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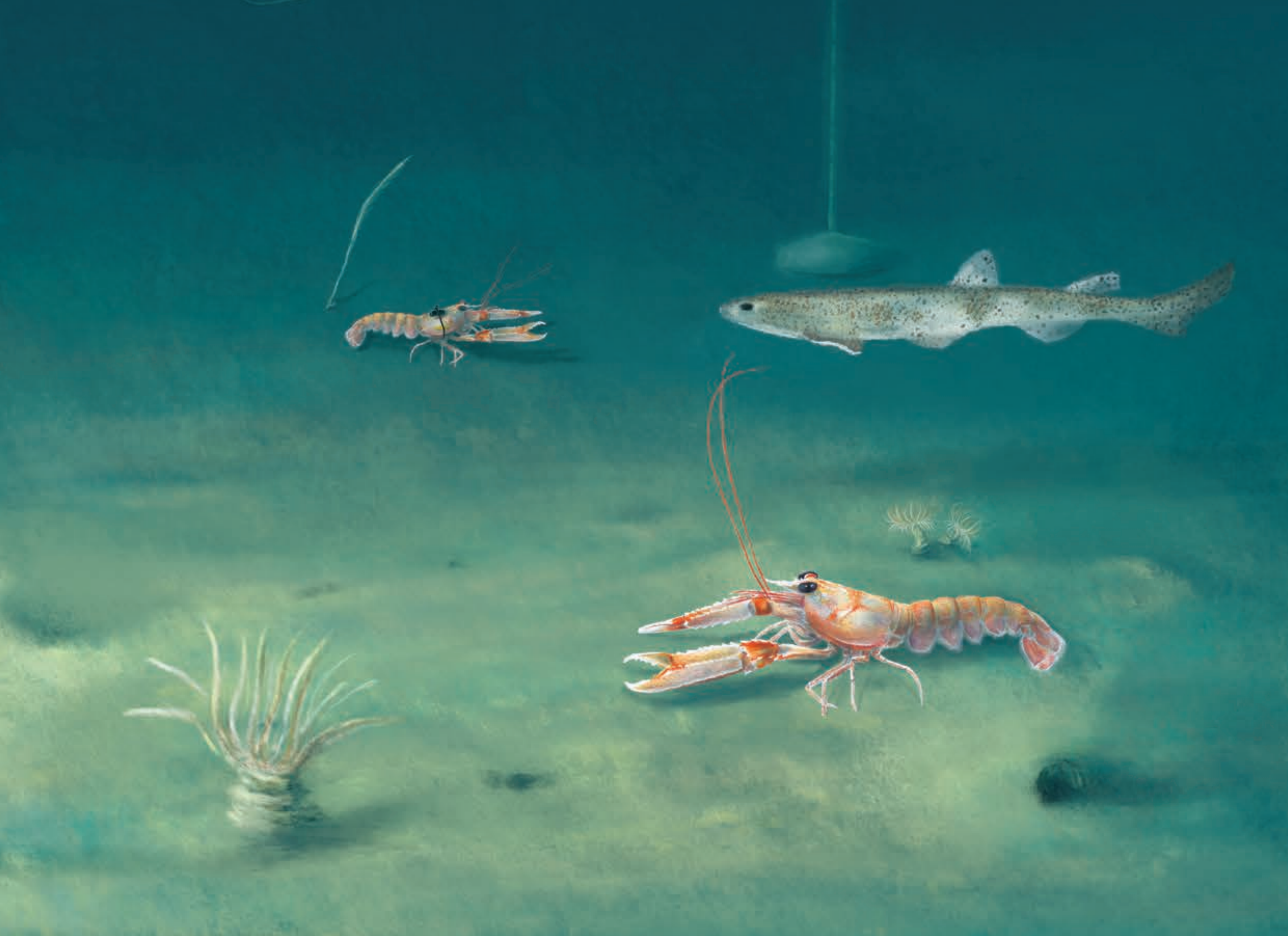

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“How inappropriate to call this planet Earth

when it is quite clearly Ocean.”

Arthur C. Clarke

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Abstract

Oceans provide a wide range of benefits for the environment and human well-being. Marine resources, in particular, are crucial sources of food for billions of people worldwide and contribute significantly to the global economy. In the Mediterranean Sea, considered a hotspot of marine biodiversity, fisheries have played a significant role as a traditional livelihood in many local communities for centuries. Fisheries provide employment and income for thousands of fishers and support local economies and regional trade. However, as with many other regions across the globe, the Mediterranean Sea faces numerous threats that affect marine biota and resources. These threats include habitat destruction, pollution, invasive species, climate variability, and one of the main challenges, overfishing. Overfishing, alongside illegal fishing practices and destructive fishing methods, undermines fish stocks and has detrimental effects on marine habitats and ecosystems functionality and services. In order to ensure sustainability in the future, it is needed to achieve a balance between the economic necessity of fishing activity and the conservation of marine resources and ecosystems. In the Mediterranean Sea, several measures have been implemented to promote sustainable fisheries, such as fishing quotas, individual size limits, gear regulations, and the promotion of responsible fishing practices. In the western Mediterranean Sea, despite these measures, recent studies suggest that these management strategies alone are clearly insufficient for the recovery and sustainability of valuable fishing stocks, such as the Norway lobster (*Nephrops norvegicus*). Other measures, such as spatial closures, could be a useful tool to achieve both conservation and fisheries goals at recovering these declining populations and achieving sustainable fisheries. To address this issue, a pilot no-take fishery reserve was established in the northwestern Mediterranean Sea in September of 2017, specifically targeting the recovery of the overexploited population of Norway lobsters inhabiting deep-sea habitats at 400 m depth. The main objective of this Ph.D. thesis is to evaluate the effects and effectiveness of the no-take fishery reserve as a tool for restoring overexploited demersal fishing stocks.

The thesis begins by updating the biological parameters of the Norway lobster population in the northwestern Mediterranean (study area). It aims to present the latest information regarding the fishery and the current status of the population while observing any potential changes that may have occurred over time. The decline in total landings and the decrease in the size at which 50% of females reach maturity indicate signs of overexploitation of this species. This thesis also identified the potential predators of Norway lobster in the Mediterranean Sea. Predators play a crucial role in all ecosystems, and acknowledging its population density is essential for predicting fluctuations in prey populations. By combining genetics and stable isotope analyses, this thesis identifies potential predators of Norway lobsters and incorporates predator density information within the no-take reserve assessment. The main predators identified were the cephalopods *Sepietta oweniana* and *Abralia veranyi*. The efficiency of the no-take fishery reserve size was also evaluated to ensure that the design of the pilot reserve was suitable for the recovery of Norway lobsters. Through a combination of acoustic tags and recapture-tag experiments, the spatial ecology of Norway lobster has been described

revealing and confirming its territorial and solitary behavior, suggesting that small-size no-take reserves could be appropriate for this species. The effectiveness of the no-take reserve was assessed using a before–after control–impact (BACI) approach. Experimental surveys were conducted in both the no-take reserve and an adjacent control area where fishing activities continued. These reserve and control areas were monitored before the establishment of the no-take fishery reserve and four years after the date of closure. To provide an alternative non-invasive methodology to traditional trawling surveys, video-surveys using Remotely Operated Vehicles (ROVs) were conducted after two and a half years after the closure to compare the no-take reserve with the control area. Both the video-surveys and traditional surveys indicated that the Norway lobster population within the no-take reserve shows signs of recovery in terms of total abundances and population biological indicators. The abundance, biomass, and size structure of Norway lobsters within the reserve were higher compared to the control area and with larger individuals. The recovery was not limited to Norway lobsters alone. Other species, such as the teleost *Helicolenus dactylopterus*, *Trigla lyra*, *Coelorhynchus caelorinchus*, and the sessile cnidarian of the family Cerianthidae, also showed signs of recovery within the no-take reserve. However, one potential predator of Norway lobsters, the demersal shark *Scyliorhinus canicula*, showed higher biomass within the no-take reserve, but with no changes in abundance. The video-surveys conducted within the no-take reserve not only provided information on the recovery of species but also offered insights into species behavior and the recovery of seafloor integrity within the reserve. This non-invasive method allowed for a more comprehensive understanding of the effects of the no-take reserve on the ecosystem. Overall, the results from both traditional surveys and video-surveys support the effectiveness of the no-take reserve in promoting the recovery of the Norway lobster population, as well as other species, and the restoration of the marine ecosystem within the reserve area.

In the thesis, several scenarios of a network of no-take fishery reserves have been simulated using a planning decision tool, such as the software *Marxan*. These scenarios incorporated a dynamic management approach that comparing the outcomes of a static network consisting only of permanent reserves. The dynamic scenarios involved a combination of permanent no-take reserves and temporal closures. The results of the simulations showed that the dynamic scenarios, which included both permanent reserves and temporal closures, achieved all conservation goals at a lower opportunity cost compared to the static network. This approach offers valuable management options for achieving sustainable fisheries and conservation goals.

Overall, this thesis highlights the potential of spatial management measures, particularly the establishment of no-take reserves, to contribute to the fisheries recovery and sustainability, as well as the conservation of marine ecosystems. While the Norway lobster population was used as a case study, the approach can be applied to many other species and their habitats and contribute to addressing the global concern about declining fishing stocks.

Resumen

Los océanos proporcionan innumerables beneficios tanto para el medio ambiente como para el bienestar humano. Concretamente, los recursos marinos son una fuente crucial de alimento para millones de personas en todo el mundo y contribuyen significativamente a la economía mundial. En el Mar Mediterráneo, considerado un punto caliente de biodiversidad marina, la pesca ejerce un rol importante definiendo el estilo de vida tradicional de muchas comunidades locales desde hace siglos. La pesca proporciona empleo e ingresos a miles de personas del sector pesquero, apoyando también a las economías locales y al comercio regional. Sin embargo, al igual que está ocurriendo en muchas otras regiones del mundo, el Mar Mediterráneo está sufriendo una presión importante que está afectando a la biota y a la disponibilidad de recursos marinos. Esta presión es inducida por diferentes factores que incluyen la destrucción del hábitat, la contaminación, la introducción de especies invasoras, la variabilidad climática, y, sobre todo, la sobrepesca. La sobrepesca, junto con las prácticas pesqueras ilegales y los métodos de pesca destructivos, ocasionan efectos perjudiciales como la disminución de stocks pesqueros y la alteración de los hábitats marinos y la funcionalidad y los servicios del ecosistema. Para garantizar la sostenibilidad en el futuro, es esencial lograr un equilibrio entre las necesidades económicas de la actividad pesquera y la conservación de los recursos y ecosistemas marinos. En el Mar Mediterráneo se han aplicado varias medidas de gestión para fomentar la pesca sostenible, como por ejemplo la aplicación de cuotas pesqueras, límites de tamaño en los individuos capturados, regulación de los artes de pesca, y hasta la promoción de prácticas pesqueras responsables. Aun así, a pesar de estas medidas, algunos estudios recientes sugieren que estas estrategias por sí solas no son suficientes para la recuperación y sostenibilidad de las poblaciones pesqueras valiosas, como la de la cigala (*Nephrops norvegicus*). Otras medidas, como el uso de cierres permanentes de caladeros pesqueros, podrían ser una herramienta útil para alcanzar los objetivos tanto de conservación como de gestión pesquera en la recuperación de poblaciones en declive y la consecución de una pesca sostenible. Para abordar esta cuestión, en septiembre de 2017 se estableció una reserva marina de interés pesquero dónde se cesó la actividad de pesca en el noroeste del Mar Mediterráneo, dirigida específicamente a la recuperación de la población de cigala que se encuentra en hábitats de aguas profundas de 400 m. En esta tesis doctoral, el principal objetivo es el de evaluar los efectos y la eficacia de esta reserva marina como herramienta para restaurar poblaciones demersales sobreexplotadas.

Esta tesis doctoral empieza evaluando los parámetros biológicos de la población de cigala en el Mediterráneo noroccidental (zona de estudio), proporcionando información actualizada sobre la pesquería y el estado de la población, y observando los posibles cambios a lo largo del tiempo. El descenso de los desembarcos totales de cigala en los puertos y la disminución de talla en la que el 50% de las hembras alcanzaban la talla de primera madurez sexual indicaron posibles signos de sobreexplotación en la población de cigala. En esta tesis también se identificaron los depredadores potenciales de la cigala en la zona de estudio. Los depredadores desempeñan un papel crucial en todos los ecosistemas, y además la densidad de sus poblaciones puede hacer fluctuar la abundancia de otras especies, sobre todo la de sus presas. Mediante la combinación de marcadores genéticos y de isótopos estables, se identificaron los depredadores de las cigalas, para

incorporar luego esta información durante la evaluación de la reserva. Los principales depredadores identificados fueron los cefalópodos *Sepietta oweniana* y *Abralia veranyi*. También se evaluó si el tamaño de la reserva marina era el adecuado para garantizar la recuperación de las poblaciones de cigala. Mediante una combinación de marcas acústicas y experimentos de marcaje y recaptura, se ha descrito la ecología espacial de la cigala, revelando y confirmando su comportamiento territorial y solitario, sugiriendo que reservas marinas de tamaño medio-pequeño garantizarían la protección de esta especie. La eficacia de la reserva marina se evaluó mediante el enfoque *before–after control–impact* (BACI). Se realizaron muestreos experimentales de arrastre tanto en la reserva como en una zona cercana a ésta, llamada área control, en el cual las actividades pesqueras estaban permitidas. Los muestreos se realizaron en las dos zonas antes del establecimiento de la reserva, y al cabo de cuatro años de protección. Para proporcionar una metodología no invasiva como alternativa a los estudios tradicionales con redes de arrastre, se realizaron transectos visuales mediante un vehículo operado remotamente (ROV, *Remotely Operated Vehicle*). Las dos evaluaciones indicaron que la población de cigalas dentro de la reserva marina mostraba signos de recuperación. La abundancia, biomasa y estructura de tallas de las cigalas dentro de la reserva eran superiores a las de la zona de control, con presencia de individuos de mayor tamaño. La recuperación no se limitó únicamente a las cigalas, sino que otras especies, los teleósteos *Helicolenus dactylopterus*, *Trigla lyra*, *Coelorhynchus caelorinchus* y los cnidarios sésiles de la familia Cerianthidae, también mostraron signos de recuperación dentro de la reserva. De los depredadores potenciales de la cigala, solo el tiburón demersal *Scyliorhinus canicula* mostró una mayor biomasa dentro de la reserva, pero sin cambios en su abundancia. La evaluación realizada mediante el ROV no sólo proporcionó información sobre la recuperación de las especies, sino también sobre su comportamiento y la recuperación de la integridad del fondo marino en la reserva. Este método no invasivo permitió comprender mejor los efectos de la reserva en el ecosistema. En general, los resultados de los estudios tradicionales y de los transectos visuales no-invasivos con ROV respaldan la eficacia de la reserva de prohibición de pesca demersal para promover la recuperación de la población de cigalas, así como de otras especies, y la restauración del ecosistema marino dentro de la zona de la reserva.

Después de la evaluación de los efectos de la reserva marina, en esta tesis se simularon varios escenarios de una red de reservas de interés pesquero utilizando una herramienta de planificación espacial, el software *Marxan*. Estos escenarios incorporaban un enfoque de gestión dinámica que comparaba los resultados de una red estática formada únicamente por reservas permanentes con escenarios dinámicos que incorporaban una combinación de reservas permanentes y de cierres temporales. Los resultados de las simulaciones mostraron que los escenarios dinámicos, alcanzaban todos los objetivos de conservación con un coste de oportunidad inferior al de la red estática. Este enfoque ofrece valiosas opciones de gestión para alcanzar objetivos sostenibles de pesca y conservación.

En general, esta tesis destaca el potencial de las medidas de gestión espacial, en particular el establecimiento de reservas marinas con cese total de la actividad pesquera, para contribuir a la recuperación y sostenibilidad de las pesquerías, así como a la conservación de los ecosistemas marinos. Aunque se ha utilizado la población de cigalas como caso de estudio, el planteamiento puede aplicarse a muchas otras especies y contribuir a abordar la preocupación mundial por el declive de las poblaciones pesqueras.

Resum

Els oceans proporcionen innumerables beneficis tan pel medi ambient com pel benestar humà. Concretament, els recursos marins són una font essencial d'aliment per milions de persones d'arreu del món, i contribueixen significativament a l'economia mundial. En el Mar Mediterrani, considerat un punt calent de biodiversitat marina, la pesca defineix l'estil de vida tradicional de moltes comunitats locals des de fa segles. La pesca ha proporcionant treball i ingressos a milers de persones del sector pesquer, recolzant també a les economies locals i al comerç regional. Tot i així, igual que està passant a altres indrets del món, el Mar Mediterrani està patint una pressió molt forta que està afectant a la seva biota i a la disponibilitat dels recursos marins. Aquesta pressió és induïda per diversos factors que inclouen la destrucció de l'hàbitat, la contaminació, les espècies invasores introduïdes, la variabilitat climàtica, i sobretot, la sobrepesca. La sobrepesca, juntament amb les pràctiques il·legals i els mètodes de pesca destructius, estan ocasionant efectes perjudicials com el declivi de molts dels estocs pesquers i l'alteració dels hàbitats marins i la funcionalitat i els serveis dels ecosistemes marins. Per garantir la sostenibilitat en el futur, és essencial aconseguir un equilibri entre les necessitats econòmiques de l'activitat pesquera i la conservació dels recursos i els ecosistemes marins. En el Mar Mediterrani s'han aplicat varies mesures per fomentar la pesca sostenible, com per exemple l'aplicació de quotes de pesca, límits en la mida dels individus capturats, regulació de les arts de pesca, i la promoció de pràctiques pesqueres més sostenibles. Tot amb l'aplicació d'aquestes mesures, alguns estudis recents han suggerit que aquestes estratègies no son suficients per tal de recuperar i aconseguir una pesqueria sostenible per a aquelles especies valuoses per la pesca, com per exemple, la de l'escamarlà, *Nephrops norvegicus*. Altres mesures de gestió, com el dels vedats pesquers, podrien ser una eina útil per assolir els objectius tan de conservació com de pesca en la recuperació de poblacions en declivi i la consecució d'una pesca sostenible. Per abordar aquesta qüestió, a setembre de 2017 es va establir una reserva marina d'interès pesquer on va cessar l'activitat de pesca en el nord-oest del Mar Mediterrani, dirigida específicament a la recuperació de la població de l'escamarlà que habita en aigües profundes de 400 m. En aquesta tesis, l'objectiu principal és el d'avaluar els efectes i la eficàcia d'aquesta reserva marina com a eina per restaurar poblacions demersals sobreexplotades.

Aquesta tesis doctoral comença avaluant els paràmetres biològics de la població d'escamarlà en el Mediterrani nord-occidental (zona d'estudi), proporcionant informació actualitzada sobre les pesqueries i l'estat de la població, i observant els possibles canvis al llarg del temps. La disminució de les descarregues totals d'escamarlà als ports i la disminució de la mida en la que el 50% de les femelles arriben a la talla de maduresa sexual van suggerir possibles senyals de sobreexplotació de la població en aquesta zona. En aquesta tesis doctoral també es van identificar els depredadors potencials de l'escamarlà en la zona d'estudi del Mar Mediterrani. Els depredadors tenen un paper crucial en tots els ecosistemes, a més, la densitat de les seves poblacions pot fer fluctuar l'abundància d'altres espècies, sobretot el de les seves preses. Mitjançant la combinació genètica i l'anàlisi d'isòtops estables es van identificar els depredadors potencials dels escamarlans, per incorporar després aquesta informació durant l'avaluació de la reserva. Els principals depredadors identificats van ser els cefalòpodes *Sepietta oweniana* i *Abralia veranyi*. També es va avaluar l'eficàcia de la mida de la reserva marina per

garantir que el disseny de la reserva era adequat per a la recuperació de la població d'escamarlà. Mitjançant una combinació de marques acústiques i experiments de re-captura, s'ha descrit l'ecologia espacial de l'escamarlà, revelant i confirmant el seu comportament territorial i solitari, suggerint que les reserves marines de mida mitjana-petita són suficients per tal de protegir aquesta espècie. L'eficàcia de la reserva marina es va avaluar mitjançant l'enfocament *before–after control–impact* (BACI). Es van realitzar mostrejos experimentals d'arrossegament tant a la reserva com a una zona propera a aquesta, anomenada l'àrea control, en què les activitats pesqueres estaven permeses. Els mostrejos es van fer a les dues zones abans de l'establiment de la reserva, i al cap de quatre anys de protecció. Per proporcionar una metodologia no invasiva alternativa als estudis tradicionals amb xarxes d'arrossegament, es van realitzar mostrejos mitjançant vídeos gravats utilitzant vehicles submergibles teledirigits (ROV, *Remotely Operated Vehicles*). Les dues avaluacions van indicar que la població d'escamarlans dins de la reserva marina mostrava signes de recuperació. L'abundància, biomassa i estructura de talles dels escamarlans dins de la reserva eren superiors a les de la zona de control, amb presència d'individus més grans. La recuperació no es va limitar únicament als escamarlans, sinó que altres espècies, els teleostis *Helicolenus dactylopterus*, *Trigla lyra*, *Coelorhynchus caelorinchus* i els cnidaris sèssils de la família Cerianthidae, també van mostrar signes de recuperació dins de la reserva. Dels depredadors potencials de l'escamarlà, només el tauró demersal *Scyliorhinus canicula* va mostrar una biomassa més gran dins de la reserva de veda, però sense canvis en l'abundància. L'avaluació realitzada mitjançant ROV no només va proporcionar informació sobre la recuperació de les espècies, sinó també sobre el seu comportament i la recuperació de la integritat del fons marí dins de la reserva. Aquest mètode no invasiu va permetre comprendre millor els efectes de la reserva a l'ecosistema. En general, els resultats dels estudis tradicionals i dels transsectes visuals no-invasius amb ROV donen suport a l'eficàcia de la reserva de prohibició de pesca per promoure la recuperació de la població d'escamarlans, així com d'altres espècies, i la restauració de l'ecosistema marí dins la zona de la reserva.

Després d'avaluar la reserva marina, en aquesta tesi es van simular diversos escenaris d'una xarxa de reserves d'interès pesquer utilitzant una eina de planificació espacial, el software *Marxan*. Aquests escenaris incorporaven un enfocament de gestió dinàmica que comparava els resultats d'una xarxa estàtica formada únicament per reserves permanents amb escenaris dinàmics que incloïen una combinació de reserves permanents i de tancaments temporals. Els resultats de les simulacions van mostrar que els escenaris dinàmics aconseguien tots els objectius de conservació amb un cost d'oportunitat inferior al de la xarxa estàtica. Aquest enfocament ofereix valuoses opcions de gestió per assolir objectius sostenibles de pesca i conservació.

En general, aquesta tesi doctoral destaca el potencial de les mesures de gestió espacial, en particular l'establiment de reserves marines, per contribuir a la recuperació i la sostenibilitat de les pesqueres, així com a la conservació dels ecosistemes marins. Tot i que s'ha utilitzat la població d'escamarlans com a cas d'estudi, el plantejament es pot aplicar a moltes altres espècies i contribuir a abordar la preocupació mundial pel declivi de les poblacions pesqueres.

Chapter 1.
General introduction

1.1. Marine fishery resources

1.1.1. Importance worldwide and global concerns

The global marine fishery refers to the commercial harvesting of fish from the oceans and seas. Indeed, fisheries produce essential resources globally for human well-being by providing basic food supplies, employment opportunities, livelihoods, economic activity, and recreational opportunities (FAO, 2022). Although fishing is an ancient activity that has played a crucial role in human societies since the dawn of civilization, it was during the 19th century when this human activity expanded due to the increase in fishing effort brought by the use of new technologies and improvements (Fig. 1.1A; Blanco et al., 2007).

Fishery resources are used for many purposes (such as bait, meal production, and fish oil), but they are primarily used for human consumption, representing approximately 80% of the total resources in both developed and developing countries (Vannuccini, 2004). Fishing resource consumption per capita is influenced by changing consumer preferences, technological advancements, and income growth. Global consumption of all fishery resources (marine, inland, and aquaculture) has increased significantly, consuming more than five times the quantity consumed 60 years ago (Fig. 1.1B; FAO, 2022).

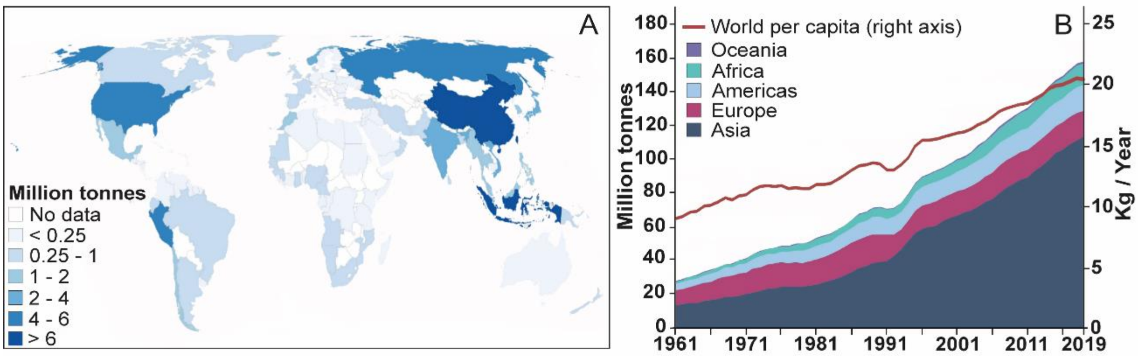


Figure 1.1. Global production and consumption of fishery resources. A) Marine capture production in million metric tons (tonnes) averaged from 2018 to 2020 by country, and B) fisheries food consumption (including marine, inland, and aquaculture resources) by continent from 1961 to 2019. Both figures are adapted from FAO, 2022.

The state of fishery resources has been monitored since the creation of the FAO Fisheries and Aquaculture Division in the early 1960s. The FAO reports that the global consumption of marine resources is continuously increasing along with captures (Fig. 1.2A), but fishing stocks within biologically sustainable levels present a negative trend over the years, reaching only 64.6% of the total fishery stocks in 2019 (FAO, 2022; see Fig. 1.2B).

There are several concerns about marine fishery resources as unsustainable fishing practices, such as bottom trawling, which can cause critical and irreversible damage to marine ecosystems (Pauly et al., 2002; Froese et al., 2018). These practices also generate high levels of bycatch, which refers to the unintentional capture of non-target species, many of which have commercial value (Tsagarakis et al., 2014). Many developing countries also face significant problems related to illegal, unreported, and unregulated fishing. This type of fishing operates outside the laws and regulations, contributing to overfishing, undermining conservation efforts, and impacting the livelihoods of fishers. The unpredictable effects of climate change also affect marine ecosystems (Brander, 2007; Cheung et al., 2013). Changes in temperature, acidity, and oxygen levels can alter the distribution, behavior, and productivity of fishing stocks. Activities like coastal development and pollution further impact the health of many species and marine ecosystems (Collins et al., 1998; Garcia and de Leiva Moreno, 2003; Lipton and Strand, 2011). They can destroy essential habitats for other marine species, such as coral reefs, seagrass beds, and mangroves. However, one of the main stressors is overfishing, which occurs when stocks are harvested at a rate that exceeds their natural replenishment rate. Overfishing has led to critical declines in fishery resources in many parts of the world and, in some cases, the collapse of entire fish stocks (Costanza et al., 2017; Rousseau et al., 2019). Indeed, the 70% of animal protein consumed worldwide comes from already overexploited fishery stocks, and this percentage is projected to increase over the next decades (Jackson et al. 2001; Pikitch et al. 2014).

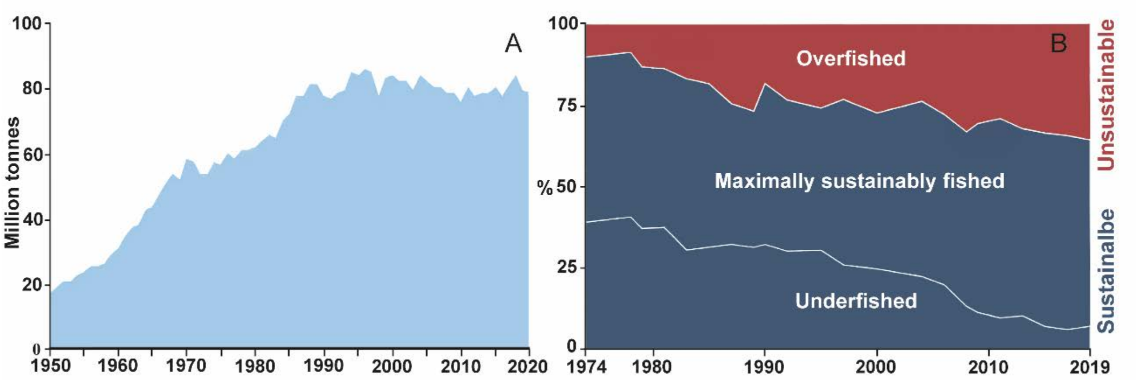


Figure 1.2. Status of fishery marine resources over time and globally: A) World marine capture fisheries represented in live weight equivalent (million tonnes). B) Global trend in the status of the world's marine fishery stocks from 1974 to 2019. Both figures were modified from FAO, 2022.

1.1.2. Fisheries in the Mediterranean Sea

A recent study about commercial fish and invertebrates in the Mediterranean and the Black Sea revealed that 85% of their stocks were overexploited (Demirel et al., 2020). The Mediterranean Sea fishing activity produces almost half of all fishing landings in the European Union (EEA 2015, European Commission, 2018), and for centuries, it has been subjected to anthropogenic pressures that have significantly intensified in recent decades due to the advancements in technology facilitating the intensive exploitation of natural resources (Claudet et al., 2010; Colloca et al., 2017).

The Mediterranean Sea supports a variety of fisheries, including bottom and pelagic trawls, purse seines, gill nets, longlines, trammel nets, and other small fishing gear (UNEP-MAP-RAC/SPA, 2013). Among these, the bottom trawling fleet is particularly significant along the Spanish-Mediterranean coasts and one of the main drivers of ecosystem change (Danovaro et al., 2017; Lizaso et al., 2020). Specifically, on the Catalan coast (northwestern Mediterranean Sea, where this thesis was developed), 221 bottom trawlers are operating, and the total landings amounted to around 6,500 tons in 2020 (Generalitat de Catalunya, 2020; ICATMAR, 2023). Bottom trawling involves dragging a large net with heavy weights over the seabed, resulting in the capture of various species in its path. Mediterranean bottom trawling fisheries are typically multi-species, characterized by a diverse range of species and the absence of large single-species stocks (UNEP-MAPRAC/SPA, 2013).

Three groups of vessels can be identified: coastal trawlers targeting various species (e.g., red mullet, common squid, curled octopus, European hake, monkfish); trawlers operating in the shelf-break and upper slope areas with Norway lobster as the primary target species; and trawlers operating in lower slope areas and submarine canyons targeting blue and red shrimp (Martín et al., 2014).

Bottom trawling is considered the most intensive and extensive worldwide fishing practice and is a source of direct physical disturbance to the seabed, with great impact on demersal and benthic deep-water ecosystems (Tillin et al., 2006; Halpern et al., 2008; Olsgard et al., 2008). Furthermore, bottom trawling has detrimental effects on benthic habitats, causing structural damage to species and altering seabed morphology, sediment characteristics, and water turbidity (Palanques et al., 2014; Demestre et al., 2018; Kroodsma et al., 2018). By resuspending sediments and disturbing sessile fauna, trawling negatively impacts natural processes and hinders the restoration of impacted ecosystems to their baselines (Cook et al., 2013). This fishing method is considered non-selective, leading to significant by-catch and discards (e.g., Damalas et al., 2018), and it is a significant contributor to the depletion of fish stocks and the alteration of benthic biodiversity (Sciberras et al., 2018). Nearly all of the target species in these fisheries are overexploited and face a high biological risk of collapse (STECF, 2020).

The future viability of fishing as an economic, social, and cultural activity is uncertain due to the increasing percentage of unsustainable fishery resources (Pauly et al., 2003). Despite a decrease in fishing pressure over the past decade, resulting in the recovery of some fish stocks (Cardinale et al., 2013; Fernandes and Cook, 2013), there is still a long way to go to achieve a global recovery of the overexploited populations (Froese and Proelß, 2010; Cardinale et al., 2013). This historically intense fishing activity has had a global impact, generating a global concern about overfishing practices (Costanza et al., 2017; Froese et al., 2018; Rousseau et al., 2019). Therefore, developing effective management strategies specially focused on stock recovery is essential for the sustainable exploitation of marine resources (Lillebø et al., 2017).

1.1.3. Fisheries management

To achieve sustainable fishery management, it is critical to ensure the long-term viability of fishery resources, prevent ecological consequences, and meet the needs of both present and future generations. Fisheries management has evolved to ensure that fisheries operate in a manner that provides immediate benefits while avoiding excessive or irreversible damage to fish stocks, ecosystem diversity, integrity, and structure. The goal is to enable the ecosystem to continually provide a full range of benefits in the future.

Fishery management in Mediterranean European waters is generally based on effort limitation, gear regulation, and biological scientific advice (Sardà, 1998a ; Sánchez Lizaso et al., 2020). However, the implemented strategies have not been sufficient or may have been based on models with unrealistic biological parameters that need to be updated, as resources are still overexploited or show signs of decline (Beddington et al., 2007; Cardinale et al., 2017). For some fisheries, such as multispecies fisheries, catch and effort limitations may be poor management tools as they land many species due to bycatch and discard many more (Hilborn et al., 2004). Inefficient fisheries management results from poor fishing regulations, weak enforcement, and a lack of relevant biological knowledge (Beddington et al., 2007; Petter Johnsen and Eliasen, 2011). Achieving sustainable management has been challenging due to scientific uncertainty, conflicts between short-term social and economic needs and longer-term sustainability, poor management practices, and insufficient capacity within the management.

In order to conserve demersal stocks and ensure sustainable operations in the Western Mediterranean Sea, a multiannual plan has been implemented. This plan, known as the West Med MAP (Regulation EU 2019/1022 of the European Parliament and Council of June 20; European Commission, 2019), covers the northern Alboran Sea, Gulf of Lions, Tyrrhenian Sea, Balearic Archipelago, Corsica, and Sardinia, spanning between Spain, France, and Italy. The plan focuses on regulating the main target species, including Norway lobster (*Nephrops norvegicus*), blue and red shrimp (*Aristeus antennatus*), deep-water rose shrimp (*Parapenaeus longirostris*), giant red shrimp (*Aristaeomorpha foliacea*), European hake (*Merluccius merluccius*), and red mullet (*Mullus barbatus*) stocks. The aim is to restore these stocks to maximum sustained yield (MSY) by 2025 while ensuring their social and economic viability. The primary approach to achieving this goal is through the reduction of fishing effort, which can involve measures such as reducing fishing time (days at sea) or the number of fishing vessels. However, it has been acknowledged that solely reducing fishing effort has proven insufficient for stock recovery (Sola et al., 2020). Therefore, additional measures and strategies may be required to effectively restore and sustain the demersal stocks in the region.

An ecosystem-based approach to fisheries management, which considers the entire ecosystem rather than just the target species, may be more effective in achieving sustainable management (Pikitch et al., 2004). A wider approach, referred to as an ecosystem approach to fisheries (EAF), attempts to bring together new insights to address the limitations of conventional fisheries management. Additionally, spatial closures are another ecosystem-based measure that is being applied. These spatial closures cease fishing activity in a selected area and can help address the overfishing pressure (including discards and bycatch), avoid habitat loss, and develop an ecosystem-oriented mindset (Hilborn et al., 2004; Pikitch et al., 2004). There is an urgent need to identify effective management strategies to achieve sustainable fisheries that can protect marine biodiversity for both conservation and fisheries goals (Jupiter et al., 2017).

1.2. Spatial closures and marine protected areas

Spatial closures, such as no-take fishery reserves and marine protected areas (MPAs), have in many cases proven to be effective measures for restoring overexploited fishery stocks and achieving sustainable fisheries and biodiversity conservation (Abesamis and Russ, 2005; Di Franco et al., 2016; Giakoumi et al., 2017), providing many benefits for both of them (Fig. 1.3). Although the primary aim of MPAs is the conservation of nature (Day et al., 2019), they can also recover fishing resources (Kerwath et al., 2013; Bourlat et al., 2021), benefiting habitats and animal communities (Ardron et al., 2014; Langton et al., 2020).

Empirical evidence has shown direct increases in population density, biomass, and individual body size of overexploited species in well-enforced and effective MPAs, especially no-take marine reserves where all extractive uses are banned (Linares et al., 2012; Sala and Giakoumi, 2018; Lenihan et al., 2021). Moreover, the benefits of these management measures can also occur when the enhanced biomass inside the MPA is exported towards the protected area boundaries. This process, called spillover, can be achieved through the dispersal of adults, larvae, or eggs outward to nearby fisheries (Kerwath et al., 2013; Marshall et al., 2019; Di Lorenzo et al., 2020).

Figure 1.3. Benefits from Marine Protected Areas (MPAs). Together, these benefits mean more marine life, higher productivity, functional food webs, healthier ecosystems, and sustainable fisheries management.

1.2.1. Concerns about effectiveness

Different studies have revealed that not all MPAs are truly effective in achieving their conservation targets (Bennett and Dearden, 2014; Chaigneau and Brown, 2016). Ineffective protected areas are generated because of inadequate size or poor management and enforcement (Halpern, 2003; Clements and Hay, 2017; Pendleton et al., 2018). It is therefore crucial to evaluate MPA management to enhance its effectiveness in achieving the goals and objectives set for the protected area (Hockings et al., 2000; Pomeroy et al., 2005; Vigo et al., 2020). The size and spacing of no-take marine reserves must ensure the persistence of populations inside the reserves. Reserves must be designed based on spatial ecological knowledge for targeted species (Blowes and Connolly, 2012).

Determining the trophic role of a particular organism is pivotal to understanding its ecological function in the ecosystem and to designing effective management actions. This involves identifying the environmental factors and biotic interactions that could influence or play an essential role in population dynamics and species distribution (D'Amen et al., 2018). Recognizing these factors could also be useful in predicting how marine ecosystems will respond to changing environmental conditions (Wisz et al., 2013). Among biotic interactions, predator-prey interactions are key in affecting species' spatial patterns (Ritchie et al., 2012). Predators play an important role in all ecosystems, influencing the dynamics of species at lower trophic levels (Estes, 1996; Ritchie and Johnson, 2009).

Ecosystem modeling, which also considers consumer-prey interactions, is widely used for ecosystem-based fishery management (Buchary et al., 2002). These holistic approaches include analyzing the type and magnitude of the species interactions involved and the biomass and abundance at several trophic levels, from plankton to apex predators (Fogarty, 2014). This entails a prior understanding of the prey-predator interactions that exist in the environment to be managed. Similarly, in assessing the effectiveness of marine protected areas (MPAs), evaluating predator densities is crucial, even in small MPAs, as an increase in predators could prevent the restoration of overexploited species (Clements and Hay, 2017) or a lack of them could lead to habitat regime shifts (Daskalov et al., 2007). Nevertheless, the trophic role that individual species play within marine ecosystems is often unclear, precluding the prediction of the consequences of their removal or recovery. In the case of ecosystem-based fisheries management, a lack of knowledge of biotic interactions could lead to a misinterpretation of the consequences of overfishing, resulting in inconsistent trophic patterns constraining the viability of stocks and their predators (Shackell et al., 2010).

Assessment via a BACI (before–after control–impact) design is a powerful tool in environmental impact assessment (Jones et al., 1992) and the most rigorous design for assessing MPA effectiveness (Ojeda-Martínez et al., 2011; Sciberras et al., 2013). By implementing BACI approaches, ecological variables and population metrics can be studied before and after protection measures are implemented (Fig. 1.4). This can contribute to novel insights regarding the accurate effects of management measures (Sørdalen et al., 2018, 2020; Pitcher et al., 2009). To evaluate the effectiveness of the

MPA, population indicators are measured, with abundance and biomass being the most representative (Moland et al., 2013; Rife et al., 2013; Smokorowski and Randall, 2017).

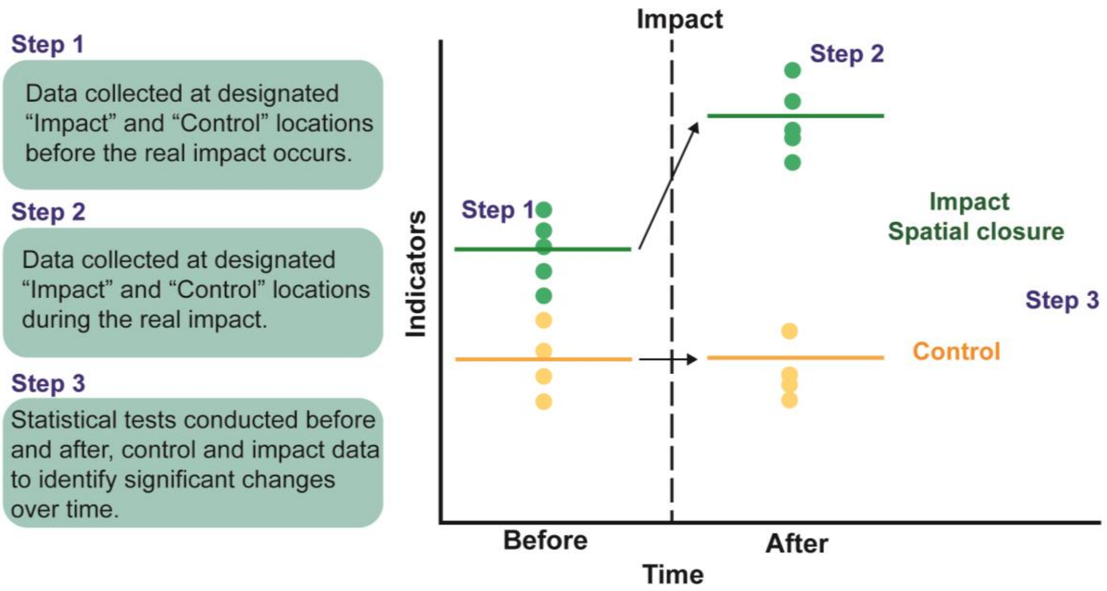


Figure 1.4. Before–after control–impact (BACI) design.

1.2.2. Designing networks of protected areas

The use of MPA networks is a conservation method that has garnered much recent attention. The general aim of MPA networks is to strategically plan MPAs to achieve greater benefits than individual protected areas (Grorud-Colvert et al., 2014). A properly designed MPA network can overcome individual protected areas for a variety of ecological, economic, and social management goals (Gaines et al., 2010). These networks are composed of protected areas that are linked, either physically through the movement of organisms or water flow, or through common management institutions and personnel for monitoring (Almany et al., 2009; Planes et al., 2009). MPA networks aim to protect linked habitats and target species in a wider region, protecting areas that would act as a source of larval recruits for key species (Planes et al., 2000).

Designing effective MPA networks while minimizing negative impacts on fisheries (e.g., through displacement of fishing activity) is a challenge. Achieving benefits from these spatial measures requires spatial information on habitat, species distribution, larval, juvenile, and adult movements, as well as source-sink dynamics of larval production and recruitment (Crowder et al., 2000; Botsford et al., 2003). Marine reserves can be economically profitable due to distributing the fishing effort more efficiently to patches of dynamic productivity (Costello et al., 2010). However, this can be achieved using systematic conservation planning approaches (Margules and Pressey, 2000; Possingham et al., 2006) and optimization decision-support tools (e.g., Klein et al., 2010; Giakoumi et al., 2011).

1.3. The Norway lobster *Nephrops norvegicus* in the northwestern Mediterranean Sea as a case study

1.3.1. Biology and behavior

The Norway lobster (*Nephrops norvegicus*, Linnaeus, 1758) is a decapod crustacean that inhabits muddy habitats on the continental shelf and slope throughout the northeast Atlantic Ocean and the Mediterranean Sea (Ungfors et al., 2013; see Fig. 1.5). Due to its burrowing behavior, suitable habitat for this demersal crustacean consists of sandy-muddy sediments. The Norway lobster is a benthic crustacean that is distributed at depths from 10 to 800 m (Bell et al., 2013; Johnson et al., 2013). Atlantic populations are mainly found on the continental shelf (Eiríksson, 2014), whereas in the Mediterranean Sea, the highest abundance is present on the upper and lower depths of the continental slope, between 300 and 600 m deep (Maynou and Sardà, 1997; Abelló et al., 2002).

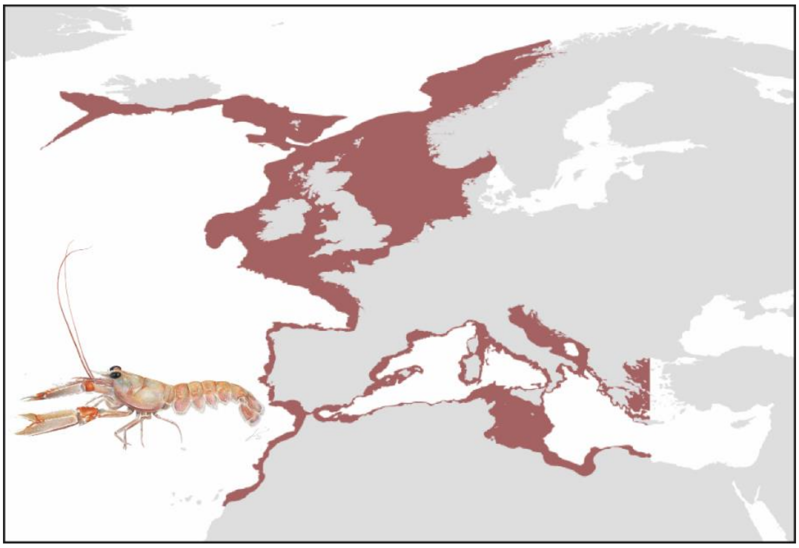


Figure 1.5. Spatial distribution of Norway lobster (*Nephrops norvegicus*) in Europe waters and the northeast Atlantic Ocean. Source FAO. Norway lobster illustration by J. Mir-Arguimbau.

1.3.2. Current fishery situation in the Mediterranean Sea

In the Mediterranean Sea, most stocks (close to 62.5%) are fished at their maximum sustainable levels or even above (Tsikliras et al., 2015; FAO, 2022). This sea is highly exploited by bottom trawlers that operate at depths between 50 and 800 m (Gorelli et al., 2011; Lucchetti et al., 2021). One of the main targets of bottom trawling is the Norway lobster, as it is one of the most valuable fishery stocks in European waters (Bell et al., 2006; Aguzzi and Sardà, 2008; Ungfors et al., 2013). Its global capture production in European waters has reached approximately 60,000 tons per year for the last 30 years (Bianchini et al., 1998; Chapman, 1980; FAO, 2022; Ungfors et al., 2013). In the Mediterranean Sea, Norway lobsters are captured by bottom trawlers, in which other demersal commercial species are also fished, such as European hake (*M. merluccius*), anglerfish (*Lophius budegassa* and *Lophius piscatorius*), white octopus (*Eledone cirrhosa*), blue whiting (*Micromesistius poutassou*), and deep-water rose shrimp (*P. longirostris*) (Sardà, 1998a). In the Mediterranean Sea, the current management approach involves regulation through the implementation of a minimum conservation reference size (MCRS) of 20 mm Cephalotorax Length (CL), caught using a square codend with a mesh size of 40 mm (Regulation (UE) 1380/2013, 11/12/2013; Regulation (EU) 2019/1241, 20/06/2019). The assessments of this stock are conducted by the General Fisheries Commission for the Mediterranean (GFCM) (Cardinale et al., 2021) and the Scientific, Technical and Economic Committee for Fisheries (STECF, 2016) through assessment models that need biological parameters.

This benthic crustacean has been the focus of many studies due to its ecological and economic value (Issifu et al., 2022; Aguzzi et al., 2023). However, the Norway lobster stocks in the western Mediterranean Sea are experiencing signs of overexploitation due to high trawling pressure (Fig. 1.6; Sardà, 1998a; Rotllant et al., 2005; **Chapter 2.1** of the present thesis). This crustacean is a burrowing species whose galleries provide habitat structures for other demersal species (Roberge and Angelstam, 2004; Aguzzi and Sardà, 2008). Although these galleries may offer some protection from trawling, the severe impacts trawling generates on the seabed make Norway lobsters highly vulnerable to this fishing activity (Campbell et al., 2009).

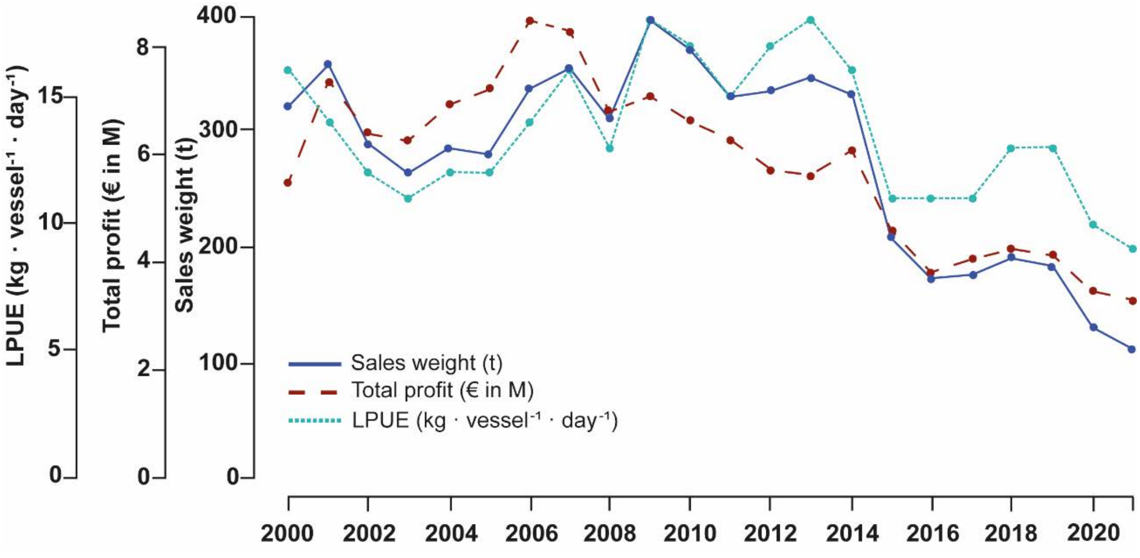


Figure 1.6. Annual landings of Norway lobsters in Catalonian coast. Annual sales weight in tones (t) (dark blue line), annual total profits from landings in € in M (red-dashed line), the LPUE represented as biomass in kg of Norway lobsters landed per day and per vessel (light blue-dashed line), and the fishing effort represented in days per vessel. This is a modified figure from **Chapter 2.1**.

1.3.3. Evaluation of a pilot no-take reserve and study area

A pilot no-take fishery reserve was established in September 2017 in response to the declining situation of Norway lobster stocks in the northwestern Mediterranean Sea. The reserve ceased all fishing activity through an agreement between the two local fishery associations (Roses and Palamós), and it was afterwords designated as a Marine Protected Area (MPA) by the Spanish Government in 2020 (Order APA/753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753To).

The no-take reserve protecting 10 km^2 of area was located on the northern flank of the Palamós canyon at 351–475 m in depth, where bottom trawling targeting Norway lobster stocks has been carried out for around a century (Sardà, 1998b; Puig et al., 2012). Most of the studies in this thesis were conducted in this no-take reserve and in a control area. This control area was ecologically and geomorphologically equivalent to the no-take reserve, but fishing activity was still undergoing (Fig. 1.7).

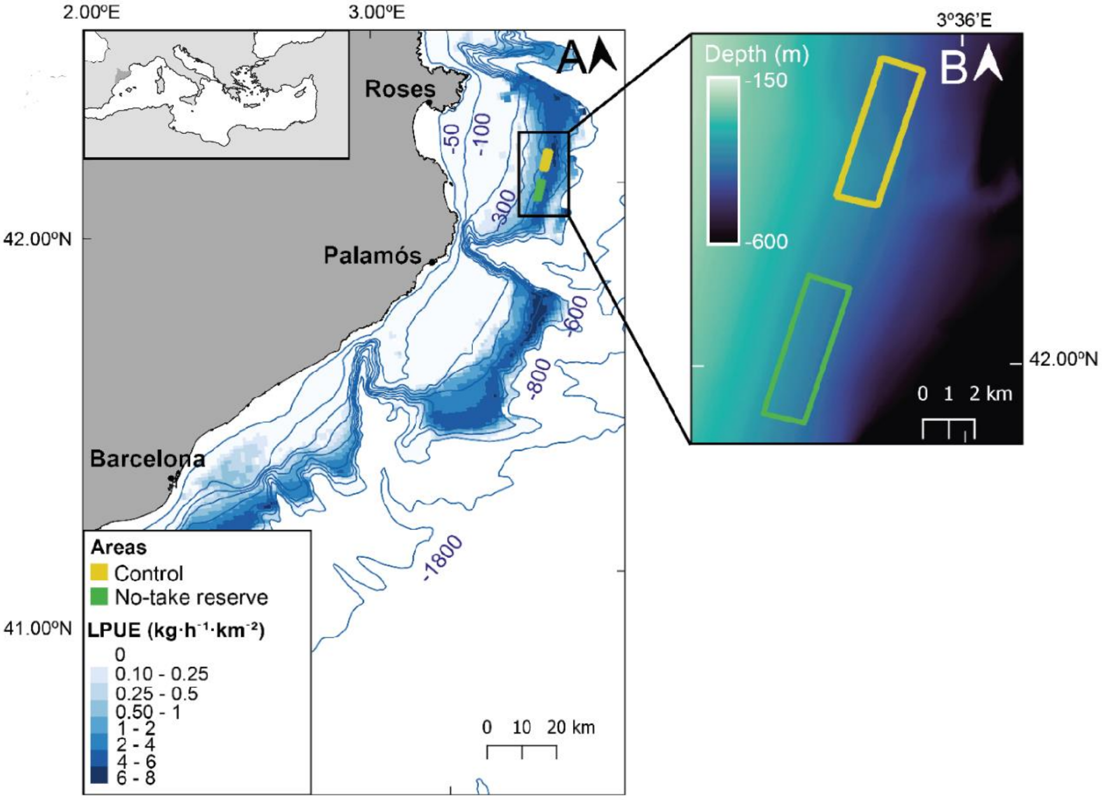


Figure 1.7. The study area shows A) the spatial distribution of Norway lobster in the Catalan Sea and the locations of the no-take reserve and the control area. Data obtained by combining landing data with Vessel Monitoring Survey (VSM) information. B) Fine bathymetry of the no-take reserve and the control area.

1.4. Objectives and structure of the Ph.D. thesis

The general objective of the present Ph.D. thesis is to evaluate the effectiveness of a no-take reserve intended to recover the overexploited Norway lobster population in the northwestern Mediterranean Sea. Based on this information, several potential scenarios for a network of no-take reserves were developed to recover the overfished populations of this crustacean and the benthic community.

In particular, to accomplish this general objective, this Ph.D. thesis defined six specific objectives, corresponding to six different chapters that cover three main questions:

Question 1: How is the current status of the Norway lobster population in the northwestern Mediterranean Sea?

1. **To update the biological parameters and the fishery status of the Norway lobster in the northwestern Mediterranean Sea.**
   The Norway lobster is one of the most valuable European fisheries resources, with daily landings in almost all riverine countries of the Mediterranean Sea and northeast Atlantic Ocean (Bell et al., 2013; Johnson et al., 2013). In the Mediterranean Sea, fishing pressure is affecting the status of many fishery stocks that are being overexploited, involving ecological, economic, and social issues (Cardinale et al., 2017). To perform an adequate stock assessment and provide advice on maximum sustainable yield, reliable biological parameters of the species are required. In **Chapter 2.1**, we aim to update these biological parameters: the size at onset of maturity (SOM), the length-weight relationship, and the individual size distribution. Besides updating these indicators, we compare our results with parameters obtained in previous studies in the same area, the GSA06, to evaluate possible shifts in time in these parameters.

   This specific objective, addressed in **Chapter 2.1**, is now under review in a peer-reviewed journal as follows:
   Vigo, M., Galimany, E., Poch, P., Santos-Bethencourt, R., Sala-Coromina, J., Bahamón, N., Aguzzi, J., Navarro, J., and Company, J.B. (under review). An update of the population status of Norway lobster, *Nephrops norvegicus* (Decapoda, Nephropidae) in the northwestern Mediterranean Sea. ***Under Review* in *ICES Journal of Marine Science***.

Question 2: How effective is the pilot no-take fishery reserve for recovering Norway lobsters, coexisting megafauna, and the seabed as a whole?

2. **To identify the potential predators of Norway lobsters in the northwestern Mediterranean Sea.**
   In order to enhance our understanding of ecosystem functions and their responses to natural and anthropogenic impacts, it is crucial to identify and study biotic and trophic interactions (Wisz et al., 2013). Predation is one of the most important interactions that influences other species' spatial patterns (Ritchie et al., 2012). In the Mediterranean Sea, it is still unknown which species prey on Norway lobsters. For this reason, to understand the effects of the no-take reserve on all species that can

interact with Norway lobsters, it is crucial to identify which species could be its potential predators.

This specific objective, addressed in **Chapter 2.2**, was published in a peer-reviewed journal:
Vigo, M., Navarro, J., Giménez, J., Andón, N., Martínez-Lage, A., Rotllant, G., and Company, J.B. (2022). Using molecular and stable isotope markers to identify the main predators of *Nephrops norvegicus* in Mediterranean deep-water ecosystems. ***Marine Ecology Progress Series*** 695, 95-108 (https://doi.org/10.3354/meps14110).

3. **To analyze Norway lobster movement patterns and home areas to determine if the no-take reserve size is adequate to protect them.**
Marine protected areas (MPAs) are effective measures for conservation and achieving sustainable fisheries, reversing the decreasing trend of some overexploited species (Melaku Canu et al., 2021). MPAs can help maintain healthy populations and preserve habitats, although the size of the MPA is crucial as it can determine the range of protection (Moffitt et al., 2011). As the effectiveness of MPAs depends on an optimal size design, it is essential to know the behavior and spatial ecology of the species (Blowes and Connolly, 2012). To evaluate if the no-take reserve size was ideal for Norway lobsters, we estimated the spatial movements, home areas, and daily activity patterns of these crustaceans in the no-take reserve by using acoustic-tracking and tagging-recapture procedures.

This specific objective, addressed in **Chapter 2.3**, was published in a peer-reviewed journal:
Vigo, M., Navarro, J., Masmitja, I., Aguzzi, J., García, J.A., Rotllant, G., Bahamón, N., and Company, J.B. (2021). Spatial ecology of Norway lobster *Nephrops norvegicus* in Mediterranean deep-water environments: implications for designing no-take marine reserves. ***Marine Ecology Progress Series*** 674, 173-188 (https://doi.org/10.3354/meps13799).

4. **To evaluate the effects of the no-take reserve using a BACI approach with experimental trawling surveys.**
The no-take reserve was evaluated using a before–after control–impact (BACI) assessment, a powerful tool with the most rigorous design for assessing MPA effectiveness (Sciberras et al., 2013). We conducted two experimental trawling surveys commonly used to study the species composition of deep habitats. The first survey was in September 2017 (before), before the closure of the no-take reserve, and the second was in September 2021 (after) in two areas: the no-take reserve (impact) and a fished area (control). We evaluated the effect of protection on the Norway lobster population and the coexistent megafauna in terms of abundance, biomass, and body size. We examined the spillover effect (Sala and Giakoumi, 2018), exporting Norway lobster biomass from the no-take reserve towards its boundaries.

This specific objective, addressed in **Chapter 2.4**, is under review in a peer-reviewed journal:

Vigo, M., Navarro, J., Rotllant, G., Bahamón, N., Carreton, M., Quevedo, J., Rojas, A., and Company, J.B. (2023). Before-after control-impact (BACI) assessment of the effects of a deep-water no-take fishery reserve to recover Norway lobster (*Nephrops norvegicus*) overfished populations and coexisting megafauna. ***ICES Journal of Marine Science*** fsad130 (https://doi.org/10.1093/icesjms/fsad130).

5. **To evaluate the effects of the no-take reserve with a non-invasive methodology using video surveys.**
   We conducted Remotely Operated Vehicle (ROV) video surveys to evaluate the status of the Norway lobster population and the coexistent megafauna species inhabiting the no-take reserve and in a fished area (control). These surveys were conducted in February 2020. We quantified the accumulation of marine debris in both study areas and assessed the seafloor integrity by quantifying and classifying the trawl mark coverage according to the degree of alteration.

   This specific objective, addressed in **Chapter 2.5**, was published in a peer-reviewed journal:
   Vigo, M., Navarro, J., Aguzzi, J., Bahamón, N., García, J.A., Rotllant, G., Recasens, L., and Company, J.B. (2023). ROV-based monitoring of passive ecological recovery in a deep-sea no-take fishery reserve. ***Science of the Total Environment*** 88320, 163339. (https://doi.org/10.1016/j.scitotenv.2023.163339)

Question 3: How would a network of no-take reserves in this area be designed, incorporating a dynamic management approach?

6. **Design different scenarios for a network of no-take reserves by comparing a static scenario with permanent closures with different scenarios using a dynamic approach.**
   Based on the results obtained in this Ph.D., we presented five scenarios for a network of no-take reserves along the Catalan Coast to achieve conservation and sustainable multi-species fishing of one of Europe's most valuable seafood stocks, Norway lobsters (*Nephrops norvegicus*). We examined and explored the benefits, opportunity costs, and trade-offs between different scenarios that depict alternative management options that range from a more traditional MPA-centered approach based on permanent closures to a combination of MPAs and priority areas for temporal closures that could act as other effective area-based conservation measures (OECMs). To do this, we used Marxan (Ball et al., 2009), an optimization decision-support tool in systematic conservation planning. By identifying priority conservation areas and coexisting megafauna species, Marxan minimized conservation's impact on fisheries while recovering Norway lobster populations.

   This specific objective, addressed in **Chapter 2.6**, is under review in a peer-reviewed journal:
   Vigo, M., Navarro, J., Hermoso, V., Navarro, J., Sala-Coromina, J., Giakoumi, S., and Company, J.B. (under review). Dynamic marine spatial planning for conservation and fisheries benefits. ***Under Review* in *Fish and Fisheries***.

1.5. General Methodology

1.5.1. Fieldwork procedures employed in the Ph.D. thesis

To accomplish **objectives 2** and **4,** addressed in **Chapters 2.2** and **2.4**, respectively, we conducted **experimental trawling surveys** on board a commercial bottom trawl vessel from Palamós (*FV Solraig*). These surveys were conducted in the no-take reserve and a control (fished) area on the northern Catalan coast. The first experimental survey was carried out in August 2017, before the establishment of the no-take reserve, and the second survey was conducted 4 years later, in August 2021. All individuals caught were identified and measured on board. The discard and the catch obtained with the cover net were stored in portable coolers and transported to the laboratory for biological examination. During these samplings, the muscle of 20 Norway lobster individuals and 249 individuals of 13 species of potential predators of Norway lobster were sampled for Stable Isotope Analyses and stomach contents.

To accomplish **objective 3**, addressed in **Chapter 2.3,** we conducted 3 **oceanographic cruises** in the no-take reserve in May-June, September, and November 2019 on board the RVs *Sarmiento de Gamboa* and *García del Cid*. During these cruises, we captured Norway lobsters using **Norway lobster creels** recovered after 10 hours at night and conducted all deck operations in dim red light. We tagged the individuals for passive recapture experiments and with acoustic transmitters. During the campaign in May-June 2019, we also deployed the array of acoustic receivers in the no-take reserve. In September 2019, we collected the array of receivers, and in November 2019, we continued with the tagging recapture experiment.

To achieve **objective 5**, addressed in **Chapter 2.5**, we conducted an **oceanographic cruise** in February 2020 aboard the RV *Sarmiento de Gamboa* to carry out the 24-hour ROV Liropus 2000 surveys. We performed six surveys in the no-take reserve and six in the control area after 2.5 years of the implementation of the no-take reserve. We quantified the presence of Norway lobsters and other coexistent megafauna species, as well as the burrows built by Norway lobsters, trawling impact marks, terrestrial vegetation, and marine litter.

1.5.2. Laboratory work

Determination of Norway lobster population parameters

A biological examination of the individuals collected during the experimental trawling surveys was conducted at the laboratory. The following measures were taken: cephalothorax length (CL, in mm), total weight (W, in g), and the total weight without claws (in g). Maturity stages of females were determined by macroscopic examination of the colors of the ovaries, modified from the histological scale proposed by Rotllant et al., 2005: Stage I, white-immature, slender, and thin ovaries; Stage II, resting and berried females, cream-yellowish; Stage III, beginning of maturation, small, light green; Stage

IV, big, thick, and light green ovaries; Stage V, dark green, advanced maturation in the pre-spawning phase.

Identification and determination of the population parameter of the coexistent megafauna species

All individuals were identified at species level, classified taxonomically, counted, weighed, and measured (total length TL for fish, in cm; preanal length AL for filiform-shaped fish species as macrourids, in cm; cephalothorax length CL for crustaceans, in mm; and mantel length ML for cephalopods, in cm).

DNA extraction and amplification from the stomach contents of potential predators

All collected stomachs were dissected using ethanol-sterilized tools, and the DNA extraction from the stomach contents was performed using the NZY Tissue gDNA Isolation Kit (NZYTech) following the manufacturer's instructions and the Phenol-Chloroform Extraction (PCI) methodology (Fig. 1.8). DNA extraction quality was analyzed with the NanoDrop ND-1000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA). We designed primers whose sequence corresponded to a mitochondrial gene from the 16S subunit of the ribosomal ribonucleic acid (following Palero et al., 2009) to identify only predation on Norway lobster. We used the program PRIMER3Plus (Untergasser et al., 2007) to design the primers: R 5'-ACG CTG TTA TCC CTA ARG TAA CTT-3' and F 5'-GGT GTA GAT TAA 167 GGA ATT CG-3'.

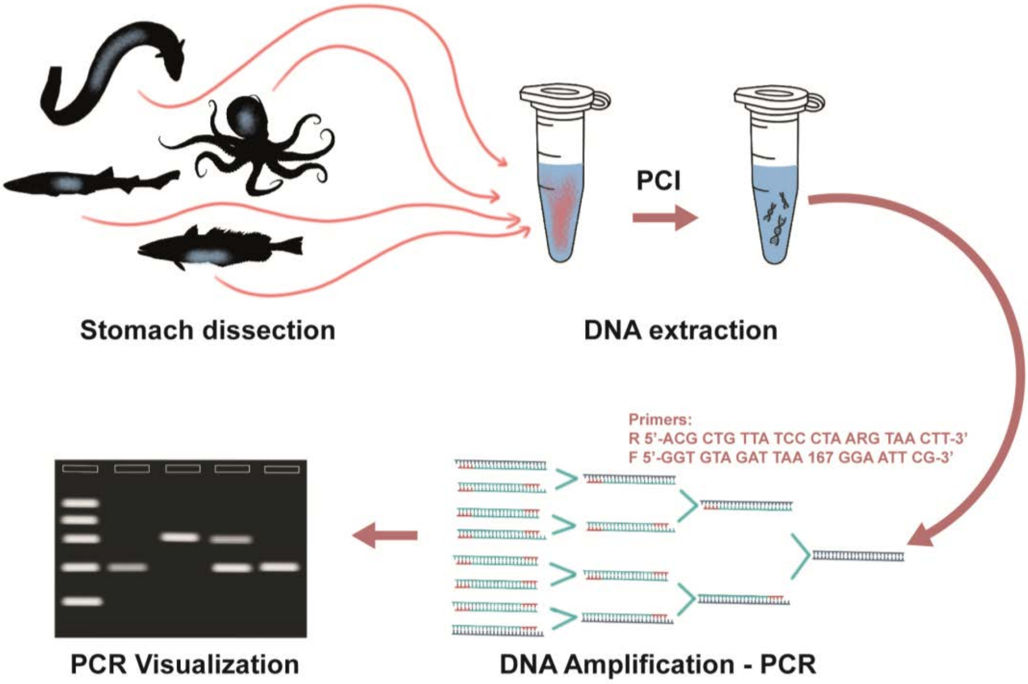


Figure 1.8. The procedure of DNA extraction and amplification of potential predators of Norway lobsters. Representing the stomach dissections to obtain stomach content samples for DNA analyses, the DNA extraction following the Phenol-Chloroform Extraction (PCI) methodology, the amplification of the DNA using the PCR (Polymerase Chain Reaction) technique and the Primers designed to identify Norway lobster DNA, and finally, the visualization of the PCR that amplified the Norway lobster DNA from each stomach content.

Stable Isotope Analyses (SIA)

Stable isotopes are biochemical tracers that focus on assimilated versus ingested prey material. It was a complementary tool to the identification of Norway lobsters in the DNA extraction and amplification of potential predators. It is used for investigating trophic relationships by integrating feeding across longer time scales, from weeks to months, depending on the tissue analyses (see Fig. 1.9; Davis and Pineda-Munoz, 2016; Young et al., 2015). Stable isotopes of carbon (denoted as $\delta^{13}C$) and nitrogen (denoted as $\delta^{15}N$) were analyzed for Norway lobsters and their potential predators. All muscle tissues were freeze-dried and powdered. Between 0.28 and 0.33 mg of the powdered tissue was packed into tin capsules, which were analysed in the Laboratorio de Isótopos Estables of the Estación Biológica de Doñana (LIE-EBD, Spain; http://www.ebd.csic.es/lie/index.html). We estimated the isotopic values of each potential predator as it would present with a specialized diet of Norway lobster (see a similar approach in Popa-Lisseanu et al., 2007). For these predictions, different diet-tissue discrimination factor values based on published studies were used for cephalopods ($\Delta\delta^{13}C$ = -0.20 ± 0.5 ‰, $\Delta\delta^{15}N$ = 3.37 ± 0.95 ‰; Golikov et al., 2020), bony fish ($\Delta\delta^{13}C$ = 1.3 ± 0.1 ‰, $\Delta\delta^{15}N$ = 3.35 ± 0.2 ‰; Caut et al., 2009, and sharks and rays ($\Delta\delta^{13}C$ = 0.49 ± 0.32 ‰, $\Delta\delta^{15}N$= 1.95 ± 0.26 ‰; Hussey et al., 2010). We finally combined the molecular results obtained from DNA amplification and the trophic markers to observe the importance of each potential predator.

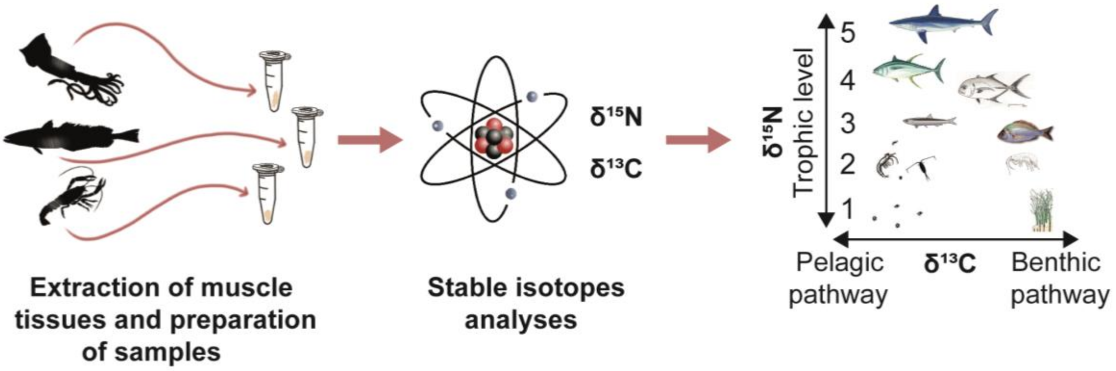


Figure 1.9. Procedure of the isotope stable analyses followed by the interpretation of the results.

Identification and quantification of Norway lobsters and all individuals recorded in the video surveys

All burrow systems built by Norway lobsters are characterized by the shape and appearance of burrow openings that occasionally number two or three in a system and are easily identified (Chapman, 1980; Tuck et al., 1994). All burrow systems recorded were also quantified in order to evaluate the population of Norway lobsters by two approaches: individual counting and burrow system counting (Fig. 1.10A). The marine debris, including plastics, metals, and terrestrial vegetation, was also quantified and identified. The surveys with ROV Liropus were used to record trawl marks and annotated according to the time they were present in the videos and classified into six categories of seafloor impact due to trawling (Fig. 1.10B).

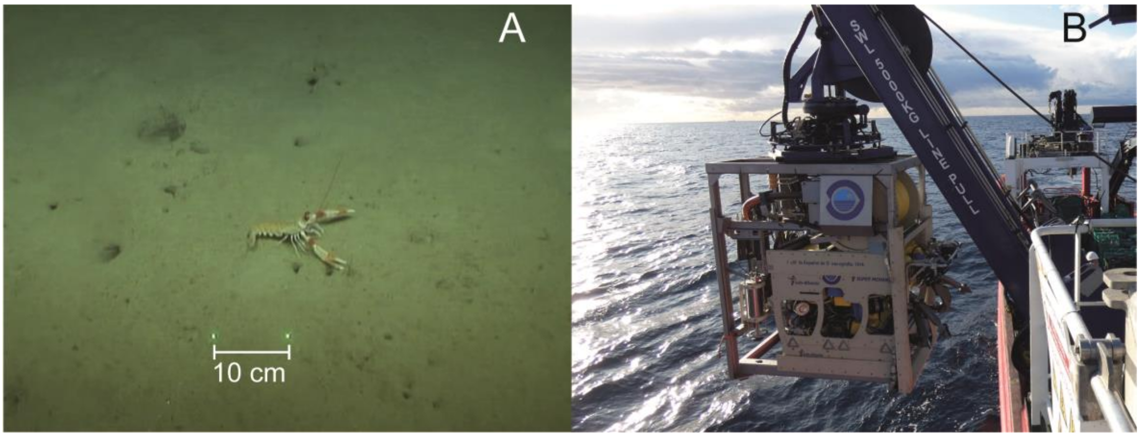


Figure 10. Non-invasive methodology for monitoring areas. A) ROV Liropus equipped with a forward-facing video camera (HD Kongsberg OE14-502) positioned below four Halogen 250 W Deep Sea Power & Light (DSPL) lights. B) Norway lobster recorded by the ROV, which also had two parallel green lasers with 10 cm separation.

1.5.3. Fishing data compilation and analysis

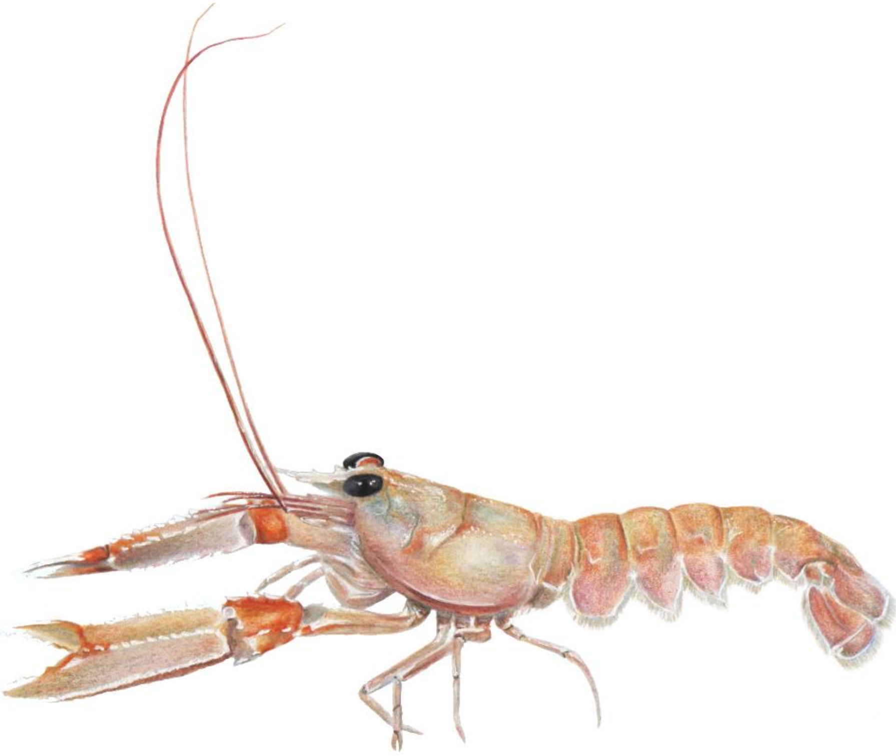
Monthly and annually, Norway lobster landings (kg) and Landings per Unit Effort (LPUE, kg/day/vessel) were collected from the Fisheries Department Service of the Autonomous Government of Catalonia from 2000 to 2021. We also obtained annual and seasonal landings data (kg) from previous studies (Sardà, 1998b; Aguzzi et al., 2007) at Barcelona harbor from 1979 to 1994. These data were used to evaluate the Norway fishery trend over time to know the actual situation of the fisheries.

Monthly landings data from Norway lobsters and other 12 coexistent demersal species and taxa were combined with Vessel Monitoring System (VMS) to obtain the spatial distribution of these species on the northwestern Mediterranean Sea from 2008 to 2021. Landings were standardized to LPUE based on fishing effort (time of fishing activity, kg/h/km^2). The 12 taxa classified were the Teleostei argentine (Argentinidae spp.), blackbelly rosefish (*Helicolenus dactylopterus*), megrim (*Lepidorhombus boscii*), anglerfish (*Lophius* spp.), European hake (*M. merluccius*), blue whiting (*M. potassou*), forkbeard (*Phycis* spp.), gunards (Triglidae spp.), the Cephalopoda white octopus (*E. cirrhosa*), bobtails (*Sepietta* spp.), variety of squids and the Crustacea deepwater pink shrimp (*P. longirostris*).

Chapter 2.
Results

2.1. An update of the population status of a commercially valuable European crustacean, the Norway lobster *Nephrops norvegicus*, in the highly exploited northwestern Mediterranean Sea

Maria Vigo, Eve Galimany, Patricia Poch, Ricardo Santos- Bethencourt, Joan Sala-Coromina, Nixon Bahamón, Jacopo Aguzzi, Joan Navarro, Joan B. Company



Under Review. ICES Journal of Marine Science.

Abstract

The Norway lobster *Nephrops norvegicus* is one of the most valuable fishery resources in many coastal countries of the Mediterranean Sea and the northeast Atlantic Ocean. In the Mediterranean Sea, several stocks are being overexploited with ecological, economic, and social consequences. To perform an adequate stock assessment and provide advice on maximum sustainable yield, reliable biological parameters of the species are required. Considering that biological parameters may change with time in overexploited populations, in the present study conducted in the northwestern Mediterranean Sea, we updated key biological parameters of Norway lobsters: size at which 50% (L50) of females were in reproductive condition, length-weight relationships, and individual size structure. Moreover, daily landings were combined with the spatial position of the vessels tracked by their Vessel Monitoring System, to obtain information about the geographical distribution and time series of Landings Per Unit of Effort (LPUE) as well as landings from 2008 to 2021. Our results may indicate overexploitation of the resource, revealing a severe reduction in size at 50% maturity, an earlier spawning and brooding period, and a clear decrease of LPUE over time.

Keywords: fisheries management, fishing resources, landings, revisiting biological parameters, size at onset of maturity.

2.1.1. Introduction

The future of fishing as a viable economic, social, and cultural activity is uncertain (Pauly et al., 2003). It is estimated that between 40% and 50% of tropical and temperate ecosystems exceed the thresholds for the sustainability of fisheries and, therefore, are considered overexploited (Link and Watson, 2019). Despite a decrease in fishing pressure over the past decade, leading to the recovery of some fish stocks (Cardinale et al., 2013; Fernandes and Cook, 2013), there is still a long way towards achieving a global recovery of overexploited populations (Froese and Proelß, 2010; Cardinale et al., 2013). For example, in the Mediterranean and the Black Seas, a recent study with 54 commercial fish and invertebrate species revealed that 85% of their stocks were overexploited (Demirel et al., 2020). A key to achieve best management practices is to implement science-based management (Pikitch et al., 2004). To achieve this goal, it is imperative to obtain biological parameters of the target species, in order to comprehend the temporal changes in their abundance, distribution, and biology, which may be subject to different alterations, depending on the degree of exploitation (Ligas et al., 2011; Galimany et al., 2015).

The Norway lobster, *Nephrops norvegicus* (Linnaeus, 1758), is a benthic crustacean inhabiting muddy bottoms at depths from 10 to 800 m, distributed in northeastern Atlantic and Mediterranean waters (Bell et al., 2013; Johnson et al., 2013). Atlantic populations are mainly found on the continental shelf (Eiríksson, 2014), whereas in the Mediterranean Sea, the highest abundance is present on the upper and lower depths of the continental slope, between 300 and 600 m depth (Maynou and Sardà, 1997; Abello et al., 2002). It is one of the most valuable European fishing resources with a great commercial importance across its entire distribution (Sardà, 1998a; Bell et al., 2013; Ungfors et al., 2013). Its global capture production in European waters has reached approximately 60,000 tonnes per year for the last 30 years (Bianchini et al., 1998; Chapman, 1980; Ungfors et al., 2013; FAO, 2022). In the Mediterranean Sea, Norway lobsters are captured by bottom trawlers, in which other demersal commercial species are also fished, such as European hake (*Merluccius merluccius*), anglerfish (*Lophius budegassa* and *Lophius piscatorius*), white octopus (*Eledone cirrhosa*) and blue whiting (*Micromesistius poutassou*) (Sardà, 1998a).

Fishery management in Mediterranean European waters relies on biological scientific advice, involving effort limitation and gear regulation (Sardà, 1998a; Sánchez Lizaso et al., 2020). Although many European Atlantic fisheries incorporate output limits through total allowable catches (TACs), as the implementation of TACs on Northeast Atlantic stocks of Norway lobsters (EU, 2020), these measures encounter difficulties in their implementation and demonstrate no efficiency when applied to diverse and mixed fisheries, which constitute most fisheries in the Mediterranean Sea (Bellido et al., 2015; Sánchez Lizaso et al. 2020). In fact, in the Mediterranean Sea, just a few species, such as the bluefin tuna (*Thunnus thynnus*) and the swordfish (*Xiphias gladius*), are currently managed through TACs (Lleonart and Maynou, 2003; McKenzie et al., 2009; Oceana, 2016). Norway lobster stocks for northern European waters are assessed in Europe by the International Council for the Exploration of the Sea (ICES) through an expert Working

Group, such as the ICES Working Group on *Nephrops* Surveys (WGNEPS) (Leocádio et al., 2018). These assessments consist in a combination of fishery dependent data from landings and fishery independent data from video surveys, UnderWater TeleVision (UWTV) (Morello et al., 2007; Dobby et al., 2021). In the Mediterranean Sea, stock assessments are conducted by the General Fisheries Commission for the Mediterranean (GFCM) (Cardinale et al., 2021) and the Scientific, Technical and Economic Committee for Fisheries (STECF, 2016). As UWTV surveys still are not implemented in the Mediterranean Sea, the evaluation of the stock is through assessment models that need biological parameters. However, these evaluations may rely on assessment models (e.g. to estimate fishing mortality for which average yield is equal to maximum sustainable yield, MSY) featuring biological parameters that require updating, which is relevant as many resources are overexploited or show signs of decline (Rindorf et al., 2016; Cardinale et al., 2017). In the case of Norway lobster, this crustacean has striking differences concerning the level of exploitation and biological characteristics (such as growth rate, density, or size structure of the population) depending on the geographical variations of the habitat, exploitation patterns, population density, and substrate characteristics (Maynou, 1998; Sardà et al., 1998; Aguzzi et al., 2003; Aguzzi and Sardà, 2008). For example, in the northwestern Mediterranean Sea (the northern half of the FAO geographical subarea 6 - GSA06), where Norway lobsters are one of the most valuable stocks for the bottom trawl fishery, former studies on its biology suggested a size reduction of the individuals caused by fishing pressure (Sardà, 1998b; Rotllant et al., 2005). The prevailing management approach for this crustacean involves regulation through the establishment of a minimum conservation reference size (MCRS), set at 20 mm of Cephalothorax Length (CL) in the Mediterranean Sea with a mesh size of 40 mm square codend (Regulation (UE) 1380/2013, 11/12/2013; Regulation (EU) 2019/1241, 20/06/2019). Notably, the estimated size at 50% maturity in Catalan waters was already approximately 30 mm CL in 1998, as documented by Orsi Relini et al. (1998). Consequently, obtaining updated biological information as well as updated data about the population status is especially crucial considering that the most recent available biological data for this region were assessed two decades ago. Therefore, in the present study, we aim to revisit the main biological parameters of the Norway lobster in the Catalan Sea, to provide relevant data for a revised assessment of this stock, acknowledging its status in terms of exploitation. In particular, we estimated length distribution, length-weight relationships, demographic structure, and reproduction, and evaluated trends in landings and income over the past two decades by comparing our present results with those of previous studies in the area.

2.1.2. Material and Methods

Study area and data collection

This study was conducted in the northwestern Mediterranean Sea along the Catalan coast (Fig. 2.1.1), where Norway lobster inhabits muddy substrates from 80 to 550 m on the lower shelf and upper-middle slope of the continental margins (Abello et al., 2002). Within this region, the bottom trawl fleet is composed of 221 vessels, which operate five days a week during a maximum of 12 h in daylight hours, commercializing the landings daily upon the arrival of the trawlers at the respective base port to which each vessel is affiliated (BOE, 502/2020).

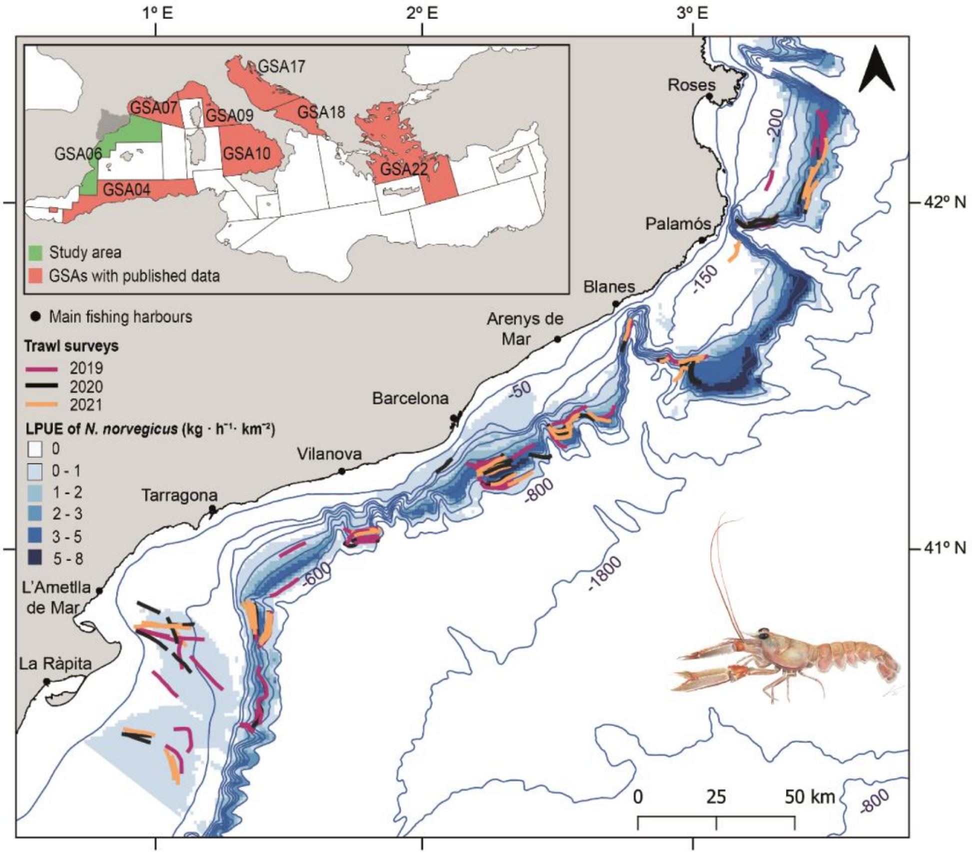


Figure 2.1.1. Spatial distribution of the annual averaged LPUE (Landings Per Unit Effort) of Norway lobsters in the Catalan Sea (northwestern Mediterranean) from 2019 to 2021, obtained by combining Vessel Monitoring System (VMS) information and official daily landing data (European Commission, 2022). Trawl surveys conducted in the study are represented in the map (in purple, black, and orange for years 2019, 2020 and 2021, respectively). Note: for comparison purposes, FAO subgeographical areas (GSA) are indicated. Grey land indicates the study area along the Catalan coast in the northern part of GSA06, in green. Other GSAs with available data of Norway lobster stocks are indicated in orange. Norway lobster illustration by Joan Mir-Arguimbau.

To evaluate the current population status and revisit the main biological parameters of Norway lobsters we used three distinct types of datasets. These encompassed two separate datasets containing landings data and fishing effort, sourced from public repositories, along with a third dataset collected directly on-board commercial bottom trawlers.

Daily landings dataset and LPUE time series

Landings data on Norway lobsters (monthly and annually) and fishing effort (vessel per day) from 2000 to 2021 were obtained from the Fisheries Department Service of the *Generalitat de Catalunya* (autonomous government of Catalonia, NE Spain). We also obtained annual and monthly landings data (kg) from previous studies (Sardà, 1998b; Aguzzi et al., 2007) at Barcelona harbor from 1979 to 1994. We compared the temporal evolution of Barcelona harbor's landings (kg) in that period with landings from the same port from 200 to 2021. In order to examine temporal changes in monthly landings, we conducted a comparative analysis of three distinct time series. These include the period from 1979 to 1994, exclusively focusing on Barcelona harbour landings, a selected timeframe spanning 2005 to 2010 encompassing landings data from the *Generalitat de Catalunya,* and the time series of catches gathered from the monthly commercial bottom trawlers during the years 2019 to 2021 (further details below).

Temporal spatial overlap of LPUE

To estimate the spatial overlap between years of the N. norvegicus presence from 2008 to 2021, we combined daily landings data on Norway lobsters, sourced from the Service of the *Generalitat de Catlunya*, but incorporating information on fishing spatial effort using the Vessel Monitoring System (VMS) for daily vessel positioning following the methodology described in Sala-Coromina et al. (2021). Data regarding fishing spatial effort before 2008 was not available because VMS data were enforced from 2005 and the first 2–3 years of the VMS implementation data is not 100% reliable. Landings were standardized based on fishing effort (duration in hours of fishing activity) and referred to as Landing Per Unit Effort (LPUE). It is important to note that when estimating spatial overlap, the fishing effort (measured as the duration of recorded fishing activity in hours) differs from the fishing effort (measured as vessels or landings per day) from the previously obtained data used to compare the temporal evolution of landings. The measurement in hours for fishing effort enhances the spatial localization of fishing activities. We represented the spatial distribution of yearly LPUE with a heatmap to observe the bathymetric range (every 25 m, from 50 m to 800 m depth) from 2008 to 2021, comparing the LPUE data based on Cohen's Kappa coefficient. This pairwise statistic (McHugh, 2012) indicates how much the same spatial units (sites defined by a grid within the study area) overlap in terms of presence of Norway lobsters between years. Cohen's Kappa values range from − 1 to + 1, though it usually falls between 0 and 1, where 0 indicates a random agreement, and + 1 indicates complete agreement (in contrast to −1, indicating complete disagreement) (Landis and Koch, 1977). To calculate the spatial similarity between the different yearly LPUE distributions, we used the *"*irr" package (Gamer et al., 2019). We evaluated the overlap of LPUE between years in the bathymetry range (i.e., every 25 m; see above) by using Spearman´s correlation through the "stats" package (R Core Team, 2023). The values of this correlation coefficient range from -1 to 1 indicating the direction and the strength of the relationship between 2 variables, being stronger the closest to -1 or 1, and independent variables closer to 0.

Data collection through commercial bottom trawlers

Biological sampling of Norway lobster individuals was conducted from January 2019 to December 2021 on board commercial bottom trawlers, harbored in nine of the most important ports of the study area (Fig. 2.1.1). All sampled individuals resulted from a total of 157 hauls, 54 carried out in 2019, 51 in 2020 and 52 in 2021. These surveys were conducted at a frequency of approximately 3 to 4 surveys per month, covering all the Catalan coast throughout the entire year. Trawling vessels were equipped with a commercial fishing net of 40–50 mm squared mesh size at cod-end, according to regulation CE Nº 1967/2006. All biological parameters were measured on-board and, whenever available, 90 individuals covering all commercial categories (30 individuals from each category, i.e. small, medium and large) were collected and transported to the Institute of Marine Sciences laboratory (ICM-CSIC) for further examination. The measures taken were Cephalothorax Length (CL in mm) and weight (W, in g), and all individuals were sexed. Males and females can be distinguished by the position of the genital apertures and the shape of the first pair of pleopods (Powell and Eriksson, 2013). In the case of females, the ovaries weight (in g) and the maturity stage were also annotated.

Population structure

Size-frequency distributions were constructed per 1 mm size class for each sex, using density plots. To test for differences in mean size between males and females, we conducted non-parametric Kruskal-Wallis tests. A Kolmogorov-Smirnov two sample tests were also used to detect differences between sexes in size distributions. We obtained size distribution data from 1974 and 1994 in the same GSA06 (Sardà, 1998b) to compare the Norway lobster population over time.

Length-weight relationships were analyzed for each sex, separately and combined, using the equation (Ricker, 1973; Pauly, 1984):

$$W = a \cdot CL^{b} \tag{1}$$

where W is the body weight (in g), CL is the cephalothorax length (in mm), a is the intercept of the regression curve, and b is the slope of the scaling exponent, indicating the pattern of growth: i.e. negative allometry ($b < 3$), isometry ($b = 3$), or positive allometry ($b > 3$). The relationships between length and weight were estimated with “FSA” R package (Ogle et al., 2023).

Maturity and reproduction stages

Sex ratio was evaluated seasonally from the surveys performed only in the upper slope (200–500 m), where Norway lobsters are found in higher abundances (Sardà, 1998a). G-tests (Gadj) (Sokal and Rohlf, 1981) were carried out to test for significant differences in sex ratio. Then, male and female percentages by season were estimated. From the total of the sampled females, we estimated the percentage of pleopods egg-bearing (i.e., berried) females per season.

Females were classified into 5 maturity stages, based on the macroscopic examination of the colors from the ovaries, modified of a histological scale from Rotllant et al. (2005): Stage I white-immature, slender and thin ovaries; Stage II resting (also refers to berried females), cream-yellowish; Stage III beginning of maturation, small, light green; Stage IV big, thick and light green ovaries; Stage V dark green, advance maturation in pre-spawning phase. All berried females, that are categorized as Stage II of maturity, were also identified and quantified.

The Gonadosomatic Index (GSI), indicating the maturity status of females, was calculated from the ratio of ovary weight over total body weight (Strange, 1996):

$$GSI = gonad\ weight / body\ weight \times 100 \tag{2}$$

For the estimation of size at 50% maturity, we considered the females sampled all year round, defining mature females from Stage II (including berried females) to females at Stage V. To estimate the size at 50% maturity, a logistic estimation of gonad maturity was run with “SizeMat” package in R program (Torrejon-Magallanes, 2020), between CL and the sexual maturity determined for both immature (Stage I) and mature (Stage II–V) females. In these analyses, a logistic curve was fitted to the data so that the CL at which 50% of females were in reproductive condition (L50) could be estimated.

2.1.3. Results

Landings trends

Over the period 2000–2021, there was a decreasing trend in both Norway lobster total landings (tonnes) and LPUE (Fig. 2.1.2A). Over the course of 21 years, the LPUE decreased by 37.81% representing a reduction of 210,647 kg in the total landings. Moreover, total incomes also decreased by 39.67%, amounting 2,190,372 € less than 21 years prior. These trends reached their lowest values in 2021 considering all Catalan Sea fisheries (Supplementary Material section Table S2.1.1). The landing trend observed at Barcelona harbor encompassed a more extensive period, from 1979 to 2021, revealing distinct transitions (Fig. 2.1.2B). Notably, the lowest landing was reported in 1992 with only 4.69 tonnes. Following this, there appeared to be an upward trajectory in landings until 2014. Starting in 2015 and coinciding with the decreasing trends in all Catalan fisheries, there was a sudden and significant decline in the stock. Regarding only Barcelona harbour, the stock showed an approximate decrease of 22.95 tonnes in 2021, accounting for a 64.29% reduction from the stock landed in 1979 (Fig. 2.1.2B).

Monthly landing patterns from 2005 to 2010 exhibited a peak in late spring months and summer, mainly in July, with mean values ranging between 33.70 and 41.10 tonnes for monthly landings from May to August (Fig. 2.1.2C). The trends observed during 2005–2010 were analogous to the landing patterns witnessed from 2019 to 2021. Upon comparing the three distinct time series of data (1979–1994, 2005–2010, and 2019–2021) for Barcelona harbor landings, it becomes evident that the highest landings across all-time series coincide and occur between May and August (Fig. 2.1.2D).

Regarding spatial overlap between years, the Cohen’s Kappa statistic indicated that the distribution of Norway lobster showed a moderate overlap, with values ranging between 0.4 and 0.6, indicating no shifts of distribution from 2008 to 2021 (see Fig. 2.1.3A and Supplementary Material section Table S2.1.2). The bathymetric range of Norway lobsters remained similar over the years, being 0.92 the lowest Spearman correlation value (see Supplementary Material section Table S2.1.3). In 2008 and 2021, 75% of the landings came from depths of 300–625 m and 300–675 m, 50% came from between 350–550 m and 375–550 m deep, and 25% came from between 400–500 and 425–500 m deep, respectively (Fig. 2.1.3B).

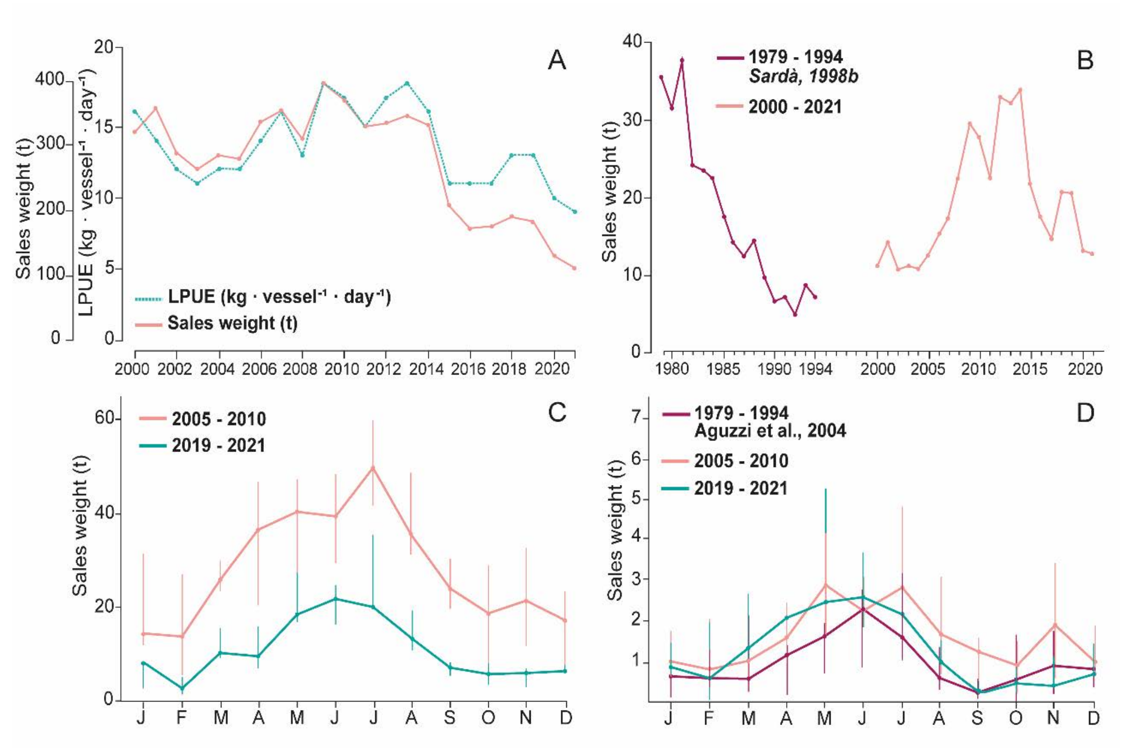


Figure 2.1.2. Annual landings of Norway lobsters from Catalan trawler vessels. (A) LPUE of N. norvegicus (kg · vessel^{-1} · day^{-1}) (light-blue-dashed line), and annual sales weight in tonnes (t) (pale orange line). (B) Norway lobster annual landings of Barcelona harbor represented by sales weight in tonnes (t) from 1974–1994 (Sardà, 1998a) and 2000–2021. (C) Average monthly sales weight in tonnes along the Catalan coast from 2005–2010 and 2019–2021. (D) Average monthly sales weight in tonnes from Barcelona harbor comparing three temporal datasets, from 1979–1994 (Aguzzi et al., 2004), 2005–2010 and 2019–2021.

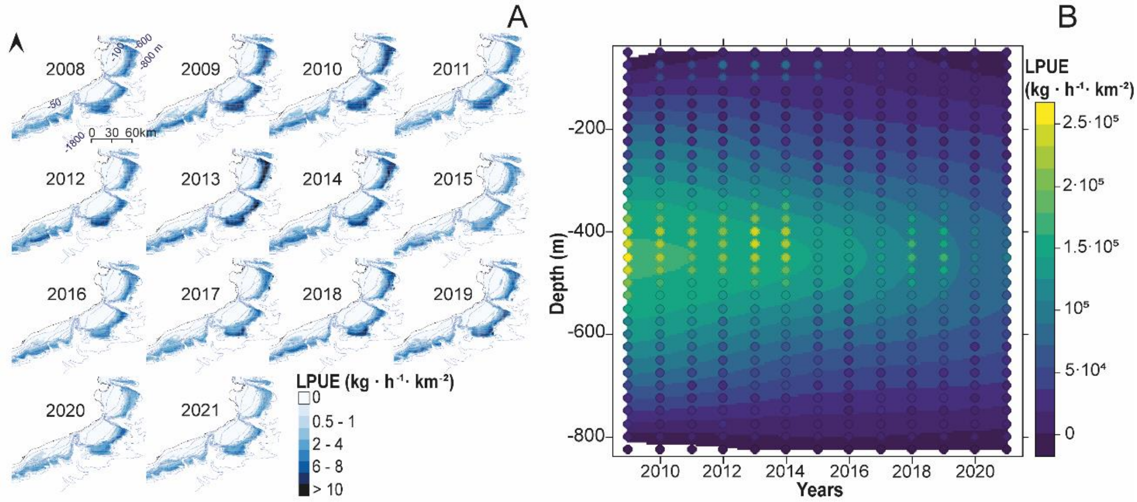


Figure 2.1.3. Distribution of the LPUE of Norway lobsters along the Catalan coast (northwestern Mediterranean Sea, Spain) from 2008 to 2021, obtained by combining Vessel Monitoring System (VMS) information and official daily landing data (European Commission, 2022). (A) Spatial distribution of the LPUE from 2008 to 2021, and (B) bathymetric range of the LPUE of Norway lobsters from 2008 to 2021. Values of LPUE accumulated per year and bathymetry are indicated in the color bar.

Population structure

From the total of 157 hauls conducted from 2019 to 2021, we collected 6,698 individuals, 4,070 males and 2,628 females (Table 2.1.1). The CL examined from the collected individuals during the sampling period ranged from 18 to 65.5 mm in males, and 18 to 60.35 mm in females, with mean weights of 40.19 ± 27.26 and 23.94 ± 14.21 g, for males and females respectively (Table 2.1.1). The size frequency distribution differed between sexes, with males having higher mean CL than females (males = 36.45 ± 7.34 mm, females = 31.16 ± 5.16 mm; $\chi^2_{1,6697} = 1352$, $p < 0.0001$; Table 2.1.1 and Fig. 2.1.4A-B). Kolmogorov-Smirnov tests also indicated a different size distribution between sexes ($D = 0.21$, $p < 0.01$). Regarding temporality, there were significant differences between years ($H=133.08$, $p < 0.01$) and between sexes ($H = 1371.72$, $p < 0.01$). Mean CLs (mm) for males were 34.34 ± 32.35 in 1974 and 30.35 ± 29.21 in 1994, whereas CLs (mm) for females were 31.51 ± 28.39 in 1974 and 27.89 ± 26.20 in 1994 (Table 2.1.1).

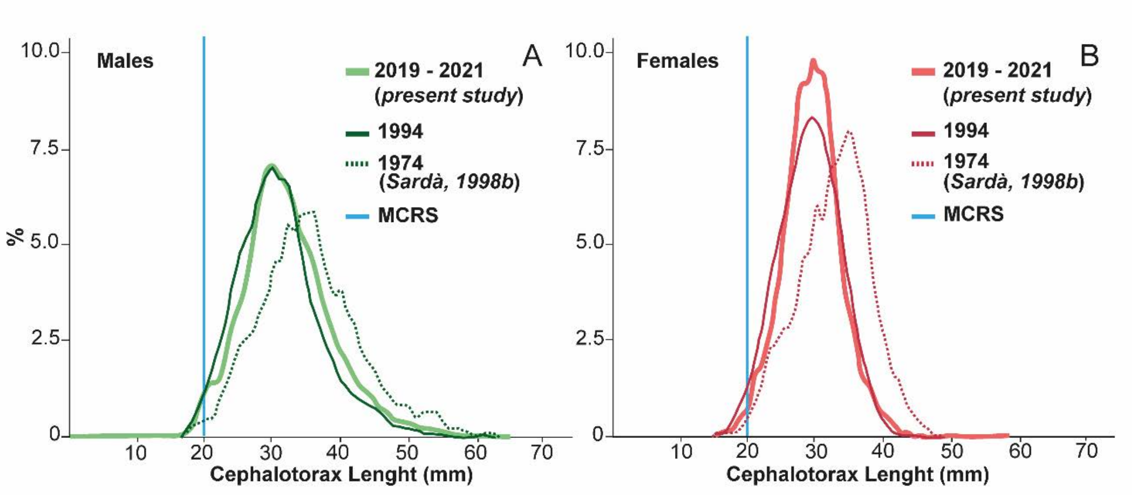


Figure 2.1.4. Plot size frequency distribution of Norway lobsters sampled from 2019 to 2021, and from 1994 and 1974 (Sardà 1998a). (A) Males size distribution. (B) Females size distribution. Blue line indicates the minimum conservation reference size (MCRS) (Regulation (UE) 1380/2013, 11/12/2013; Regulation (EU) 2019/1241, 20/06/2019).

The non-linear regressions between CL and body weight (W) for females, males, and pooled individuals had a good fit with, with high correlation coefficients ($r^2 > 0.90$; Fig. 2.1.4). Length-weight relationship for females, males, and pooled individuals were in the slope of the regression relationships; the scaling exponents (b) were similar between sexes indicating a slight positive allometric pattern for growth ($b > 3$) (Fig. 2.1.5; Table 2.1.1). The regression equation calculated by sex and pooled individuals were:

$$Log\ W_{females} = 4 \cdot 10^{-4} \cdot x^{3.1736} \tag{3}$$

$$Log\ W_{males} = 4 \cdot 10^{-4} \cdot x^{3.1766} \tag{4}$$

$$Log\ W_{pooled} = 5 \cdot 10^{-4} \cdot x^{3.1116} \tag{5}$$

The monthly commercial bottom trawling surveys carried out from 2019 to 2021 revealed that catches were notably higher during the spring months (April, May, June) and the summer months (July, August, September) (Fig. 2.1.2C). From the upper slope sampling, averaging years and surveys, and correcting the abundance per the swept trawled area, spring was the season that yielded the highest catch density (1,191 ±711 N km^{-2}), followed by summer (1,158 ± 598 N km^{-2}) (Table 2.1.2).

Table 2.1.1. Length-weight relationships for Norway lobsters obtained in the present study compared with the relationships in the same and other GSAs of the Mediterranean Sea. No.: total of specimens; a: intercept; b: slope; Sex: M are males, F females, and C combined sexes; CLmin: minimum cephalothorax length (mm); CLmax: maximum cephalothorax length (mm); CL: mean of cephalothorax length and the standard deviation (in mm); W: mean body weight of all individuals sampled and the standard deviation (in g). The Mediterranean subareas are defined following the criteria of the General Fisheries Commission for the Mediterranean (GFCM).

Source	Area	Year	No.	a	b	Sex	CLmin	CLmax	CL	W
Present Study	GSA06	2019–2021	4,070	0.0004	3.1766	M	18.00	65.50	36.45 ±7.34	40.19 ±27.26
			2,628	0.0004	3.1736	F	18.00	60.35	31.16 ±5.16	23.94 ±14.21
			6,698	0.0005	3.1166	C	18.00	65.50	34.38 ±7.06	33.83 ±24.38
Sardà, 1998	GSA06	1974	1,600			M			34.34 ±32.35	
			1,484			F			31.51 ±28.39	
		1994	13,549			M			30.35 ± 29.21	
			12,470			F			27.89 ±26.20	
Sardà et al., 1998	GSA06	1994	7,887	0.0005	3.0520	M			31.00	
			7,574	0.0008	2.9140	F			28.90	
		1995	5,806	0.0004	3.1180	M			30.50	
			4,942	0.0005	3.0750	F			27.60	
Angelini et al., 2020	GSA17	2012–2014	4,145	0.0003	3.2470	C	9.00	53.00		
			1,842	0.0003	3.2030	M			30.60 ±5.71	
			2,299	0.0013	2.7620	F			24.50 ±9.20	
	GSA17	2012–2016	2,798	0.0008	2.9670	C	17.00	75.00		
			1,466	0.0008	2.9610	M			47.06 ±6.38	
			1,332	0.0010	2.9010	F			44.33 ±6.53	
Stergiou and Politou, 1995	GSA22	1993	275	0.9229	2.9130	C	11.00	55.00		
		1994	221	0.4701	3.0850	C	16.00	68.00		
Aydin and Aydin, 2011	GSA22	2008	659	0.4800	3.2100	C	17.20	49.40	28.50	17.30
			305	0.4600	3.2700	M	19.30	49.40	29.80	20.90
			354	0.5200	3.1200	F	17.20	42.30	27.50	14.40

Table 2.1.2. Individuals of Norway lobsters by season from the surveys conducted from 2019 to 2021 in the upper slope (200–500 m). *n* indicates the number of surveys conducted in each season at the upper slope; *T* represents the total number of individuals corrected per the swept area covered (No.·km^{-2}); *M* is number of male individuals per swept area (No.·km^{-2}) and the percentage respect the total number of individuals (*T*) between brackets; *F* is number of female individuals (No.·km^{-2}) and the percentage respect the total number of individuals (*T*) between brackets; *Bd* is the number of berried females per swept area and percentage in brackets respect the total number of females estimated.

Season	*n*	*T*	*M*	*F*	*Bd*
Winter	21	1049 ± 741	651 ± 487 (62.06)	398 ± 284 (37.94)	7 ± 11 (1.76)
Spring	21	1191 ± 711	560 ± 369 (47.02)	631 ± 362 (52.98)	0 (0)
Summer	20	1158 ± 598	599 ± 306 (51.73)	559 ± 329 (48.27)	37 ± 52 (6.62)
Autumn	17	819 ± 432	533 ± 311(65.08)	286 ± 161 (34.92)	62 ± 49 (21.86)
Total	79	1053 ± 632	582 ± 365 (55.27)	471 ± 320 (44.73)	28 ± 44 (5.94)

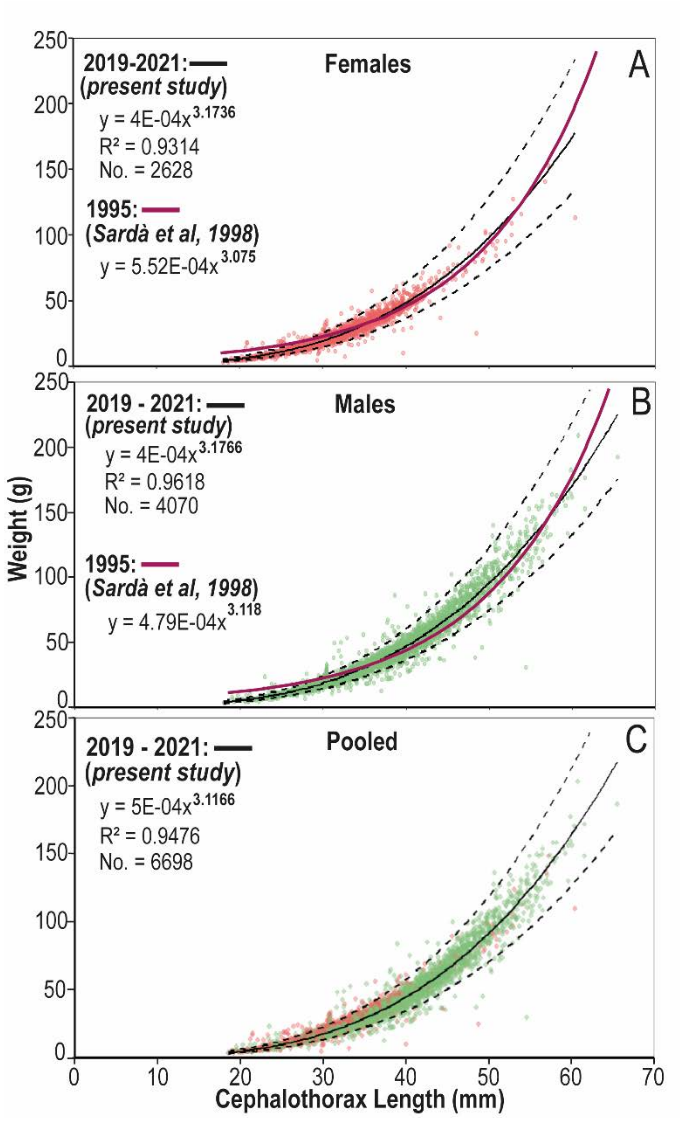


Figure 2.1.5. Relationship between length and weight of A) females (in red), B) males (in green), and C) both sexes (females in red, males in green) pooled of Norway lobsters sampled in the northwestern Mediterranean Sea. In purple line there is the non-linear regression from length-weight relationships obtained in previous studies from the same area GSA06 (Sardà, 1998b).

Maturity and reproduction stages

Sex-ratio differed from the expected equilibrium (0.50) in autumn and winter, exhibiting a lower presence of females in the landings from October to March (Table 2.1.2). In spring, females showed a higher presence than males (0.53 and 0.47, respectively). G-tests indicated significant differences between sex-ratio among seasons ($G = 90.64$, $p < 0.01$). However, similar sex-ratio was found for autumn and winter ($p = 0.18$) and spring and summer ($p = 0.05$). Overall, berried females as a percentage of total females were higher in autumn (21.86%) than in the other seasons. Moreover, G-tests conducted with berried females among seasons showed significant differences among all seasons ($G = 164.17$, $p < 0.01$).

GSI values of females between 2019–2021 were higher in summer, specifically in July and August (Fig. 2.1.6A). Afterwards, in late summer and the beginning of autumn the GSI decreased, coinciding with a higher percentage of berried females (Table 2.1.2). Additionally, GSI values are also shown by maturity stage (I–V) (Fig. 2.1.6B). Between 2002–2003, GSI monthly values demonstrated the highest values in July, August and September (Fig. 2.1.6C). The estimated size at 50% maturity for females was 25.3 mm CL, with a confidence interval of 24.8–25.7 mm CL (Fig. 2.1.7), a lower value when compared to other Norway lobster stocks evaluated within the Mediterranean Sea (Table 2.1.3).

Table 2.1.3. Comparative table of different studies performed in different GSAs with size parameters of Norway lobsters in commercial bottom trawl fishery; No.: total specimens; CL: mean cephalothorax length (mm); S50M: size at size at 50% maturity, cephalothorax length with a 50% probability of being retained. The Mediterranean subareas are defined following the criteria of the FAO organization General Fisheries Commission for the Mediterranean (GFCM).

Areas	Year	No.	CL	S50M	Studies
GSA02	1995			36	Orsi Relini et al., 1998
GSA04	2011–2012	617	62.14	33	Bekrattou et al., 2019
GSA06	1974,1977,1978	3595	15.0-60.0	30.0-31.0	Sardà, 1991
GSA06	1995			30	Orsi Relini et al., 1998
GSA06	**2019–2021**			**25.7**	**Present Study**
GSA07	1980			27	Morizur, 1981
GSA09	1995			32	Orsi Relini et al., 1998
GSA10	1995			32	Orsi Relini et al., 1998
GSA17	2012–2014	2299	24.50 ± 9.20	21.14	Angelini et al., 2020
	2012–2016	1332	44.33 ± 6.53	30.83	
GSA17-18				31.69	Mytilineou and Sardà, 1995
GSA18	1995			30	Orsi Relini et al., 1998
GSA18	2009–2011	744	33.9 ± 6.9	25.7	Marković et al., 2016
GSA22	1995			33	Orsi Relini et al., 1998
GSA22	2007	510		28.1	Mente et al., 2009
Mediterranean Sea	2003			32	ICES, 2006

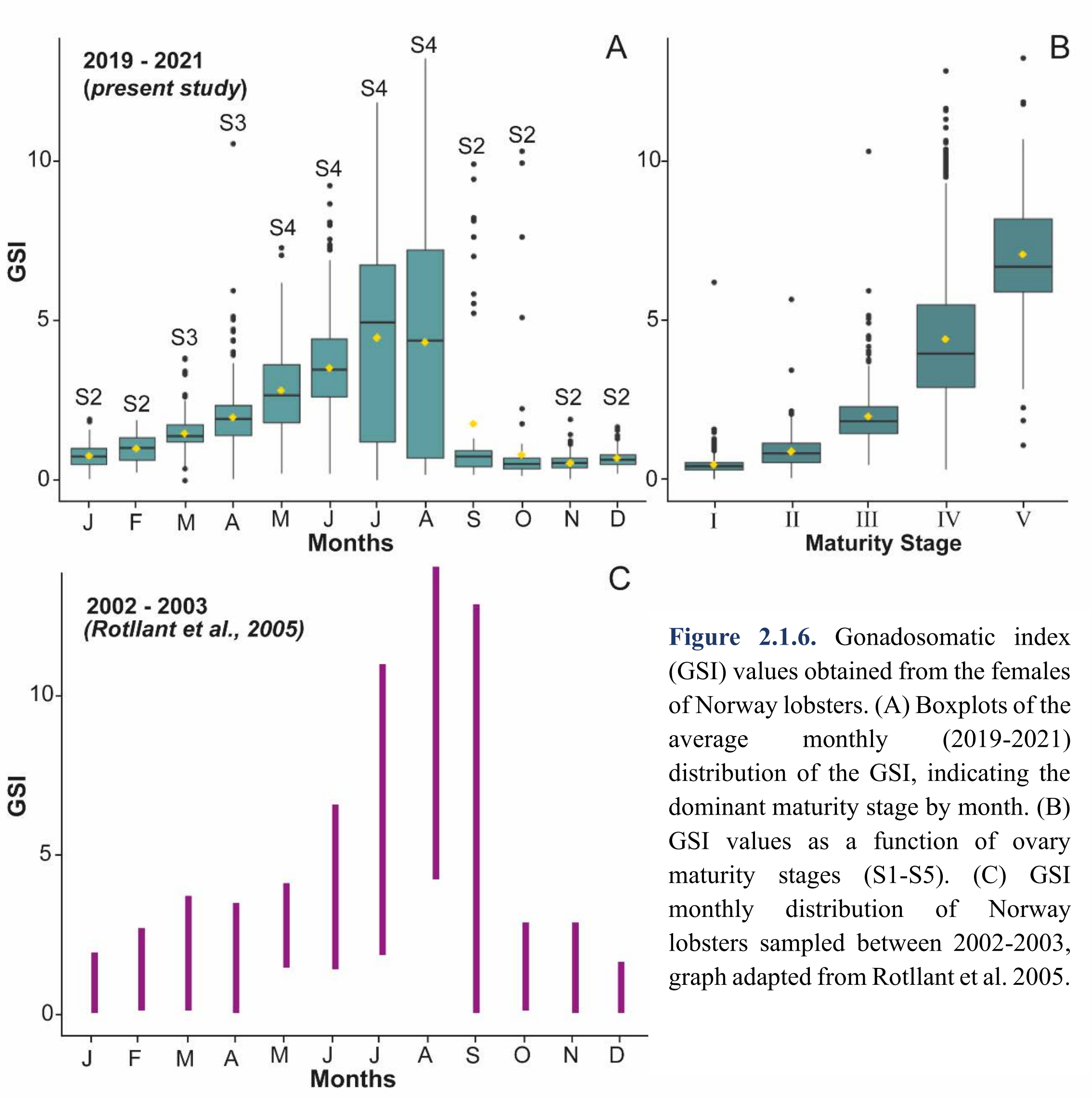


Figure 2.1.6. Gonadosomatic index (GSI) values obtained from the females of Norway lobsters. (A) Boxplots of the average monthly (2019-2021) distribution of the GSI, indicating the dominant maturity stage by month. (B) GSI values as a function of ovary maturity stages (S1-S5). (C) GSI monthly distribution of Norway lobsters sampled between 2002-2003, graph adapted from Rotllant et al. 2005.

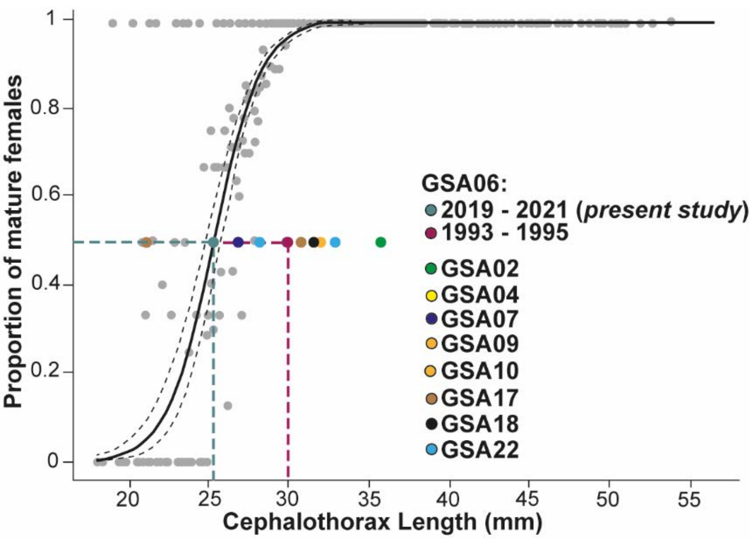


Figure 2.1.7. Length at 50% maturity (L_{50}) of Norway lobster females represented in percent mature females and confidence limits. Females collected all year, defining mature females from stage II to V, were considered. The figure presents the size at 50% maturity in this study (2019–2021), the purple dot representing the size at 50% maturity obtained in Orsi Relini et al. (1998) in GSA06, and size at 50% maturity evaluated in other GSAs in the Mediterranean Sea (see Table 2.1.3).

2.1.4. Discussion

Norway lobsters abruptly decreased in annual landings over time in the northwestern Mediterranean Sea, with a total of 65% biomass loss in just two decades (i.e., from 2000 to 2021). Moreover, we found clear evidence of a significant reduction, up to 5 mm, on size at 50% maturity for the population of Norway lobsters. However, it is important to note that this reduction in size at maturity did not translate into a decrease in mean sizes over time for both females and males. In the Mediterranean Sea, this species is mainly regulated by the minimum conservation reference size, which is limited at 20 mm CL (Regulation (UE) 1380/2013, 11/12/2013; Regulation (EU) 2019/1241, 20/06/2019), well below the size at 50% maturity reported so far (Fig. 2.1.7 and references herein). Our results may be an indicator of high fishing pressure on Norway lobsters evidencing that the management measures in place are not sufficient to manage the stock sustainably.

Spawning season and stock spatial distribution

The northwestern Mediterranean Norway lobster fishing grounds are still located from 300 to 675 m depth (Sardà, 1998a). However, we observed how the landings have extremely decreased in total numbers over the years. It is worth mentioning that, despite the fishing effort reduction in the last years (ICATMAR, 2022), the LPUE of the Norway lobster stocks is still decreasing.

Notwithstanding, landings preserve a seasonal component, probably related to the behavior of the species. Norway lobsters build burrows offering a natural mean of protection to bottom trawling activities (Aguzzi et al., 2004, 2023). A seasonal pattern in landings was observed, currently peaking in June, although in previous years the highest landings occurred in July-August. The individuals caught can be considered proportional to the number of individuals emerging from their burrows, which seems to depend on light intensity (Aguzzi et al., 2003, 2021; Vigo et al., 2021). Spring and summer are seasons where longer photoperiod duration elicits longer burrow emergence with animals wandering and encountering. Additionally, mating of Norway lobster takes place outside the burrows and occurs in spring-summer (Aguzzi et al., 2004). Later, during the brooding period, berried females hide inside their burrows all autumn until the release of larvae in early winter, showing a highly seasonal reproductive period (Farmer, 1974, 1975; Company et al., 2003; Rotllant et al., 2005). Possibly, a combination of all those factors may explain the larger catches during these periods, and lower catches in autumn and winter.

Demographic parameters as indicators of overexploitation

The population structure of Norway lobsters presents different demographic patterns in the northwestern Mediterranean due to area-dependent fishing pressure in combination with variable environmental factors such as habitat characteristics (Abello et al., 2002). Concerning landings, the largest individuals were always males. The mean sizes of individuals did not exhibit a reduction over time when compared to the mean size of individuals in 1974. However, it is important to note that the 1974 study was conducted within a specific delimited area near Barcelona, whereas the recorded sizes spanning 2019-2021 encompassed the entire Catalan coast. Despite this distinction, when considering only the comparison between these studies, there were no indications of overexploitation reflected in the mean sizes. Sex ratio was almost equal in spring and summer, yet in autumn and winter the presence of males was greater than females, coinciding with the periods in which there is a high proportion of berried females, which apparently spend more time concealed in tunnels (Farmer, 1975; Aguzzi et al., 2007).

Norway lobsters are considered a long-lived species (Hillis, 1979; Sardà, 1985; Castro, 1992), with slow growth rates ranging from 4 to 5 mm per year (Bianchini et al., 1998). Our results showed that the Length-Weight Relationship (LWR) was positively allometric for both males and females. Thus, the volumetric growth (body mass) is faster than the length growth (body length), with both sexes growing at the same speed. The LWRs can vary significantly, both temporally and spatially (Robinson et al., 2010). Other studies from the GSA06 reported a very similar a coefficient (ranging from 0.0004 to 0.0008 in Sardà et al., 1998; see Table 2.1.1), whereas the growth parameter indicated almost an isometry reaching *b* values close to 3, with most of them indicating a positive allometric pattern in both sexes (Sardà et al., 1998; Company and Sardà, 2000). Compared to other geographical areas of the Mediterranean, the only zone with negatively biometric relationship is the GSA17, corresponding to the northern and central Adriatic Sea (Angelini et al., 2020). Even if the difference is not significant, the growth rate of Norway lobsters seems to vary according to the geographical site. Growth in crustaceans is discontinuous because it depends on the frequency and increment of molting the old exoskeleton (Green et al., 2014). These two factors respond differently to environmental conditions, such as water temperature, which is a major factor influencing marine species, both in physiological and ecological aspects (Kinne, 1970; Aiken and Waddy, 1986). Other factors may suppress growth such as a high density of individuals in an area, potentially stemming from a high recruitment, which, in turn, may subsequently lead to competition interactions for resources like food and space (Parslow-Williams et al., 2001; Briggs, 2002; Johnson et al., 2013).

The proportion of berried females peaked from September to December, mostly during the autumn months (October-December). This peak occurred just after the spawning period, when females achieved the highest GSI values (late summer), corresponding to the lowest catches recorded during the year. The GSI monthly values from females sampled between 2002 and 2003 from Rotllant et al. (2005) showed a similar pattern compared to the present study, indicating highest values of GSIs in July and August, but also presenting high values in September. The reproduction cycle of Norway lobsters has slightly advanced starting the spawning period already in early August. Variations of the environmental factors, such as temperature, could directly modify growth patterns (e.g. molting period), reproduction periods (e.g. earlier spawning periods), and even induce migrations of some crustacean species (Company et al., 2008; Green et al., 2014; Le Bris et al., 2017). In fact, effects such as climate change have been involved in the decline of vulnerable lobster stocks and other communities due to changes in sea water temperature and salinity (Henderson et al., 2011; Caputi et al., 2013). The lower catches observed in

August from the most recent landing data series (2019–2020) could be explained by an earlier spawning followed by the brooding period, in which females hide inside their burrows a month earlier than previously recorded data (Rotllant et al., 2005).

The breeding cycle of Norway lobsters shifts depending on the latitude, while in lower latitudes is suggested to be annual, in higher latitudes, such as Iceland, Norway lobster females have a biannual breeding (Sardà, 1991; Powell and Eriksson, 2013). Our results highlight the fact that Noeway lobster females in the Mediterranean Sea have a single spawning yearly event, with an annual and highly seasonal breeding period as observed for other species dwelling at similar water depths (Company et al., 2003). In detail, the observed spawning period occurred in late summer (end August or in early September) and hatching was from December to February, as reported in other studies (Rotllant et al., 2005; Powell and Eriksson, 2013).

The size at 50% maturity estimated for females is 25.3 mm CL, approximately 5 mm less than the maturity size (30 mm CL) proposed by Orsi Relini et al. (1998) in the same area. In the Mediterranean, the size at 50% maturity has been reported to range between 30 and 36 mm CL in Algarve (Atlantic Ocean) and the Catalan and Adriatic Seas (Mediterranean Sea), being considered the regions with the smallest sizes (Angelini et al., 2020; Orsi Relini et al., 1998). This size reduction can be also observed in other areas, such as the GSA18 and GSA22 (Orsi Relini et al., 1998; Mente et al., 2009; Marković et al., 2016), in which the size seems to have also diminished approximately 5 mm CL. Our results, though, are similar to those from Atlantic stocks, as the average size at 50% maturity is about 25.6 mm CL among different Atlantic areas (Orsi Relini et al., 1998; McQuaid et al., 2006). The variation in size can be caused by differences in growth rate, which could be conditioned by many factors, including fishing pressure. For example, Marković et al. (2016), suggested that overfishing was the cause of the decreased size at 50% maturity (25.7 mm CL) observed for Norway lobsters in the South Adriatic Sea, the same size as the one found in this research. Indeed, the abrupt decline of population abundances, which may be caused by overfishing, are often followed by shifts in size and age at first maturity (Galimany et al., 2015; Di Salvatore et al., 2019; Molinet et al., 2020).

Previous assessment studies indicate that Norway lobster populations may not be strongly affected by fishing pressure in the GSA06 and other geographical subareas (STECF, 2019). However, we hypothesize that fishing pressure is depleting the biomass stock of Norway lobsters in the northern GSA06, leaving a population with small individuals. The biology and behavior of Norway lobsters may have some resilience, but it is a sensitive species to trawl disturbance, which has resulted in decreasing the size at 50% maturity. Apparently, juveniles and berried females spend most time in their burrows, which confers a natural source of protection from bottom trawlers thereby presenting lower mortality values (Abelló et al., 2002; Pauly, 2013). However, we suggest that the removal of large males can also affect and reduce the size at 50% maturity as previously indicated for the Mediterranean stocks (Orsi Relini et al., 1998; Abello et al., 2002; Rotllant et al., 2005). It is known that larger males are subject to a great fishing pressure because they spend more time outside their burrows, and that is the reason why males often dominate

Norway lobster catches (Briggs, 1995). However, fisheries in the Catalan area are also targeting female individuals that are close to the size at 50% maturity, and also small individuals (juveniles) that will be part of the mature stock. All this information is useful to develop new management approaches to better preserve this fishing resource.

The need of new management approaches

New management measures should be applied to minimize the impact on the Norway lobster stock (Ridgway et al., 2006; Lolas and Vafidis, 2021). Here, we observed how fishing pressure may be the stress that reduced the size at 50% maturity of Norway lobsters, while fisheries were targeting individuals with lower sizes that the MCRS established for this resource, which is currently in 20 mm CL in the Mediterranean Sea. Reducing the effort in terms of decreasing the number of fishing vessels, a management strategy applied up to now, does not seem to be enough to sustainably manage the fishery. Thus, we suggest an increase of MCRS and, importantly, an improvement in trawl selectivity, which would help reduce the fishing pressure (Bahamon and Sardà, 2006; Bahamon et al., 2007) as may avoid fishing an immature part of the stock leaving larger individuals to perpetuate the fishery. For example, the addition of escape rings is helping recover the exploited stocks of southern king crab stocks *Lithodes santolla* and *Lithodes confundens* in Southern Atlantic Ocean with an increase of male individuals (no extraction of males, thus no limitation of sperm) and ovigerous females (Varisco et al., 2019; Di Salvatore et al., 2021). In fact, the size at first sexual maturity of crustaceans should determine the minimum commercial exploitation (Jewett et al., 1985) and this may be reached through different approaches, e.g. establishing improved selectivity measures by, i.e., increasing the currently commercial 40 mm square mesh codends to reach the average retention rates to the MCRS (ICATMAR, 2022). Developing sustainable harvesting guidelines requires the precise quantification of Norway lobster populations across extensive geographic regions. This is achieved through stock assessment methods that rely on animal sampling via fishery-dependent trawls or underwater video cameras (ICES, 2016). However, it is important to note that capture rates can be significantly influenced by their burrowing behavior (Aguzzi et al., 2021). The integration of novel tools, including ecological monitoring technologies, has the potential to enhance existing stock assessment methodologies (Aguzzi et al., 2022). Other effective measures may be the establishment of no-take reserves, a promising useful management tool to achieve sustainable fisheries management (Sala and Giakoumi, 2018; Melaku Canu et al., 2020; Vigo et al., 2023a; 2023b).

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2.2. Using molecular and stable isotope markers to identify the main predators of *Nephrops norvegicus* in the Mediterranean deep- water ecosystems

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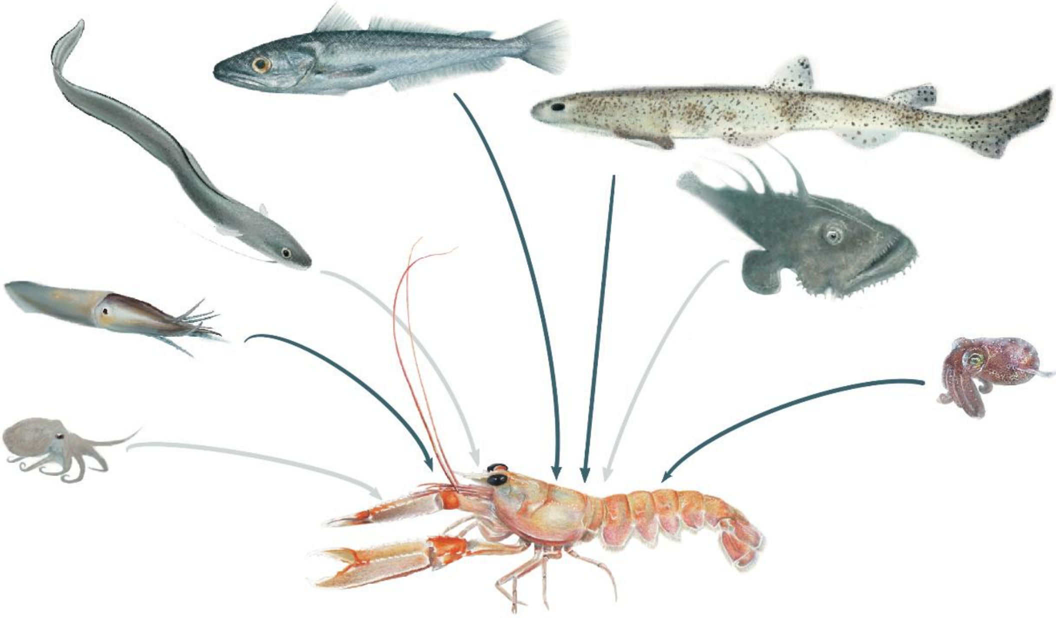

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Abstract

To obtain a better understanding of the functioning of ecosystems and how they respond to disturbance, it is necessary to identify the relevant biotic interactions and specific trophic roles. Predation is one of the most important biotic interactions that can also define the spatial patterns of other species. Many predators are considered key species for the functioning and maintenance of ecosystems, as they play an important ecological role that can influence the dynamics at lower trophic levels. The Norway lobster *Nephrops norvegicus* is one of the most valued European fishing stocks. However, its value and capture have declined over the last decade. In the Atlantic Ocean, Atlantic cod *Gadus morhua* is the main predator of Norway lobster. However, this species is not present in the Mediterranean Sea, and little is known about which species might prey on Norway lobsters in this area. Here, we combine 2 methodologies—genetic identification of stomach contents and stable isotope analyses—to identify, for the first time, the main predators of Norway lobster in the Mediterranean Sea. Moreover, we have created the Predation Index, which determines the most influential predator affecting Norway lobster population dynamics. Our results reveal that the major predators are the cephalopods *Sepietta* spp. and *Abralia veranyi*, which probably affect the early stages of Norway lobsters, followed by the elasmobranch *Scyliorhinus canicula* and the bony fishes *Merluccius merluccius, Trigla lyra*, and *Conger conger*. To evaluate possible fluctuations in the Norway lobster population, we consider the assessment of these predator populations crucial.

Keywords: ecological role, feeding ecology, fisheries, food web, Norway lobster, Predation Index, prey DNA, resource management, trophic ecology.

2.2.1. Introduction

Determining the trophic role of a particular organism is pivotal to understanding its ecological function in the ecosystem and to designing effective management actions. This involves identifying the environmental factors and biotic interactions that could in fluence or play an essential role in population dynamics and species distribution (D'Amen et al., 2018). Recognizing these factors could also be useful for predicting how marine ecosystems will respond to changing environmental conditions (Wisz et al., 2013). Among biotic interactions, predator‒prey interactions are key in affecting the spatial patterns of species (Ritchie et al., 2012). Predators play an important role in all ecosystems, influencing the dynamics of species at lower trophic levels (Estes, 1996; Ritchie and Johnson, 2009).

Ecosystem modelling, which also considers consumer‒prey interactions, is being widely used for ecosystem-based fishery management (Buchary et al., 2002). This holistic approach includes the type and magnitude of the species interactions involved, analyzing biomass and abundance at several trophic levels from plankton to apex predators (Fogarty, 2014). This entails a prior understanding of which prey‒predator interactions exist in the environment to be managed. Similarly, in the assessment of the effectiveness of marine protected areas (MPAs), evaluating predator densities is crucial, even in small MPAs, as an increase in predators could prevent the restoration of overexploited species (Clements and Hay, 2017) or a lack of them could lead to habitat regime shifts (Daskalov et al., 2007). Nevertheless, the trophic role that individual species play within marine ecosystems is still often unclear, precluding the prediction of the consequences of their removal or recovery. In the case of ecosystem-based fisheries management, a lack of knowledge of biotic interactions could lead to a misinterpretation of the consequences of overfishing, resulting in inconsistent trophic patterns constraining the viability of stocks and their predators (Shackell et al., 2010).

Despite the importance of this ecological information, there is still a huge knowledge gap regarding the main predators of some well-studied marine species. This is the case for Norway lobster *Nephrops norvegicus* in the Mediterranean Sea. This demersal decapod is one of the most important crustacean species for the European fishing industry, being considered an important target species across European waters. It is a common decapod crustacean distributed in the northeast Atlantic Ocean and the Mediterranean Sea, inhabiting the muddy bottoms of the continental shelves and slopes, at depths from 10 to 800 m (Johnson et al., 2013; Ungfors et al., 2013). The management of this stock involves a mixture of EU regulations (Common Fisheries Policy; CFP) and national legislation, though Norway lobster stocks seem to have been fished above scientific advised levels (Sardà, 1998a; Letschert et al., 2021). Over the last decade the Mediterranean stocks of Norway lobsters from the northwestern Mediterranean Sea (Spanish waters) have declined in abundance (from 400 t in 2009 to 200 t in 2019). In the Mediterranean Sea, most management policies are not successfully enforced, as the current state of the stocks is not reviewed (Sardà, 1998a). To better understand the temporal changes in species abundance, distribution and biology, this approach to fisheries management needs to be changed. Moreover, to prevent possible trade-off consequences due to fluctuations of other species populations that may be associated with Norway lobsters, it is essential to understand their ecological role and importance as a trophic resource for predators. Despite the large amount of research conducted on Norway lobsters, knowledge about its main predators in the Mediterranean Sea is scarce. In the Atlantic waters, its main predator is the Atlantic cod *Gadus morhua* (Chapman, 1980; Brander and Bennet,1986; Dombaxe, 2002), which is distributed within a similar depth range (Johnson et al., 2013). In contrast, information about its main predators in the Mediterranean Sea, where the Atlantic cod is not present, is limited to only a few studies that suggest that cephalopods, some demersal elasmobranchs, and the bony fish *Conger conger* could be important (Coll et al., 2006; El-Amine Abi-Ayad et al., 2011; Šantić et al., 2012; Navarro et al., 2014). However, describing the diet of cephalopods and elasmobranchs, and identifying specific prey using traditional stomach content analyses, is complicated because they usually have empty stomachs and, in the case of cephalopods, it is difficult to identify stomach contents due to the high efficiency of their beaks in crushing food and their rapid enzymatic stomach activity (Guerra, 1978; Ibáñez et al., 2021). For this reason, the actual trophic importance of Norway lobsters for these predators may be underestimated.

As an alternative to stomach content analysis, the use of trophic indicators such as molecular or stable isotope analyses (SIA) could help to determine the diet composition of marine predators (Guerreiro et al., 2015; Olmos-Pérez et al., 2017). In the case of molecular techniques, it is possible to determine the presence of a specific prey by detecting its DNA in the stomach contents of a potential predator (Dunshea, 2009). Also, stable isotopes of nitrogen (denoted as $\delta^{15}N$) and carbon (denoted as $\delta^{13}C$) have been used extensively to study the trophic ecology of marine predators (Shiffman et al., 2012; Navarro et al., 2013; Giménez et al., 2021). This approach is based on the fact that $\delta^{15}N$ and $\delta^{13}C$ values are transformed from dietary sources to consumers at predictable ratios (Kelly, 2000): the incorporation of the carbon isotope ratio ($^{13}C/^{12}C$) of primary producers into consumer tissues and the enrichment of the nitrogen isotope ratio ($^{15}N/^{14}N$) due to the incorporation of the heavy isotope of nitrogen (^{15}N) by the consumer from its diet. Stable isotopes alone cannot completely resolve the consumption of Norway lobsters due to the limitation of the technique (i.e. simulated predators based on a predator that only feeds on Norway lobsters). Combination with other techniques, such as DNA analysis, is beneficial and enhances the interpretation of the results. A more precise interpretation would be possible if stable isotope information on all putative prey were available to infer diet through stable isotope mixing models. The combination of different methodologies could solve complex ecological questions by providing more accurate information about the structure and functioning of marine food webs and be a useful tool to validate results. Moreover, due to the different integration time of each of these 2 methodologies, their combination could provide information about the trophic importance of a particular prey at the short-term scale (DNA integrates in days due to rapid digestion times; Aguilar et al., 2017) and the long-term scale (SIA in muscle tissues integrates ~2 to 8 mo of the food consumed by a predator, depending on the species; Vander Zanden et al., 2015). For example, in SIA of muscle tissues, the isotopic half-life ($\ln(2)/\lambda$, days), defined as the time required to reach 50% equilibration with the diet, averages 47 d in the Atlantic cod *G. morhua* (Ankjærø et al., 2012), 147 d in the red rock lobster *Jasus edwardii* (Suring and Wing, 2009) and 105.3 d in the leopard shark *Triakis semifasciata* (Kim et al., 2012; Malpica-Cruz et al., 2012).

In the present study, our principal objective was to identify the main predators of Norway lobsters in the deep-sea ecosystems (315 to 475 m depth) of the western Mediterranean Sea using both molecular and stable isotope techniques. We also considered possible predators of the early stages of Norway lobster, such as the cephalopods *Sepietta* sp. and *Abralia veranyi*, which are smaller than adult Norway lobsters. Moreover, we estimated the predation impact on Norway lobsters to portray the significance of the predator−prey interactions taking into account the predator density, which could adversely affect prey consumption (Arditi et al., 2001). For this purpose, a Predation Index (PI) combining the results of this study and the density of each predator identified in the study area was calculated to elucidate the real importance of each predator in the Norway lobster fishing grounds.

2.2.2. Material and Methods

Fieldwork procedures

The study was conducted in the northwestern Mediterranean Sea, in a deep-sea Norway lobster fishing ground (300 to 500 m depth; Fig. 2.2.1). This area is composed of muddy habitats of the upper slope of the continental shelf margin, which is crossed by several submarine canyons. These submarine canyons are major geomorphological structures of the western Mediterranean Sea, hosting a fishing ground of great economic importance for the local and regional fisheries (Fernandez-Arcaya et al., 2017).

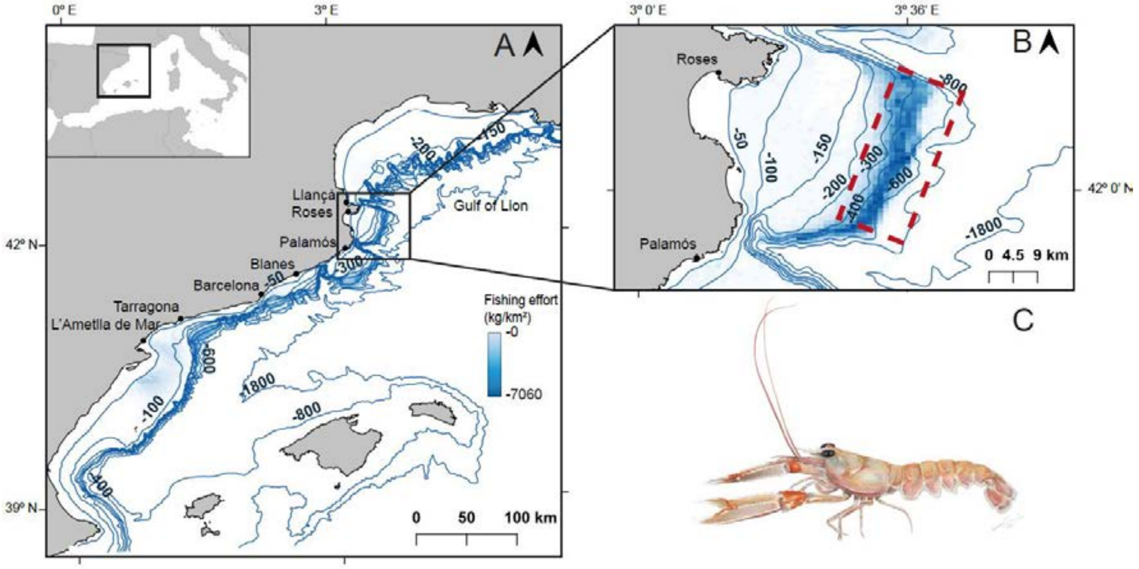

Figure 2.2.1. (A) Study area of Norway lobsters *Nephrops norvegicus* in the northwestern Mediterranean Sea, Spain. (B) Spatial distribution of Norway lobsters along the Catalan coast, obtained by combining Vessel Monitoring System (VMS) information and official landing data from the time period 2005−2018 (European Commission, 2002–2018, Garcia et al., 2016), and the study area (red rectangle). (C) Norway lobster (illustration by Joan Mir-Arguimbau).

To collect potential predators and estimate their abundance, a total of 28 experimental hauls (18 hauls in September 2017 and 10 in September 2019) were performed in this area using commercial trawling gears (square mesh size of 40 mm) covered with a net with a diamond mesh size of 12 mm to collect the maximum number of species and sizes. The headline height of the trawl was around 1.3 m, and the horizontal trawl opening was about 22 m. The total wire of the fishing trawl was between 850 and 950 m. Towing was maintained at a constant speed (2.4 to 2.5 knots) and the duration of each haul ranged between 1 h 31 min and 1 h 44 min. All hauls were conducted in local daylight, coinciding with the diurnal emergence of Norway lobsters on the continental slope of these deep-water habitats (Aguzzi et al., 2003; Vigo et al., 2021).

Abundance of potential predators of Norway lobsters

The total catch was classified into Norway lobsters and the different species of its potential predators. The abundances of Norway lobsters and the different predators were estimated considering the swept area, which is the area that the trawl net has towed, in km^2 following the equation:

$$A = V \times BT \times H \times 1852 / 10^6 \tag{1}$$

where A is the total number of individuals per km^2, V is the average speed of the trawls (knots), BT is the towing time (h), H is the horizontal opening of the net (m) and the constant 1852 is the equivalent in nautical miles to make the conversion to km^2 (Sparre and Venema, 1998).

Muscle and stomach content sampling

A total of 20 Norway lobster individuals and potential predators (cephalopods [n = 133], bony fish [n = 78], and elasmobranchs [n = 38]) were collected from the fishing hauls. They were identified at the species level and frozen on board until their dissection at the Institut de Ciències del Mar (ICM - CSIC). In the laboratory, all collected individuals were weighed (in g) and measured (standard body measures in mm: mantel length [ML] for cephalopods, total length [TL], standard length [SL], or anal length [AL] for fish species). We obtained 269 muscle samples, 20 from Norway lobsters and 249 from the potential predators of Norway lobster, which were later frozen and preserved for stable isotopic determination. We also extracted the stomach contents of these potential predators and kept the contents in ethanol-sterilized sample pots.

Extraction and amplification of DNA from the stomach contents of predators

All collected stomachs were dissected using ethanolsterilized tools and DNA extraction from the stomach contents was performed using the NZY Tissue gDNA Isolation Kit (NZYTech) following the manufacturer's instructions. DNA quality was analyzed with the NanoDrop ND-1000 spectrophoto meter (Thermo Fisher Scientific).

We designed primers with sequences corresponding to a mitochondrial gene from the 16S subunit of the ribosomal ribonucleic acid (following Palero et al., 2009) to identify predation only on Norway lobster. We used the program PRIMER3Plus (Untergasser et al., 2007) to design the primers: R 5’-ACG CTG TTA TCC CTA ARG TAA CTT-3’ and F 5’-GGT GTA GAT TAA GGA ATT CG-3’.

We followed the protocol of the NZYTaq 2x Colourless Master Mix (NZYTech) using a thermocycler with pre-programmed temperatures and times. The optimal PCR conditions consisted of an initial denaturation at 95°C for 5 min, followed by 19 cycles of 95°C for 30 s, 58°C for 30 s, 72°C for 30 s; 20 cycles of 95°C for 30 s, 61°C for 30 s, 72°C for 30 s; and a final step at 72°C for 5 min to make sure that all DNA extracts were amplified. Finally, the sample was stored at 12°C to preserve the reaction for the short term. PCR products were visualized on 2% agarose gels prior to cloning and sequencing to verify amplicon presence and size. We analyzed the results as binary variables: the absence of bands was classified as no detection (value 0) and the presence of a band was considered detection of Norway lobster (value 1).

Stable isotopic analysis

All muscle samples (Norway lobster and its potential predators) were freeze-dried and powdered, and 0.28 to 0.33 mg of each sample was packed into tin capsules. Stable isotopic analyses were performed at the Laboratory of Stable Isotopes of the Estación Biológica de Doñana CSIC (www.ebd.csic.es/lie/index.html). Samples were combusted at 1020°C using a continuous flow isotope ratio mass spectrometry system (Thermo Electron) by means of a Flash HT Plus elemental analyzer interfaced with a Delta V Advantage mass spectrometer. This applies international standards run every 9 samples: LIE-CV and LIE-PA, previously normalized with the international standards IAEA-CH-3, IAEACH-6, IAEA-N-1, and IAEAN-2. Stable isotope ratios were expressed in the standard δ-notation (‰) relative to Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N2 ($\delta^{15}N$). Based on laboratory standards, the measurement errors (SD) were ±0.1 and ±0.2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. The C:N ratio of all tissues was always lower than 3.5‰, and hence, no correction of the $\delta^{13}C$ values was required to account for the presence of lipids in muscle samples (Logan et al., 2008).

To compare the differences in the $\delta^{13}C$ and $\delta^{15}N$ values between potential predators we used Kruskal-Wallis and Wilcoxon post-hoc tests, using the statistical software R version 4.0.3 (R Core Team 2020).

Identification of the potential predators of Norway lobster using isotopic values

Based on the stable isotope values, we estimated the qualitative importance of Norway lobster for each sampled predator. This approach consisted of determining whether the isotopic niche of a potential predator overlapped with that of a hypothetical predator (bony fish, elasmobranch, or cephalopod) that only feeds on Norway lobsters. If so, then we could assume that this predator includes Norway lobsters in its diet (see a similar approach in Popa-Lisseanu et al., 2007). We also checked whether Norway lobster was segregated from the other crustaceans present in the study area. For this, we revised all the published data on the stable isotope values of the cohabiting crustaceans present in the study area, confirming that Norway lobster was segregated in its stable isotope values from the other cohabiting crustaceans (see Fig. S2.2.1 in the Supplementary Material).

As isotopic niche, we calculated 3 different kernel utilization density (KUD) estimators that contained 50%, 75%, and 95% of the isotopic niche of each species. KUD is estimated across a regular network of equally spaced points, with the extent of the grid larger than that of the observations (Venables and Ripley, 2002; Eckrich et al., 2020). The contour lines used are defined in relation to the Euclidean distance of each observation to the centroid in bivariate space (Robinson, 2021). For these predictions, different diet-to-tissue discrimination factor values based on published studies were used for cephalopods ($\Delta\delta^{13}C = -0.20 \pm 0.5‰$, $\Delta\delta^{15}N = 3.37 \pm 0.95‰$; Golikov et al., 2020), bony fish ($\Delta\delta^{13}C = 1.3 \pm 0.1‰$, $\Delta\delta^{15}N = 3.35 \pm 0.2‰$; Caut et al., 2009), and sharks/rays ($\Delta\delta^{13}C = 0.49 \pm 0.32‰$, $\Delta\delta^{15}N= 1.95 \pm 0.26‰$; Hussey et al., 2010). We used the “rKIN” package (rKIN; https://github.com/salbeke/rKIN) in R version 4.0.3 (R Core Team 2020) to compute the KUDs and calculate their overlap.

Combining molecular and trophic markers

We combined and plotted the results for the percentage of stomachs containing Norway lobster DNA (% DNA) for each of the different potential predators and the 95% contour of the KUD overlap (K 95%) of the isotopic niches estimated from the isotopic values for each predator. Species with low values for both metrics should not be considered as predators of Norway lobsters, while species with high values could be major predators of Norway lobsters. Species that appear in the lower-right section of the plot (only high values of % DNA) could be casual predators of Norway lobsters with short-term predation importance. On the contrary, if species appear in the upper-left section of the plot (high values of K 95%, stable isotopes), they present a long-term marker, indicating that they had preyed on Norway lobsters in the past months (~2 to 8 mo).

Estimating the impact of each predator on the population of Norway lobsters

By using % DNA or K 95%, we estimated the relative importance in number (I) of each potential predator of Norway lobsters by calculating the percentage of abundance of each predator in relation to the abundance of all predators together. The abundance of predators was obtained from the fishing surveys conducted in the study area. The importance index (Ix) was obtained with the following equation:

$$Ix\ (\%) = [(PAx/100) \times (E/100)] \times 100 \qquad (2)$$

where PA is the percentage of abundance of a specific predator x in relation to the abundance of all potential predators and E is the % DNA or the K 95%. For each predator, we estimated a Predation Index (PI) based on the average I values obtained with % DNA and K 95%.

2.2.3. Results

DNA Results

From the 249 stomachs of 20 potential predator species (see Table 2.2.1), Norway lobster DNA was detected mainly in the cephalopods *Todaropsis eblanae* (% DNA = 73.33%), *Abralia veranyi* (72.73%), *Sepietta* sp. (66.67%), *Pteroctopus tetracirrhus* (50 %), *Todarodes sagittatus* (42.86%), and *Illex coindetii* (38.46%). In bony fish, Norway lobster DNA was detected mainly in *Lophius budegassa* (75 %), *Merluccius merluccius* (35.71%) and *Conger conger* (33.33%). In the other 13 potential predators analyzed, less than 25% of individuals had Norway lobster DNA in their stomachs, and it was absent in 7 of the species (Table 2.2.2).

Table 2.2.1. Results obtained from the stable isotope analyses of each species considered as potential predators of Norway lobster. N: is the number of individuals or samples; δ13C (‰): mean ± SD values; δ15N (‰): mean ± SD values.

Species	n	Body mass (g)	δ^{13}C (‰)	δ^{15}N (‰)
CRUSTACEA				
Nephrops norvegicus	20	26.39 ±7.52	-19.91 ±0.46	5.86 ±0.36
CEPHALOPODS				
Abralia veranyi	9	4.89 ±1.15	-19.76 ±0.55	10.34 ±0.56
Eledone cirrhosa	16	223.10 ±93.71	-18.97 ±0.28	8.27 ±0.46
Illex coindetii	12	139.71 ±58.03	-19.20 ±0.30	9.74 ±0.77
Rossia macrosoma	20	76.91 ±31.94	-18.49 ±0.41	8.20 ±0.22
Octopus saluti	2	282.50 ±307.59	-18.87 ±0.21	7.31 ±0.65
Pteroctopus tetracirrhus	4	412.50 ±251.58	-18.44 ±0.19	7.09 ±1.12
Scaeurgus unicirrhus	2	56.36 ±0.00	-19.15 ±0.08	8.04 ±0.41
Sepietta oweniana	20	9.89 ±14.30	-19.33 ±0.17	9.55 ±0.24
Sepietta sp.	18	5.20 ±2.20	-19.32 ±0.22	9.57 ±0.27
Todarodes sagittatus	9	205.40 ±306.10	-19.24 ±0.30	9.85 ±0.85
Todaropsis eblanae	15	121.37 ±35.19	-19.38 ±0.23	9.46 ±0.37
BONY FISH				
Conger conger	29	197.29 ±229.51	-18.63 ±0.27	9.30 ±0.44
Lepidopus caudatus	2	46.00 ±0.00	-20.16 ±0.00	9.35 ±0.00
Lophius budegassa	4	435.00 ±189.47	-18.62 ±0.32	10.51 ±0.28
Merluccius merluccius	14	353.14 ±124.38	-19.01 ±0.19	9.79 ±0.33
Molva macrophtalma	10	29.90 ±7.47	-19.24 ±0.19	10.12 ±0.41
Trigla lyra	18	79.61 ±12.44	-18.86 ±0.24	9.46 ±0.37
ELASMOBRANCHS				
Galeus melastomus	10	15.44 ±4.21	-18.65 ±0.13	8.43 ±0.21
Scyliorhinus canicula	30	207.83 ±102.86	-17.80 ±0.48	8.71 ±0.28
Raja clavata	1	260.00	-17.76	9.08
Raja polystigma	3	77.50 ±10.61	-18.05 ±0.64	7.85 ±1.19
Raja sp.	2	46.00 ±0.00	-17.67 ±0.29	8.71 ±0.32

Stable isotope results

When comparing the stable isotopic values of Norway lobster and its potential predators, we found that Norway lobster was completely segregated from them all in δ^{15}N and δ^{13}C values (Fig. 2.2.2). Among predator species, we found significant differences (Kruskal Wallis tests, $p < 0.05$) in both δ^{15}N and δ^{13}C values (Table 2.2.1, Fig. 2.2.2). The species that presented the lowest values of δ^{13}C and were the most significantly different from Norway lobsters (−19.91 ± 0.46‰) (based on Wilcoxon post-hoc tests, $p < 0.05$) were the bony fishes *C. conger* (−18.63 ± 0.27‰) and *Trigla lyra* (−18.86 ± 0.24‰), and the elasmobranchs *Scyliorhinus canicula* (−17.80 ± 0.48‰), *Raja* sp. (−17.80 ± 0.48‰), and *Galeus melastomus* (−18.65 ± 0.13‰). For δ^{15}N values, the predators most segregated from Norway lobsters (5.86 ± 0.36‰) and with the highest values of δ^{15}N (based on

Wilcoxon post-hoc tests, $p < 0.05$) were the cephalopod *A. veranyi* (10.34 ± 0.56‰), the bony fish *L. budegassa* (10.51 ± 0.28‰), and the elasmobranch *S. canicula* (9.13 ± 0.23‰) (see Table 2.2.1).

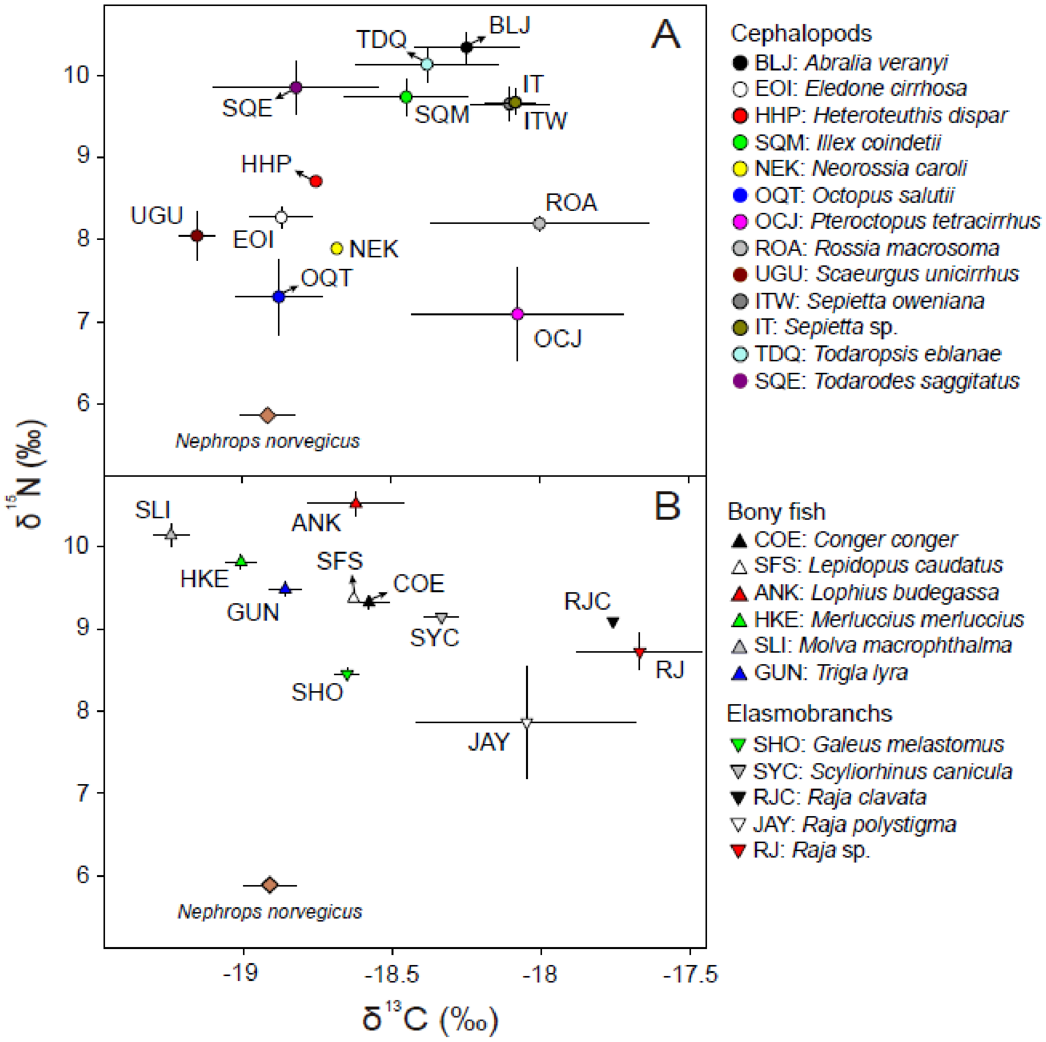

Figure 2.2.2. Mean and standard error of δ^{15}N and δ^{13}C values of Norway lobsters and potential predators sampled in the northwestern Mediterranean Sea. (A) Cephalopods; (B) bony fish.

Regarding the 95% contour of KUD overlap between the isotopic area of a potential predator that consumes only Norway lobster and each predator species (Figs. 2.2.3 and 2.2.4), we found higher K 95% values for the elasmobranch *G. melastomus* (64.3%) and the cephalopods *Sepietta* spp. (58.1%) and *S. oweniana* (55.9%), representing the species most likely to be specialized predators of Norway lobsters. Other predators that presented relevant overlap values were the cephalopod species *Eledone cirrhosa* (34.5%), *A. veranyi* (30.3%), and *Todarodes sagittatus* (25.9%) (Table 2.2.2). The K 95% of the other 14 sampled predators, including all bony fishes and the rest of cephalopods and elasmobranchs, was lower than 25% (Table 2.2.2, see Figs. 2.2.3 and 2.2.4).

Table 2.2.2. Results obtained from the DNA determination and overlap between the isotopic niches of the potential predators and the simulated predator generated from the Norway lobster isotopic values. N: number of individuals analyzed; K 95%: 95% of probability of isotopic area overlap between the simulated predator and the species analyzed in kernel utilization densities; DNA%: percentage of individuals that contained Norway lobster DNA in their stomach; A: abundance (ind·km^{-2}) in the study area; PI: Predation Index value obtained based on DNA % and K̄ 95% values of each species (see Material and Methods).

Species	K95%	DNA%	A	PI
CEPHALOPODS				
Abralia veranyi	30.3	72.7	274	4.94
Eledone cirrhosa	34.5	0	11	0.04
Illex coindetii	23.9	38.4	59	0.76
Rossia macrosoma	8	19.5	35	0.16
Octopus saluti	0	0	2	0
Pteroctopus tetracirrhus	22.8	50	0	0
Scaeurgus unicirrhus	9.9	0	2	0
Sepietta oweniana	55.9	15.0	848	6.42
Sepietta sp.	58.1	66.7	233	4.45
Todarodes sagittatus	25.9	42.9	5	0.08
Todaropsis eblanae	22.1	73.3	15	0.30
BONY FISH				
Conger conger	25.0	33.3	21	0.19
Lepidopus caudatus	14.0	0	0	0
Lophius budegassa	0	75.0	13	0.21
Merluccius merluccius	0	35.7	161	1.21
Molva macrophtalma	0	0	77	0
Trigla lyra	15.8	0	393	0.49
ELASMOBRANCHS				
Galeus melastomus	64.3	10	91	0.75
Scyliorhinus canicula	6.4	9.1	762	1.8
Raja sp.	21.8	0	1	0

Short- and long-term markers of Norway lobster in the diet of its predators

The potential predators *Sepietta* spp. and *A. veranyi* presented high values for both % DNA and K 95% (Fig. 2.2.5A). For other predators, such as *G. melastomus,* the trophic marker of Noray lobster was high for K 95% and low for % DNA (Fig. 2.2.5A), while some, such as *L. budegassa*, presented high % DNA values and low K 95% values (Fig. 2.2.5A).

Abundance of predators in the study area and their estimated predation impact on Norway lobsters

The most abundant predators in the Norway lobster grounds were the cephalopods *Sepietta oweniana* (848 individuals [ind.] km^{-2}), *A. veranyi* (274 ind. km^{-2}), *Sepietta* spp. (233 ind. km^{-2}), the bony fish *Trigla lyra* (393 ind. km^{-2}), and the elasmobranch *Scyliorhinus canicula* (762 ind. km^{-2}) (see Table 2.2.2).

The PI, which incorporates the importance of % DNA and K 95% in relation to the relative abundance of each potential predator in the environment, was higher for the cephalopods

Sepietta oweniana (6.42%), *A. veranyi* (4.94%), and *Sepietta* spp. (4.45%), followed by the shark *Scyliorhinus canicula* (1.81%) and the bony fish *M. merluccius* (1.21%) (see Table 2.2.2, Fig. 2.2.5B).

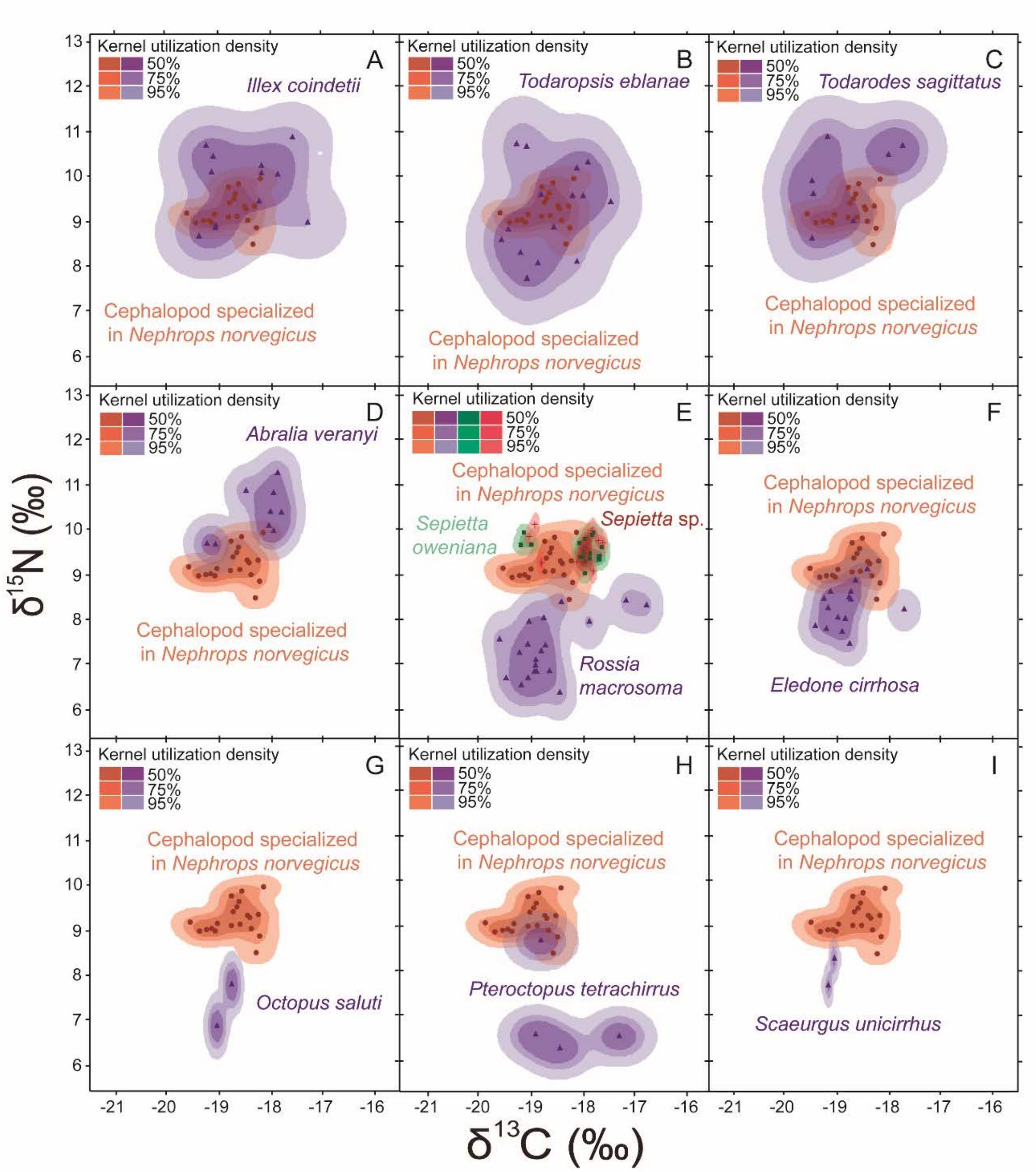

Figure 2.2.3. (A−I) Isotopic niche and overlap of a potential cephalopod that only feeds on Norway lobsters *Nephrops norvegicus* and 11 cephalopods inhabiting deep-water ecosystems of the northwestern Mediterranean Sea. Niche size and overlap estimates were generated for the 50%, 75%, and 95% contour levels of the kernel utilization densities. The potential predators that only feed on Norway lobsters represent the isotopic niche of the expected stable isotope values of 20 Norway lobster individuals corrected for specific-group isotopic fractionation factors.

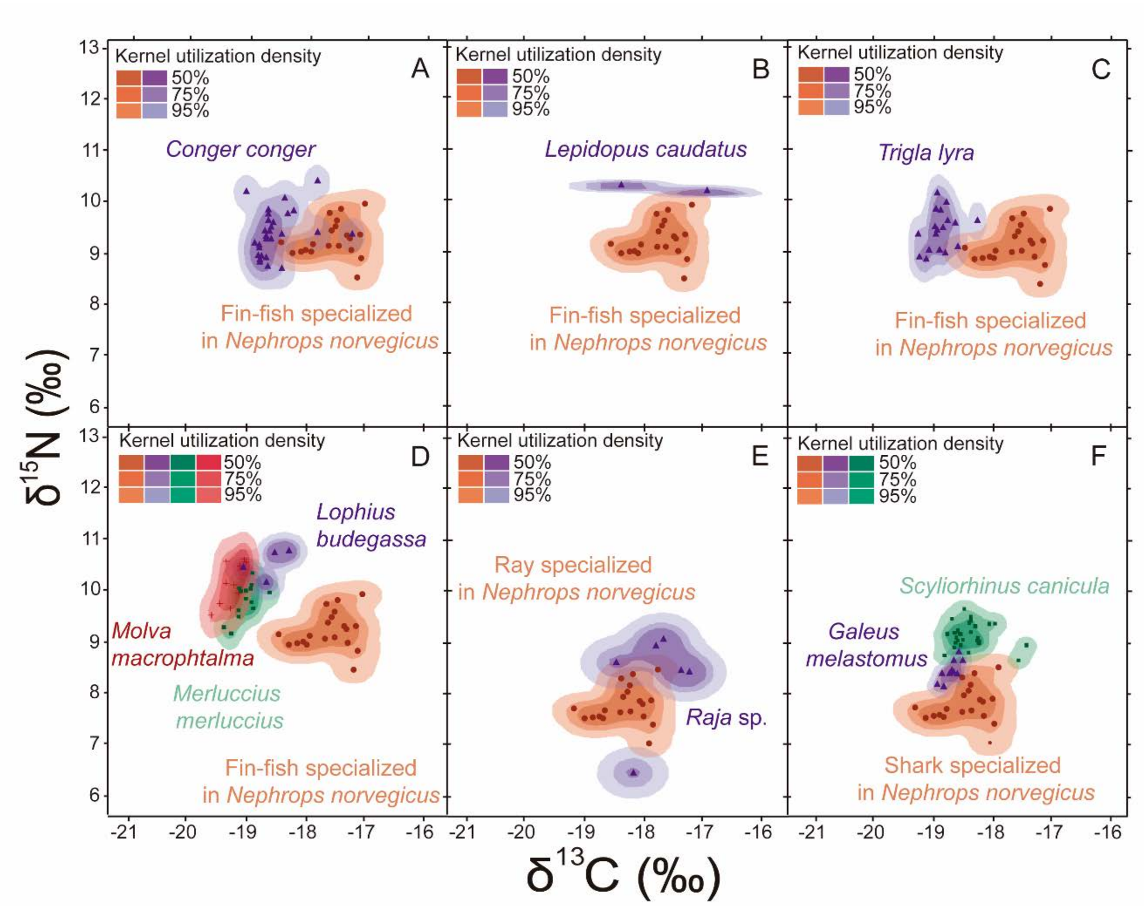

Figure 2.2.4. Isotopic niche and overlap of a potential bony fish, ray and shark that only feed on Norway lobsters and (A–D) 6 bony fishes, (E) rays *(Raja* spp.), and (F) 2 shark species inhabiting deep-water ecosystems of the northwestern Mediterranean Sea. See Fig. 2.2.3 for an explanation of the niche size and overlap estimates and the potential predators.

2.2.4. Discussion

In the present study, we identified the main predators of Norway lobsters in the deep-sea Mediterranean waters combining 2 methodologies: genetic determination of stomach contents and stable isotope analysis. Our results demonstrate that the major predators of Norway lobster are the cephalopods *Sepietta* spp., as they presented high values using both methodologies. Considering only the short-term marker (% DNA), which consists of the identification of Norway lobster DNA in the stomach contents (i.e. recent consumption), we also identified the bony fish *Lophius budegassa* as a major predator. Considering only the long-term marker (K 95%), which reflects the assimilation in the muscle tissues of Norway lobsters consumed a few months ago, we identified the elasmobranch *Galeus melastomus* and the cephalopod *Sepietta oweniana*. Moreover, according to the estimated PI, which also considers the abundance of the predators in the Norway lobster grounds, the main predators are still *Sepietta* spp. and *S. oweniana*, followed by *Abralia veranyi* (see Fig. 2.2.5C). These results are useful for understanding prey–predator interactions and their ecological role in Norway lobster grounds and could also provide pivotal information for ecosystem-based fisheries management, as well as for evaluating the effectiveness of marine protected areas for the conservation of demersal species.

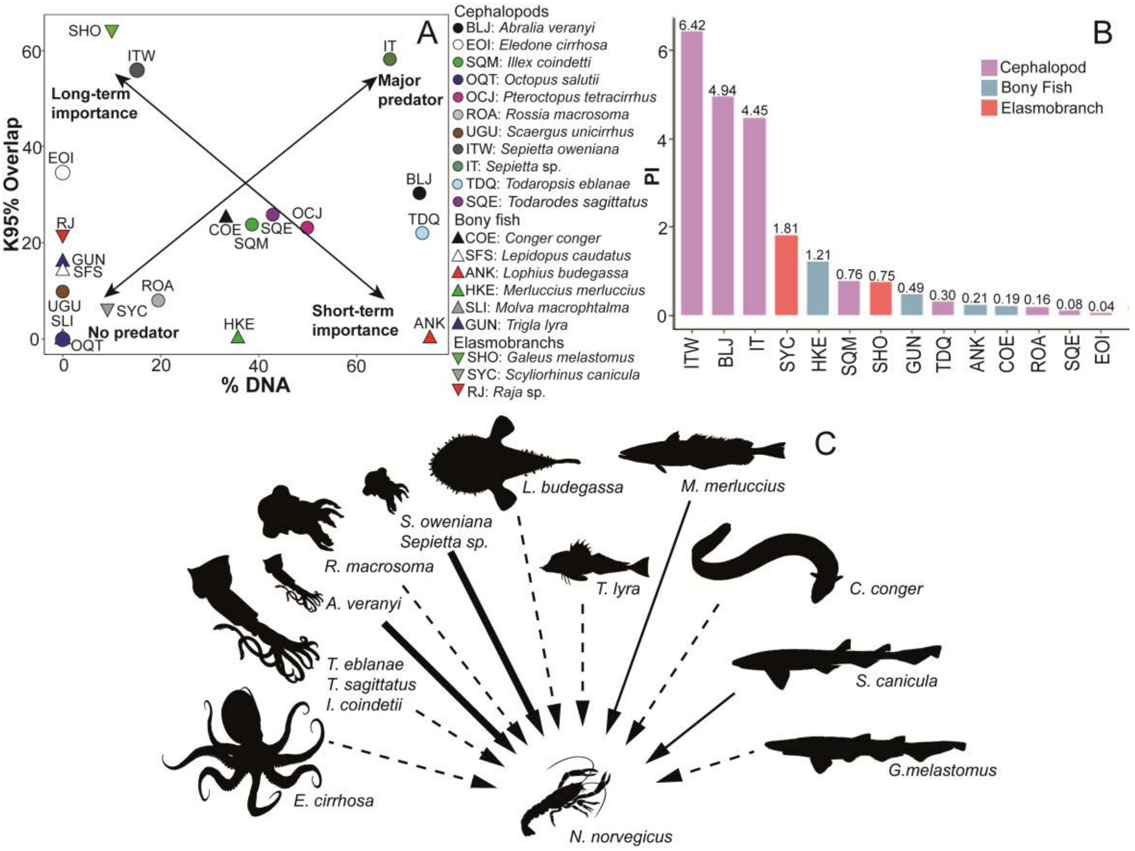

Figure 2.2.5. (A) Classification of the potential predators of Norway lobsters according to their % DNA (percentage of individuals containing Norway lobster DNA in their stomach) and K 95% (95% contour overlap between the isotopic area of the simulated predator and the potential predator) values. Long-term importance: high K 95% value; Short-term importance: high % DNA value; Major predator: % DNA and K 95% values both high; No predator: % DNA and K 95% values both low, meaning that this species does not prey on Norway lobster. (B) Predation Index for each species, from the highest value to the lowest. (C) Trophic network relating the species (silhouettes obtained from https://pngtree.com/ and http://clipart-library.com/) that prey on Norway lobsters. Solid and wider arrows: major predators; solid and thin arrows: species of moderate importance; dashed arrows: predators with minor importance.

Using genetic analyses of stomach contents, we identified species that had recently preyed on Norway lobsters, while stable isotope analyses from muscle tissue showed the assimilation of all the prey consumed by predators in recent months (Boecklen et al., 2011). As expected, all potential predators showed higher $\delta^{15}N$ values than Norway lobster, reflecting its lower position in the food web. There was isotopic variability among predators, reflecting different trophic habits. For example, within the cephalopods, we found species that occupy higher trophic levels, such as *A. veranyi* that can prey on decapods, larger fish, and other cephalopods (Guerra-Marrero et al., 2020), whereas species such as the cephalopod *Pteroctopus tetracirrhus*, which preys mainly on crustaceans such as *Alpheus glaber* and some fishes (Quetglas et al., 2009), occupy lower trophic positions (Navarro et al., 2013). The range of values found suggests that some predators can exploit resources across entire food webs. *L. budegassa* and *A. veranyi* both showed the highest values, indicating that they may prey on other potential predators, such as *Merluccius merluccius,* and even other cephalopods (Negzaoui-Garali et al., 2008; López et al., 2016; Guerra-Marrero et al., 2020; Lloret-Lloret et al., 2020). The overlap in the different isotopic niches helped us determine if the diet composition of each predator was similar to that of a predator that only consumes Norway lobsters. The most similar predators were the demersal shark *G. melastomus*, which has a diet consisting mainly of decapod crustaceans (Fanelli et al., 2009; Barría et al., 2018), and the cephalopods *Sepietta* spp. and *S. oweniana*, which tend to forage from dusk till dawn as adults, preying on demersal and benthic crustaceans (Bergström, 1985).

Even though the combined results of the genetics and isotopic niche overlap indicate some specific species as the major predators, it is crucial to keep in mind the density effects of predators, such as predation rate, on Norway lobsters (Kunert and Weisser, 2003). Predator density could indicate that some species, despite showing less importance based on genetics and isotopic analyses, could have a stronger influence on Norway lobster population dynamics and distribution due to a higher abundance within the habitat (Mchich et al., 2007). Considering the estimated PI along with the % DNA and K 95% results indicates that the major predators were the cephalopods *S. oweniana*, *Sepietta* spp., and *A. veranyi*. Though some bony fishes and elasmobranchs prey occasionally on Norway lobsters, the main predators in their grounds are cephalopods, in contrast to the Atlantic Ocean, where the main predator is the bony fish *Gadus morhua* (Björnsson and Dombaxe, 2004). The bony fish most closely related to cod in the Mediterranean is *M. merluccius*, which showed a low consumption of Norway lobsters based on the % DNA value. In the western Mediterranean, *M. merluccius* is mainly distributed between 100 and 200 m depth (Recasens et al., 1998), segregated from the habitat occupied by Norway lobsters (300 to 600 m) (Sarda, 1998), which could explain why the crustacean is only occasionally predated by this species. The trophic marker of Norway lobster for *Conger conger*, based on stable isotopes and % DNA values, was similar to that determined for *M. merluccius*, and this species has been directly observed preying on Norway lobsters (see in Supplementary Material section the Fig. S2.2.2; O'Sullivan et al., 2004; Matić-Skoko et al., 2012). However, the PI was not high enough for this fish to be defined as a major predator, probably due to its low abundance in the habitat.

Some studies have indicated that the combination of unavailability of Norway lobsters due to its burrowing behavior and the potential invulnerability of larger individuals could explain the absence of specialized predators (Smith and Herrkind, 1992; Wahle, 1992; Serrano et al., 2003). In addition, Norway lobsters are not an easy prey to catch and digest because of its exoskeleton and its low-fat content (Björnsson and Dombaxe, 2004); thus, its predation might be more a matter of prey availability than a preference (Chapman, 1980).

The identification of predators offers key information for interpreting biological linkages among species and is critical for identifying nature-based solutions for ecosystem-based management used both in fisheries and marine spatial planning. Ecosystem-based modelling can generate predictions of the ecological consequences of activities such as overfishing (Jacobsen et al., 2016). Most predators are considered keystone species in the environments they inhabit (Power et al., 1996), playing an essential ecological role in restoring ecosystems and conferring resilience against future negative impacts, such as biological invasions or climate change (Ritchie et al., 2012). The information provided in the present study could be useful for adapting and creating effective fisheries management and restoring the population of Norway lobsters in the Mediterranean Sea while preventing negative future scenarios. An improvement for fisheries management could be the parallel assessment of the major predators identified, to compare the fluctuations between populations. In the management of no-take marine reserves, predators should also be evaluated in terms of abundance and biomass, to properly assess the effectiveness of the protected area. Predators such as *Sepietta* spp. and *A. veranyi* might also directly affect the dynamics of Norway lobster populations by reducing recruitment and/or survival.

In this study, we used indirect methods and, therefore, we did not consider whether *Sepietta* spp. and other predators prey only on small-sized Norway lobster individuals or larvae. Consequently, next steps could involve assessing and testing the predation of *Sepietta* spp. and *S. oweniana* on Norway lobsters of different sizes (including larvae) and evaluating the presence of predator avoidance of larger Norway lobsters across all the predator species analyzed.

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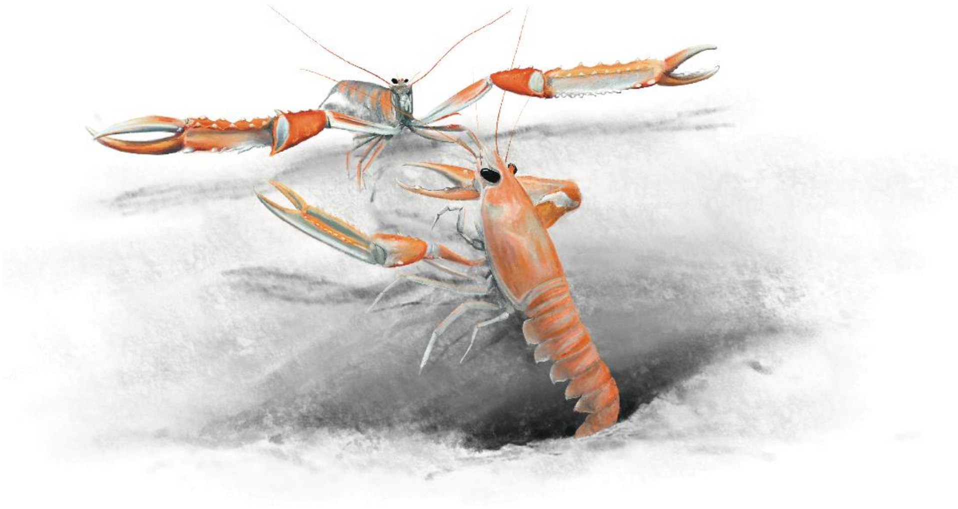
2.3. Spatial ecology of Norway lobster (*Nephrops norvegicus*) in Mediterranean deep-water environments: implications for designing no-take marine reserves

Maria Vigo, Joan Navarro, Ivan Masmitja, Jacopo Aguzzi, José Antonio García, Guiomar Rotllant, Nixon Bahamón, and Joan B. Company



Vigo, M., Navarro, J., Masmitja, I., Aguzzi, J., García, J. A., Rotllant, G., Bahamón, N., and Company, J. B. (2021). Spatial ecology of Norway lobster Nephrops norvegicus *in Mediterranean deep-water environments: implications for designing no-take marine reserves. Marine Ecology Progress Series, 674, 173–188.* https://doi.org/10.3354/meps13799

Abstract

The Norway lobster *Nephrops norvegicus* is one of the most important marine resources for European fisheries. However, overfishing has caused the stocks to decline over the last decades, particularly in the Mediterranean Sea. The implementation of no-take marine reserves could change these current trends, thus achieving a more sustainable fishery. The effectiveness of no-take reserves depends on optimal size design, and because of this, new behavioural data on the spatial ecology of the species are of pivotal importance. Here, for the first time, we investigated the spatial movements and daily activity patterns of Norway lobster in a deep-water (315−475 m depth) no-take marine reserve of 10 km^2 in the continental slope of the northwestern Mediterranean Sea, by combining acoustic tracking and tagging−recapture procedures. The results revealed the territorial behaviour of Norway lobster, centred in small exclusive individual areas where most displacements took place at midday. We found that once settled in a place, their home ranges reached approximate sizes of 17.75 to 736.25 m^2, suggesting that no-take marine areas focused on recovering Norway lobster populations do not require large extents to be effective. Tag−recapture data indicated minimal spillover of biomass, implying that Norway lobsters are site settled and do not perform large movements. Future studies on larval spread and recruitment would be necessary to focus on the possible spillover benefit for fisheries. The acoustic telemetry system used in the present experiment effectively revealed the range of movement of individuals, and thus represents a promising monitoring tool to assess no-take marine reserve sizes and reciprocal spacing for deep-water demersal resources.

Keywords: resources management, fisheries, no-take marine reserves, home range, acoustic telemetry, *Nephrops norvegicus.*

2.3.1. Introduction

The percentage of sustainable global fishing stocks have decreased considerably; for example, in the Mediterranean Sea, more than 60% of fishing stocks were estimated to be biologically unsustainable, and this percentage is projected to increase over the next decades (Jackson et al., 2001; FAO 2020). This historically intense fishing activity has had a global impact, not only by reducing biodiversity and marine resources, but also by compromising habitats (e.g. Thrush and Dayton, 2002; Puig et al., 2012) and consequently, generating global concern regarding unsustainable practices (Costanza et al., 2017; Froese et al., 2018; Rousseau et al., 2019). The Convention on Biological Diversity Aichi Target 11 aimed to implement10% of effectively protected marine areas to improve biodiversity and to also enhance social benefits (CBD, 2010). Therefore, developing effective management strategies specially focused on stock recovery and expanding marine protected area (MPA) networks is essential for the sustainable exploitation of marine resources (cf. Sustainable Development Goals; UN, 2015; Lillebø et al., 2017).

Mediterranean fishing activity produces almost half of all fishing landings in the European Union (EEA, 2015; European Commission 2018). Beyond the possible effects of climate change (Trindade-Santos et al., 2020), the use of high-impact fishing gears is one of the main drivers of ecosystem change in the Mediterranean Sea (Danovaro et al., 2017). Bottom trawl fishing (trawling) is one of the most widespread anthropogenic activities in ocean continental margin areas down to 1000 m (Palanques et al., 2006; Kroodsma et al., 2018). Trawling causes sediment resuspension and removal, eliminating sessile fauna with negative feedback on natural processes to restore a baseline condition in impacted ecosystems (Cook et al., 2013). These practices have many impacts on benthic biodiversity and constitute the main cause of depleted stocks through fishing, removing high proportions of populations (Sciberras et al., 2018). The structure of benthic communities is profoundly altered, with mobile scavengers or opportunistic predators replacing fragile epifaunal species (Tillin et al., 2006; Ramalho et al., 2020). Despite all of these consequences of trawling, the great majority of the European fleet employs this fishing method (Clarke et al., 2015).

The Norway lobster *Nephrops norvegicus* is of great importance in the European fishing industry (Ungfors et al., 2013); however, in the Mediterranean Sea, some stocks are heavily exploited, as fisheries management policies are non-adaptive and include a high proportion of undersized individuals (Sardà et al., 1998; GFCM, 2017; STECF, 2019; García-De-Vinuesa et al., 2020). Their dependency upon fragile soft muddy bottoms, where the animals dig burrows, makes lobsters particularly vulnerable to the effects of trawling (Hiddink et al., 2006); moreover, lobsters can avoid capture when they are inside or at the entrance of their burrows, which makes their de pendency stronger (Chapman and Rice, 1971). As marine ecosystem engineers, the digging behaviour of Norway lobsters provides habitat features of relevance for several other co-existing benthic species. Lobsters could therefore be a potential umbrella species, representing an effective conservation tool to protect other co-occurring species (Roberge and Angelstam, 2004).

For this reason, the demographic reduction of Norway lobster stocks could broadly affect the coexisting benthic biota (Tuck et al., 1994; Davidson and Hussey, 2019) and overall ecosystem functioning, including blue carbon sequestration (Luisetti et al., 2019).

The implementation of MPAs, such as no-take reserves, could be a useful tool for recovering the demographic status of presently over-exploited Norway lobster populations with the correct assessment and monitoring plan (GFCM, 2019; Melaku Canu et al., 2021). Although one of the primary aims of MPAs is benefiting and restoring biological diversity, they can also recover and produce healthy fishing resources (Kerwath et al., 2013; Laffoley et al., 2019; Bourlat et al., 2021), benefiting the habitat and all other inhabiting benthic species, including fragile sessile fauna (Ardron et al., 2014; Langton et al., 2020). The implementation of no-take reserves directly improves population densities and individual body sizes not only inside the no-take area, but also in surrounding zones, via biomass spillover, thus benefiting the nearby fisheries (Sala and Giakoumi 2018; Cabral et al., 2020; Sala-Coromina et al., 2021). Positive management experiments with no-take marine reserves and biomass export have already been carried out on crustacean decapod species, such as the European lobster *Homarus gammarus* and the spiny lobster *Palinurus elephas* (Goñi et al., 2010; Follesa et al., 2011; Moland et al., 2013). Presently, in the Mediterranean Sea there are no assessments of the use of no-take reserves closed year-round for the recovery of Norway lobster populations, except for the Pomo Pit area in the Adriatic (Melaku Canu et al., 2021). In the deep-water northwestern Mediterranean Sea, assessments should be carried out in habitats between 300 and 500 m depth, where intensive trawling has been taking place over the past 70 yr (Maynou, 1998; Sbrana et al., 2020).

No-take marine reserve size and reciprocal spacing ensure the persistence of populations inside the reserves (Moffitt et al., 2011). The reserves must be designed based on spatial ecological knowledge of the targeted species (Blowes and Connolly, 2012). Spatial ecology applied to conservation and management in protected areas is essential to determine the closure design of the protected area and its efficacy in defining animal movement as representative of large-movement species or site-attached species (Lea et al., 2016). To design protected areas considering the biology and behaviour of the species is crucial, as, in some cases, closed areas could lead to instabilities over long periods resulting in negative effects (Smith and Jensen, 2008). Although several aspects of the burrowing behaviour and distribution of Norway lobsters have been widely studied (e.g. Sardà and Lleopart, 1998; Haynes et al., 2016), information about their spatial ecology is still limited to territoriality and site fidelity or diel activity patterns (e.g. Aguzzi et al., 2003; Power et al., 2019).

Spatial data on movement, home ranges (i.e. where most animals live and perform their day-to-day activities) (Katajisto and Moilanen, 2006) and territorial interactions are required to determine the adequate size and location of marine reserves (Lees et al., 2020). Acoustic telemetry could provide these data for deep marine organisms, although the operational challenges it presents for deep-water and deep-sea applications are much greater than those for terrestrial or shallow habitats (e.g. Aspillaga et al., 2016; Crossin et al. 2017).

In the present study, we investigated, for the first time, the spatial ecology of Norway lobsters inhabiting a deep-water no-take marine reserve in the Mediterranean Sea. Specifically, using acoustic tracking and capture−recapture data, we examined: (1) their spatial movement patterns and home range, (2) their diel pattern of movement activity and (3) their spatial territorial interactions. All of this spatial ecological information was necessary to evaluate whether the size of this no-take marine reserve, established in 2017 to recover the depleted stocks of Norway lobsters, is adequate as a conservation measure for this target fishery.

2.3.2. Material and Methods

Study area

This study was conducted in a no-take marine reserve of 10 km^2 located between 315 and 475 m depth in muddy habitats of the continental slope margin of the northwestern Mediterranean Sea (Fig. 2.3.1). During the last 20 yr, the total catch of Norway lobsters has declined along with other resources such as European hake *Merluccius merluccius* and the deep-sea red shrimp *Aristeus antennatus*. To reverse this situation, the Spanish Government enforced a network of no-take reserves along its Mediterranean continental margin (Order APA/ 753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753). Our study area corresponded to one of those reserves, closed to all extractive activities in September 2017 and covering 10 km^2 (Fig. 2.3.1).

Passive tag-recapture experiment

A total of 216 Norway lobsters were captured inside the no-take marine reserve using prawn creels (UK-Model, Carapax Company; creel size: 58 cm length × 42 cm width × 32 cm height; Video S2.3.1 caption in the Supplementary Material section and visualization in https://www.dropbox.com/sh/fhnlzsarne25to2/AADYWcw-2hPM8IR5u9BvalPia?dl=0) during 3 surveys (May−June, September and November 2019) on-board the RVs 'Sarmiento de Gamboa' and 'García del Cid'. Creel bait consisted of salted herring and fresh chicken (following the recommendations of local creel-specialized fishermen). Creels were recovered after 10 h at night conducting all deck operations in dim red light, to avoid retinal damage to captured individuals (Loew, 1976; Shelton et al., 1985). All individuals were then transferred in complete darkness, within an individual cell of a compartmented aquarium with continuous marine water flow at 13°C. Carapace lengths (±0.05 mm) were measured and sex determined (thickness of the first pair of pleopods) for all the individuals caught. All captured specimens were labelled with 2 tags: serial numeric coded tags glued to the carapace, and numeric coded Floy Streamer Tags attached with a needle (FTSL-73 and Floy Custom UV Protected Vinyl Laminated Ovals). For tagging the individuals, the needle was sterilized with 95% alcohol and injected through the muscular tissue of the fourth abdominal segment. The first tag was used to ensure that fishermen would not miss the tagged animal and the second tag ensured that the animal would still be tagged after moulting, as was used in other studies of growth in this species (Ulmestrand and Eggert, 2001). We performed 3 different surveys conducted onboard research vessels during 2019, releasing a total of 216 tagged Norway lobsters with serial numeric coded tags (85 individuals in May−June, 105 in September and 26 in November). Tagged animals were released in the middle of the no-take marine reserve at 10 m above the seabed during the night following the capture with an auto-release device. All crews of fishing vessels operating in the study area (46 vessels) were requested to report the presence of tagged specimens in their captures.

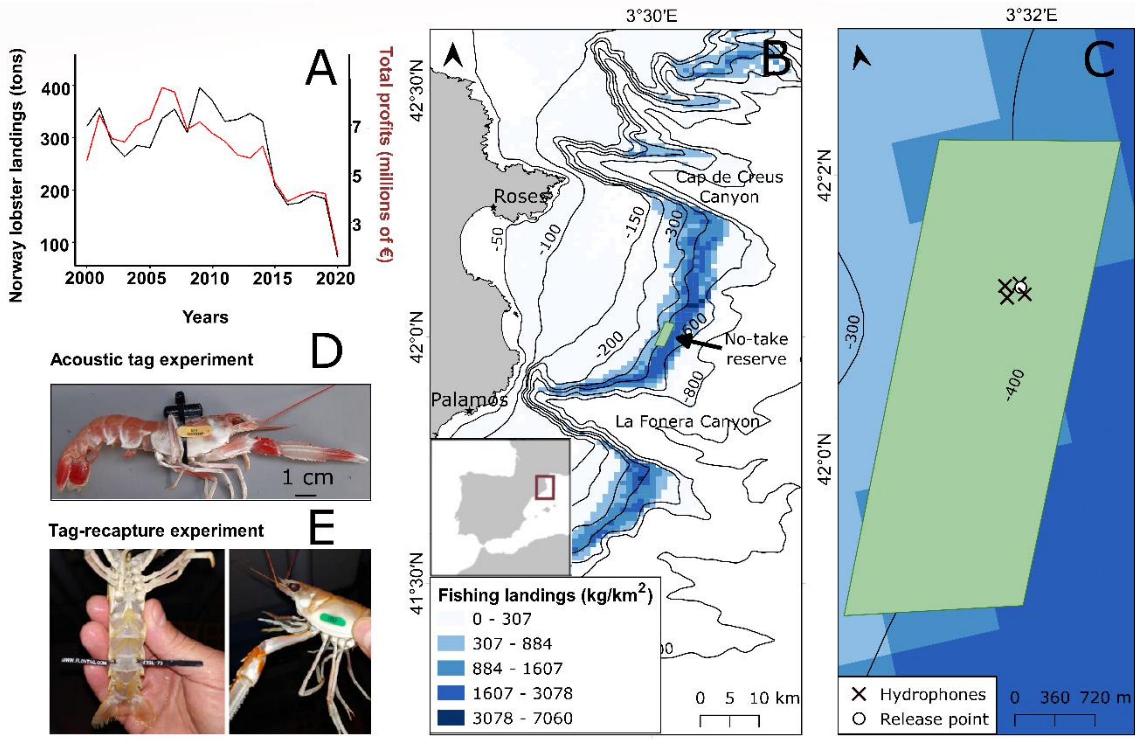


Figure 2.3.1. (A) Evolution of the total biomass and total economic gains of Norway lobster *Nephrops norvegicus* in Catalonia (northwestern Spain) between 2000 and 2020 (DGPAM 2021). (B) Spatial distribution of the accumulated catches of Norway lobster along the Catalan coast (northwestern Mediterranean Sea, Spain), obtained by combining vessel monitoring system information and official landing data in the time period 2005−2018 (Garcia et al. 2016, European Commission 2020). (C) Locations of the network of hydrophones (black crosses) and the release point (white dot). Black lines in (B) and (C) show bathymetry (m). (D) A Norway lobster equipped with a coded tag and the acoustic transmitter. (E) A Norway lobster equipped with serial numeric coded tags glued to the carapace, and numeric Floy Streamer Tags injected in the 4th abdominal segment. Tags also provide a phone number to contact in case of recapture by fisherman.

Acoustic tracking experiment

A total of 33 Norway lobsters (11 females and 22 males), ranging from 31 to 50.5 mm carapace length (Table 2.3.1), were caught by creels, sized, acclimated and tagged with serial numeric coded tags and acoustic emitters (VEMCO V7-L1-69k, Innovasea) equipped with a 255 d battery life (length = 18 mm, weight = 0.7 g) glued onto the carapace (Fig. 2.3.1). Each acoustic tag sent an acoustic signal (ping) at a frequency of 69 kHz, approximately every 120 s. Each ping emitted by the individual tags included information on the identification number (ID).

The monitoring area of the hydrophone array (2 VR2W-69k and 2 VR2AR-69k hydrophones, VEMCO) covered a radius of ~350 m from the mooring location. The 4 hydrophones were attached to the mooring at 20 m above the bottom and 150 m apart (Fig. 2.3.1). The presence of each tagged Norway lobster was reported when the acoustic ID signal was detected by at least 1 of the hydrophones (animals inside burrows were sound-shielded by the sediment), while triangulated positions were obtained when at least 3 hydro phones detected the same acoustic ID signal, time-synchronized (i.e. displacements of animals within the monitoring area) (Fig. 2.3.2).

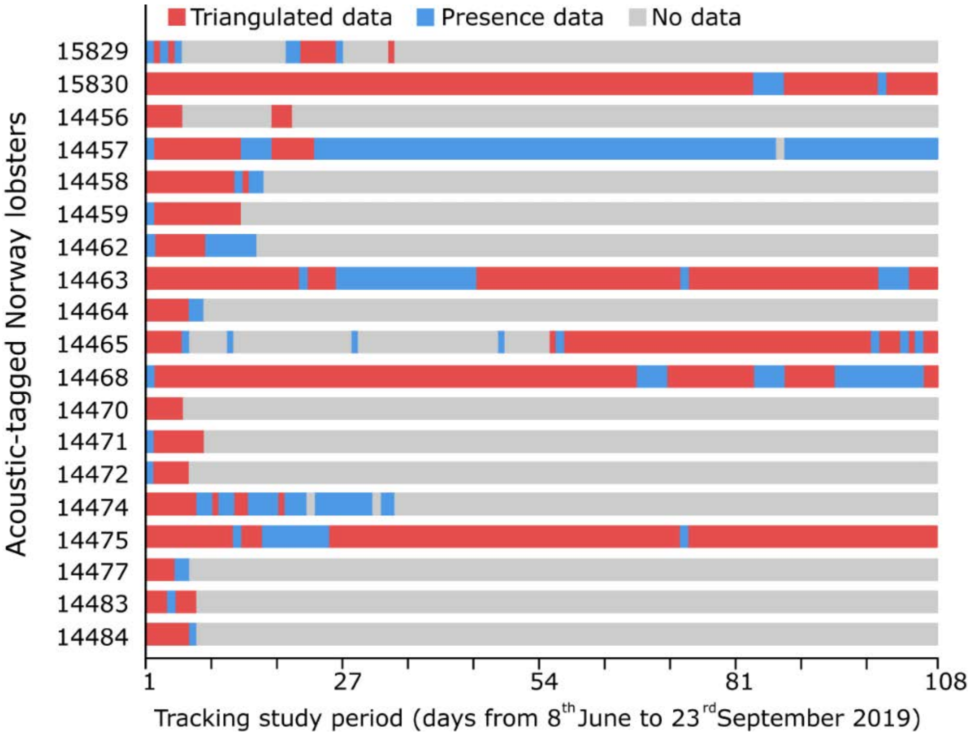


Figure 2.3.2. Overview of the data obtained from each acoustically tagged Norway lobster throughout the study period. 'Triangulation data' include triangulated detections that resulted in precise positions inside the detection area; 'presence data' refers to the number of detections obtained by any of the 4 hydrophones, with no triangulation procedures; and 'no data' indicates a lack of both triangulation and presence data.

We released all individuals at night, in the middle of the array of the 4 hydrophones moored in advance (labelled A, B, C and D, see Fig. 2.3.6) with a release system consisting of a PVC receptacle with a dissolving latch closure on the door (designed to dissolve after 5−10 min more than the estimated time for the release system to sink to the seabed) (adapted from Tuck et al., 2015; see Video S2.3.2 in https://www.dropbox.com/sh/fhnlzsarne25to2/AADYWcw-2hPM8IR5u9BvaIPia?dl=0, captions in the Supplementary Material section).

To account for the effect of clock drift of each hydrophone affecting the evaluation of tracking (i.e. the same ping can be received at different hydrophones at slightly different timings so that signals can be erroneously interpreted as a change in position), synchronizing acoustic tags (VEMCO model V7-L1-69k) were attached to each of the 4 moorings (1 m above each hydro phone) and to the release system (Masmitja et al., 2020). After the deployment, the exact position of each hydrophone was registered from the GPS and the ultra short base-line positioning methods by a remotely operated vehicle ('Liropus 2000'). After 4 mo of deployment (September 2019), the 4 hydrophones were recovered on board the RV 'Sarmiento de Gamboa' using an acoustic transponding release device, and all recorded data were downloaded.

Table 2.3.1. Details of 33 acoustically tagged Norway lobsters in a no-take reserve in the northwestern Mediterranean Sea during 2019. ID: identification number of each individual; CL: carapace length; tracking time: total days with detections; total detections: total number of pings; detections filtered: total number of detections after filtering procedures; net distance: vector sum of individual displacements; total distance travelled: sum of the length of all trajectories of an individual; total distance/track time: mean total distance travelled each day. Dashes indicate the absence of information from the individuals that were removed after data filtering and processing.

ID	CL (mm)	Sex	Tracking time (d)	Total detections	Detections filtered	Net Distance (m)	Total distanc travelled (m)	Total distance/track time ($m \cdot d^{-1}$)
14456	37.1	F	18	732	705	145.44	4,007.58	265.13
14457	32.7	F	44	6,070	6,070	2.44	11,746.71	266.97
14458	34.7	M	12	1,692	1,692	215.07	3,067.66	255.64
14459	32.7	F	11	1,379	1,379	80.56	3,319.23	301.75
14460	44.9	M	1	33	-	-	-	-
14461	40.1	M	106	40,067	-	-	-	-
14462	36	M	5	549	548	173.99	1,052.96	1.92
14463	34.05	F	106	11,509	11,509	131.31	22,733.87	1.98
14464	34.1	M	4	407	407	187.85	975.64	2.39
14465	43.4	M	106	3,092	2,975	150.88	49,352.72	16.59
14466	35.4	M	2	153	-	-	-	-
14467	40.4	M	106	15,415	-	-	-	-
14468	44	M	106	12,676	12,536	36.39	39,228.73	3.13
14469	50.5	M	2	5	-	-	-	-
14470	42	M	3	45	42	169.78	1,553.34	36.95
14471	41.2	M	6	597	597	14.14	1,942.93	3.25
14472	34.13	M	4	150	110	70.93	517.99	4.71
14473	34.3	F	83	21,043	-	-	-	-
14474	46.6	M	17	113	112	183.63	1,383.41	12.35
14475	50.4	M	106	9,919	8,815	145.14	19,626.18	2.23
14476	34.6	M	106	40,099	-	-	-	-
14477	41.44	M	2	39	39	101.11	874.06	22.41
14478	41.2	M	1	2	-	-	-	-
14479	37	F	106	28,071	-	-	-	-
14480	36.2	F	5	209	-	-	-	-
14481	34.3	F	1	8	-	-	-	-
14482	45.8	M	106	38,241	-	-	-	-
14483	37.5	F	5	36	36	151.69	543.94	22.41
14484	39.7	M	4	107	106	110.02	564.99	15.11
14485	37.5	M	16	712	-	-	-	-
15829	31.7	F	24	381	295	238.92	2,267.03	5.33
15830	37.6	M	106	22,103	22,103	20.66	23,240.88	7.68
15831	31	F	106	35,816	-	-	-	1.05

Estimation of spatial movement of Norway lobsters based on acoustic tracking

Spatial movement of acoustically tagged individuals was estimated by using a triangulation method, detecting signals simultaneously by a minimum of 3 hydrophones. The acoustic tag signal detected by each hydrophone had a different timestamp due to its position and the time of flight of acoustic signals. Therefore, using the time difference of arrival among different hydrophones, and applying regression methods such as least squares (Jin et al., 2018), the position of the sound-emitting source was computed (see Masmitja et al., 2020 for more details).

Before analysing the spatial data, it is essential first to check the data by visualization and then by filtering detections. The aim of this procedure is to eliminate possible individuals that have lost their acoustic tag or unusual detections provoked by a failure of the acoustic tag, which, if they were included in the results, would lead to misinterpretation of the behaviour. Data treatment to compile time series of spatial data was as follows. Firstly, we discarded all triangulated acoustic positions with velocities above a maximum threshold of 0.5 m s^{-1}. This threshold was estimated from the movement analyses of 4 acoustically tagged Norway lobsters caught by 3 fishing vessels at the border of the no-take reserve (Fig. S2.3.1 in the Supplementary Material section). These individuals caught were analysed in terms of velocity (m s^{-1}), total distance travelled (m), trajectories (m) and patterns of detection to be used as a control for the rest of the acoustically tagged Norway lobsters (Table 2.3.1, Fig. 2.3.3). After processing the acoustic data and performing the filtering procedures, only 19 out of 33 acoustically tagged lobsters were included in the successive spatial and waveform analyses described below.

Spatial movement descriptors in terms of total distance travelled, net distance (m) or tracked time (d), mean velocities (Table 2.3.1; Fig. S2.3.2 in the Supplementary Material section) and main trajectories were analysed using the statistical software R version 4.0.3 (R Core Team 2020), using the packages “trajr”, “moveVis”, “adehabitatLR”, and “adehabitatHR” (Calenge, 2006; 2019; McLean and Skowton Volponi, 2018; Schwalb-Willmann, 2020). Afterwards, we estimated 2 home range descriptors as proxies for analysing different types of area occupation (i.e. home range size) per individual: the 50% probability utilization distribution (UD) as a proxy of the core area (UD50) and the 90% probability UD as proxy for total home range extent (UD90), based on kernel UDs (Katajisto and Moilanen, 2006), a non-parametric density estimation of the UD. Both UD50 and UD90 were estimated with the R software package “adehabitatHR”, using the smoothing parameter selection ad hoc, and considering only the speed threshold-filtered positions for each month after release (i.e. June, July, August and September). To test differences over time in both UD50 and UD90, 1-way ANOVAs were conducted using the package “stats” in R (Bates et al., 2020). Normality and homogeneity of variances were tested with the Shapiro-Wilk normality test using the package “stats” in R and the Levene test using the package “car” in R (Bates et al., 2020; Fox et al., 2020). Mean values of UD50 and UD90 were log-transformed before testing the differences over time. Home range overlap among tagged Norway lobsters was also quantified and measured in each month through the UD overlap index (UDOI) for both UD50 and UD90 (Hurlbert, 1978), which ranges from 0 to 1 (i.e. respectively for complete spatial segregation and uniform distribution with 100% overlap for a pair of animals).

The interaction among individuals was innovatively investigated with the coefficient of association (CA) that measures the interaction between pairs of individuals in terms of spatial attraction or avoidance (i.e. values above or below a threshold of 0.5, respectively;

Bauman, 1998). The CA was calculated over different inter-individual distances of 1, 5, 15 and 50 m, using the R software package "wildlifeID" (Long, 2019).

The locomotor activity rhythms were characterized for all acoustically tagged individuals (N = 19) in terms of the total distance covered per hour (Fig. S2.3.2 in the Supplementary Material section). Waveform analyses on time series of distance data were conducted to assess the phase (i.e. activity peak) over the 24 h, as follows. Each time series (i.e. 1 per individual) was subdivided into 24 h segments. Values from all individuals were then pooled together at corresponding time intervals, resulting in a single averaged waveform (i.e. as a global activity pattern profile). That averaged curve was plotted over the 24 h made by values plus their standard deviation. On those plots, the phase of the rhythm was identified by superimposing a threshold computed by re-averaging all waveform values together (i.e. the midline estimating statistic of rhythm [MESOR]; Aguzzi et al., 2003). In the resulting waveform, all mean values above MESOR represent a significant activity increment in travelled distance.

Presence data of Norway lobster from acoustic detections

Parallel to the tracking estimation, we also computed the occupancy area of the 19 acoustically tagged individuals, by using time series detections from each of the 4 hydrophones (A−D) during 4 mo. The potential area of detection was calculated with the software QGIS 3.10 (www.qgis.org/) creating polygons with a radius of 350 m for each hydrophone and then creating a unique polygon which encompassed the 4 polygons created for each hydrophone. The total area was estimated with the same QGIS software. By analysing each hydrophone individually (without the need to triangulate), we amplified the detection range, consequently increasing the capacity to detect more Norway lobsters. As for triangulation, the furthest position estimated was at approximately 300 m from the hydrophones. Considering the range of detection as a unique area, we split it into 13 subareas according to the hydrophone ranges that overlapped. We then assigned each acoustically tagged individual to the subarea in which we found the most detections. This methodology did not provide the exact location of the individual as with the triangulation method, but it efficiently allowed us to identify the subarea in which an individual spent most of its time.

2.3.3. Results

Capture and recapture of individuals

During the whole period of the coded-tagging experiment, in which 216 individuals were labelled with serial numeric coded tags, we obtained a low recapture rate (i.e. only 5 individuals, equivalent to 2.32% of the total batch). These individuals were recaptured by a fleet of 46 trawlers fishing in the neighbouring areas and operating on a daily basis (i.e. from 07:00 to 16:00 h), 5 d wk^{-1} outside (but very close to) the borders of the no-take reserve (see Fig. S2.3.1 at the Supplementary Material section).

Acoustic tracking of individuals by triangulation

A total of 33 Norway lobsters (11 females and 22 males) ranging from 31 to 50.5 mm carapace length were instrumented with acoustic tags (Table 2.3.1). After processing all acoustic data, only 19 of these tagged lobsters (6 females and 13 males) were included in the spatial and waveform analysis. The total distance travelled per day for these individuals ranged from 1.05 to 266.97 $m\ d^{-1}$ (Table 2.3.1). The potential area of detection for triangulated acoustic data covered around 0.28 km^2 (Fig. 2.3.3). The acoustic data revealed that in June, most Norway lobsters moved randomly, reaching the edges of the area of detection. In September, only 5 of the 19 tracked individuals established themselves in the monitored area as evidenced by the continuous detection of their presence during the entire monitoring period (Fig. 2.3.4).

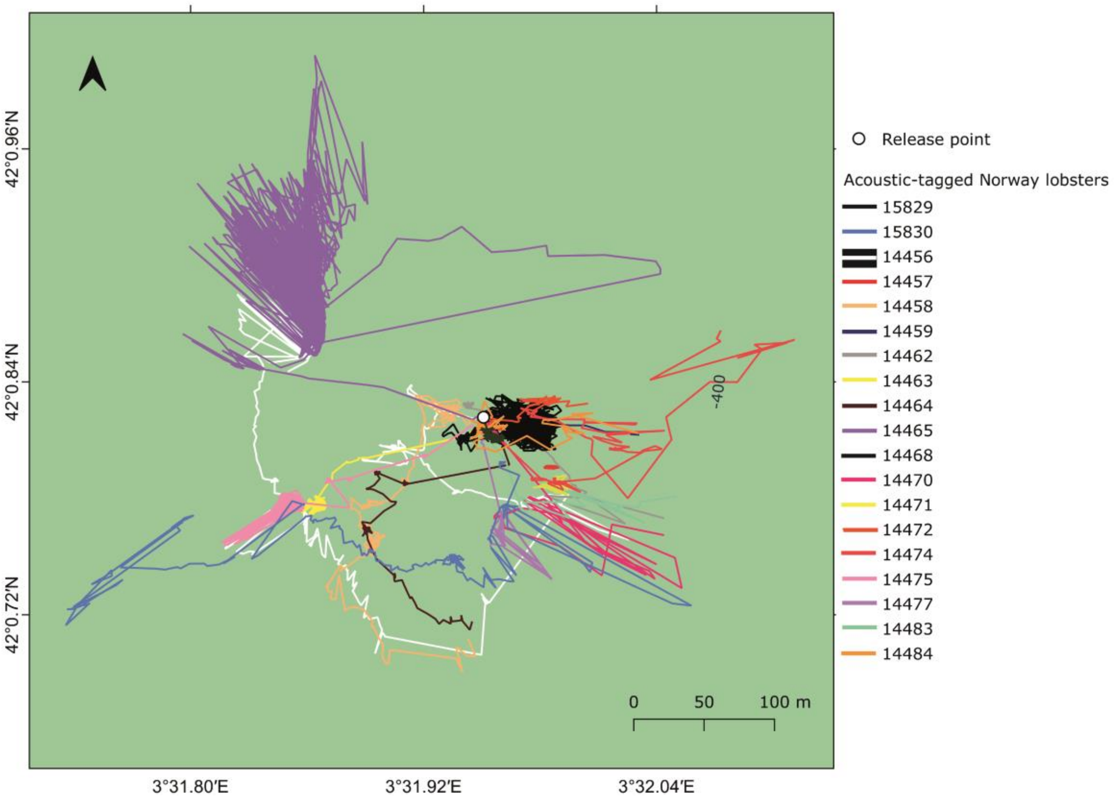


Figure 2.3.3. Individual spatial movements of 19 acoustically tagged Norway lobsters in deep waters of the northwestern Mediterranean. The location of the release point is indicated (white dot); also shown is the approximate depth (400 m).

Home ranges of Norway lobsters obtained by UD50 and UD90 estimations were significantly different over the 4 mo of tracking (UD90: ANOVA, $F_{3,30} = 5.06$, $p < 0.05$; UD50: $F_{3,30} = 5.51$, $p < 0.05$). Home ranges in June were larger (UD50: mean ± SD = 2476.32 ± 3338.67 m^2; UD90: 11223.42 ± 16 022.64 m^2; n = 19) than in the following months of July (UD50: 18.4 ± 30.62 m^2; UD90: 170.2 ± 316.74 m^2; n = 5), August (UD50: 305.6 ± 598.88 m^2; UD90: 1413.8 ± 2679.81 m^2; n = 5) and September (UD50: 278.4 ± 599.09 m^2; UD90: 1341 ± 2910.37 m^2; n = 5) (Table 2.3.2). The home range defined for all Norway lobsters was estimated by the average home ranges (UD90) obtained from individuals who stayed inside the detection area for the entire experimental period (IDs = 14463, 14468, 14475 and 15830; see Table S2.3.1 in the Supplementary Material section) and ranged from 17.75 to 736.25 m^2.

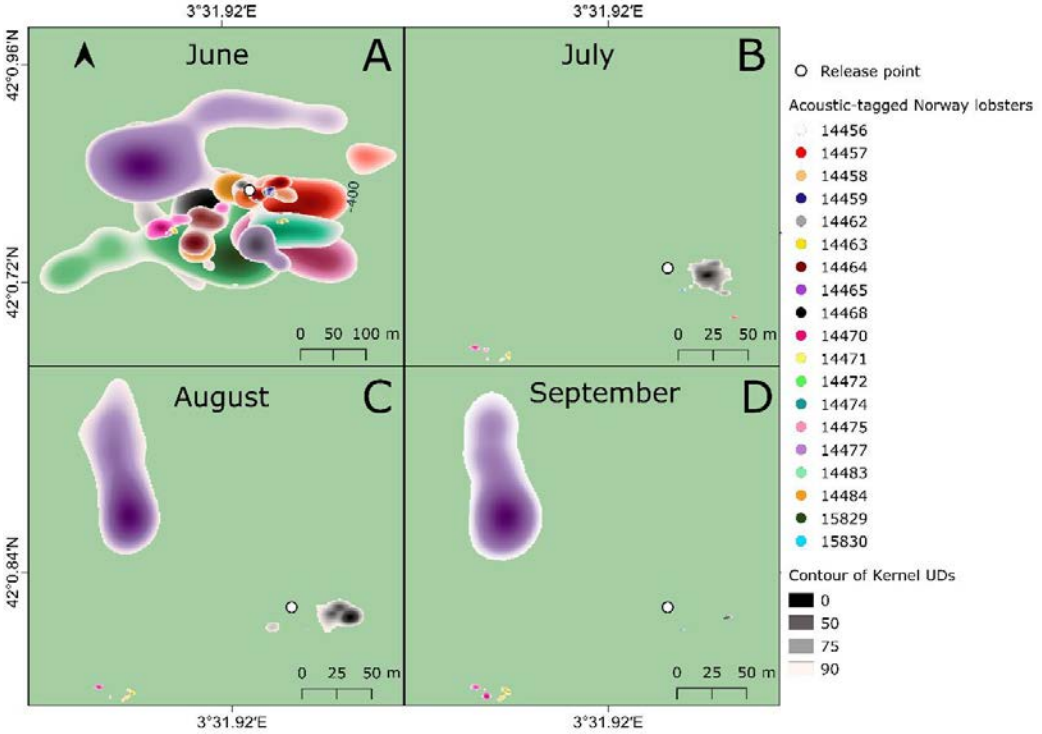


Figure 2.3.4. Home ranges of 19 acoustically tagged Norway lobsters released in 2019 represented by the gradient of kernel utilization during 4 mo of 2019 in the deep waters of the northwestern Mediterranean: (A) June, (B) July, (C) August, (D) September. Also shown in panel A is the approximate depth (400 m).

Table 2.3.2. Spatial movement metrics of 19 acoustically tagged Norway lobsters tracked in a no-take reserve in the northwestern Mediterranean Sea during 2019. UD90 (UD50): 90% (50%) probability utilization distribution as proxy of the core area (total home range) (m^2); N: sample size; min (max): lowest (highest) number of detections.

	N	Mean	SD	Min	Max
June					
UD90	19	11,223.42	16,022.64	12.00	47,022.00
UD50	19	2,476.32	3,338.67	3.00	11,140.00
Total Distance (m)	19	2,768.92	2,953.66	517.99	12,958.48
Velocity (m/s)	19	0.01	0.02	0.00	0.51
July					
UD90	5	170.20	316.74	11.00	736.00
UD50	5	18.40	30.62	2.00	73.00
Total Distance (m)	5	8,637.19	5,985.15	3,152.56	18,502.08
Velocity (m/s)	5	0.01	0.02	0.00	0.38
August					
UD90	5	1,413.80	2,679.81	4.00	6,168.00
UD50	5	305.6	598.88	1.00	1,372.00
Total Distance (m)	5	13,283.09	13,147.74	4,413.24	35,808.19
Velocity (m/s)	5	0.02	0.04	0.00	0.50
September					
UD90	5	1,341.00	2,910.37	9.00	6,547.00
UD50	5	278.40	599.09	2.00	1,350.00
Total Distance (m)	5	6,013.72	4,287.69	2,872.51	13,447.19
Velocity (m/s)	5	0.01	0.03	0.00	0.50

The UDOI metrics among the home ranges (Table 2.3.3) showed no overlap between the areas estimated with UD90, nor with UD50 or core areas. In June, when all acoustically tagged individuals were released together, home ranges presented a higher index of overlap (UDOI UD90: mean ± SD = 0.03 ± 0.08; UDOI UD50: 0.01 ± 0.01).

Mean values of the spatial interactions among individuals estimated with the CA indicated no spatial attraction between acoustically tagged Norway lobsters, as values were always <0.5. CAs were higher for some individuals only in the first month (June) than in the other months (i.e. >0.5, Table 2.3.3; the CA values for all individual interactions are indicated in Table S2.3.2 in the Supplementary Material section).

Table 2.2.3. Norway lobsters tracked (N =19) in a no-take reserve of the northwestern Mediterranean Sea during the year 2019. Number of interactions, mean, Standard Deviation (SD), minimum values (min) and maximum values (max) of the Utilization Densities Overlapping Index (UDOI) and the mean of Coefficient of Association index (CA) obtained between each pair of individuals reported per each month.

	N	Mean	SD	Min	Max
June					
UDOI (UD90)		0.03	0.08	0	0.59
UDOI (UD50)		0.01	0.01	0	0.11
Ca (1 m)		0.01	0.01	0	0.01
Ca (5 m)	**171**	0.01	0.01	0	0.02
Ca (10 m)		0.01	0.01	0	0.12
Ca (20 m)		0.01	0.04	0	0.26
Ca (50 m)		0.03	0.06	0	0.29
July					
UDOI (UD90)		0	0	0	0
UDOI (UD50)		0	0	0	0
Ca (1 m)		0	0	0	0
Ca (5 m)	**10**	0.01	0.01	0	0.01
Ca (10 m)		0.01	0.01	0	0.01
Ca (20 m)		0.01	0.02	0	0.05
Ca (50 m)		0.11	0.16	0	0.42
August					
UDOI (UD90)		0	0	0	0
UDOI (UD50)		0	0	0	0
Ca (1 m)		0	0	0	0
Ca (5 m)	**10**	0.01	0.01	0	0.01
Ca (10 m)		0.01	0.01	0	0.01
Ca (20 m)		0.01	0.02	0	0.04
Ca (50 m)		0.07	0.13	0	0.33
September					
UDOI (UD90)		0	0	0	0
UDOI (UD50)		0	0	0	0
Ca (1 m)		0	0	0	0
Ca (5 m)	**10**	0	0	0	0
Ca (10 m)		0.01	0.01	0	0.02
Ca (20 m)		0.02	0.05	0	0.17
Ca (50 m)		0.06	0.12	0	0.29

Waveform analyses, pooling together the movement data of all acoustically tagged individuals (n = 19), showed a significant increase in the travelled distance in phase with light intensity. Based on MESOR analysis (mean ± SD =15.42 ± 11.13 m^2), a major peak was identified during light hours, between 08:00 and 17:00 h GMT (Fig. 2.3.5).

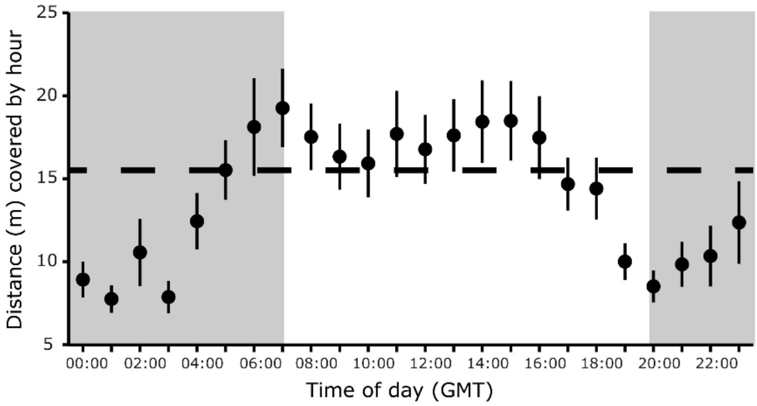


Figure 2.3.5. Overall activity patterns of 19 acoustically tagged Norway lobsters based on the mean ± SD number of meters covered per hour in relation to the time of day. The dashed horizontal line represents the midline estimating statistic of rhythm (MESOR; mean = 15.42); grey-shaded portion of the figure represents the night (before dawn and after dusk)

Norway lobster detection based on acoustic presence data

Analysing detections for each hydrophone individually, we increased the range of detection to double the triangulation area, around 0.6 km^2 (Fig. 2.3.6). The total number of acoustic detections differed among the 13 subareas classified and among the 4 months (Table 2.3.4). In June and July, acoustic detections mainly appeared in the central area, in the centre among the 4 hydrophones and in the eastern area, where only 2 hydrophones could make these detections. During August and September, the number of detections increased in the north-eastern areas.

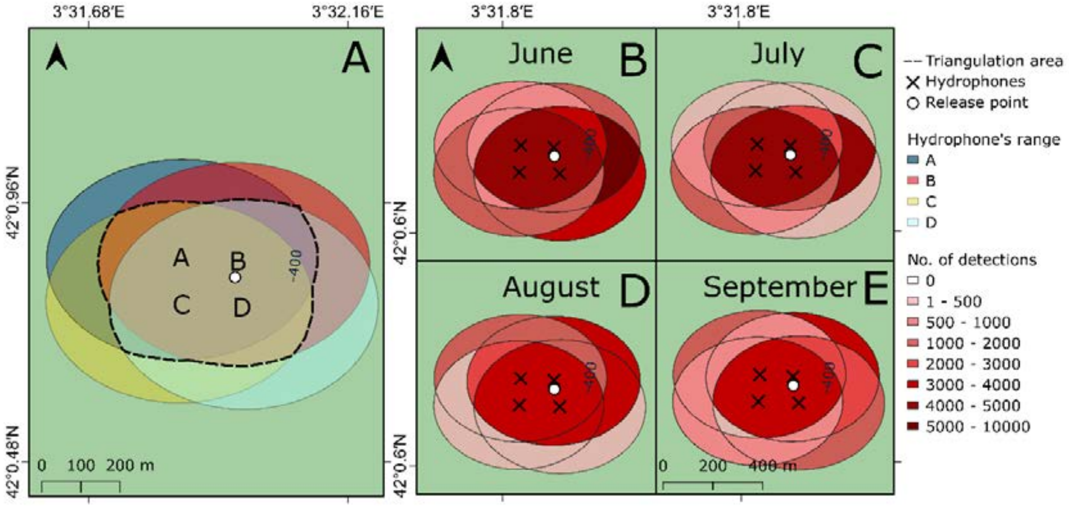


Figure 2.3.6. Detections of acoustically tagged Norway lobsters in the different sets of detection areas within the 4 moored hydrophones. (A) The range of detection of each hydrophone was ~350 m. (B−E) The number of total detections in each area is represented in 4 periods of 27 d. Also shown in each panel is the approximate depth (400 m).

Table 2.3.4. Number of total acoustic detections of the 19 acoustically tagged Norway lobsters tracked in a no-take reserve in the northwestern Mediterranean Sea during 2019 in the detection in each hydrophone group.

Detection area	June	July	August	September	Total
A	757	167	1,760	1,740	4,424
AB	642	230	1,508	970	3,350
ABC	818	1,907	2,635	997	6,357
ABCD	4,228	3,883	1,936	480	10,527
ABD	3,951	2,185	1,519	2,361	10,016
AC	1,776	644	358	840	3,618
ACD	929	667	205	316	2,117
AD	282	164	78	1,243	1,767
B	1,843	407	3,401	3,747	9,398
BC	773	379	1,044	1,539	3,735
BCD	1,997	1,389	3,186	591	7,163
BD	5,425	4,007	3,219	2,066	14,717
C	1,534	1,559	442	826	4,361
CD	1,708	570	143	524	2,945
D	3,107	302	192	1,493	5,094
Total	29,770	18,460	21,626	19,733	89,589

2.3.4. Discussion

By combining acoustic tracking and capture–recapture information, we provide the first detailed description of the spatial ecology of Norway lobsters inhabiting the deep-water Mediterranean Sea. Our results revealed that once deployed over a very small area, most individuals dispersed a few hundred metres and showed the same territorial and solitary behaviour already well described in the literature (Sbragaglia et al., 2017). Moreover, those animals displayed a clear temporal pattern of activity, which peaked during light hours at this depth (Aguzzi et al., 2003). Beyond the ecological interest, these spatial data may be valuable for designing other no-take reserves focussed on recovering deep-water populations of Norway lobsters.

Tag–recapture experiments traditionally yield low recapture rates of labelled individuals (Haynes et al., 2016). The 2.32% recapture rate in our study might suggest that most Norway lobsters remained inside the no-take reserve, in agreement with results obtained in similar studies (Haynes et al., 2016) and from the acoustic telemetry data that comprised the spatial movements obtained by triangulation of acoustic positions.

Spatial movements estimated by triangulation data showed that most Norway lobsters repeatedly travelled more than 100 m away from the re lease point, covering more than 10,000 m in 4 mo with a mean speed between 0.1 and 0.2 m s^{-1}. This locomotor displacement speed corresponds to previous reports for Norway lobsters (Newland et al., 1988). Of the 33 acoustically tracked Norway lobsters, we could only analyse 19 individuals after the filtering procedure to make sure our spatial results were accurate for this species. Some of these 19 lobsters disappeared from the detection area within the first week. Some individuals even suddenly disappeared without exiting the range of detection. Disappearance from the monitoring area can be explained by predation at different times after the release by, for example, small-spotted catshark *Scyliorhinus canicula* (Mnasri et al., 2012) or European conger eel *Conger conger* (Matić-Skoko et al., 2012), both of which are abundant in the study area (RESNEP Project). On the other hand, the transient disappearance of animals over multiple consecutive days can be explained by periods of burrow occupancy, shielding the transmission of acoustic signals to hydrophones. Burrow emergence suppression has been observed in berried female Norway lobsters, which reduce their presence on the seabed during late summer in the Mediterranean Sea (Orsi Relini et al., 1998; Aguzzi et al., 2004).

In the present study, we observed 2 home range shape patterns, one wider and irregular and the other smaller and more uniform. Differences in home range sizes and space use due to intraspecific variability that includes social behaviour and environmental factors are well documented in some crustacean decapods such as the European spiny lobster (Afonso et al., 2008; Giacalone et al., 2019). Here, all individuals were about the same size, but sex differences could not be analysed due to the low number of samples. Considering the previous facts, our results indicate that wider home ranges made by linear trajectories could be ascribed to habitat selectivity in animals that may keep looking for a suitable place to establish (Welsh and Bellwood, 2012), and in the case of Norway lobsters, to dig their burrows. Smaller home ranges may in fact be effectively larger due to the presence of bathymetric features, such as depth gradient in the no-take marine area, resulting in less uniform lines of displacement (Wiig et al., 2013).

From the beginning of the monitoring survey, some Norway lobsters appeared to settle in small areas around the release point. This fact could be explained as dominant Norway lobsters tend to show burrow-oriented behaviour, remaining close to the entrance most of the time and evicting other animals from their burrows to obtain more spatial resources (i.e. sheltering) (Aguzzi et al., 2008; Sbragaglia et al., 2017). The home range area became significantly smaller within 1 mo, as an indication of the establishment of the individuals in their burrows and the dispersal of most individuals from the detection area. We obtained an average home range size (UD90) ranging from 17.75 to 736.25 m^2, which could correspond to the usual area where the species carries out its behavioural, burrow-centred, activities. This mean home range has a high standard error because it includes the trajectories made during the first month, where all individuals were looking for a place to settle. One individual, 14465, was not included in the resulting home range calculations as it was defined by a moving behaviour, disappearing and reappearing again in the detection area. Given that Norway lobsters are territorial (Johnson et al., 2008; Sbragaglia et al., 2017), we assumed that inside the UD50 areas (core areas) each acoustically tracked individual settled in its own burrow, then explored and foraged in the area represented by the UD90, moving away from the burrow as reported in previous studies (Tuck et al., 1997).

The estimated home areas were dispersed and segregated inside the detection area over the entire study period, even in June when all individuals were released together. In addition, interactions between individuals were also scarce as a result of their territorial behaviour (Sbragaglia et al., 2017). Acoustically tagged individuals, released together at the same point, likely had a higher level of interaction at the beginning, which promoted their dispersal inside the no-take area until they experienced a sufficient intra specific pressure release and ultimately settled in burrows. However, more long-term tracking studies with variable numbers (i.e. demographic densities) of reintroduced animals are required to evaluate the effects of agonistic interactions on dynamic settling of individuals, focussing at the same time on population density-associated demographic features such as the body size as a proxy for growth (Merder et al., 2020). By complementing presence data, we doubled the detection range making possible the identification of more acoustically tagged individuals. With this methodology, we observed that many individuals that disappeared in triangulated data results remained inside the no-take marine reserve in the north-eastern detection area, near the point of release of acoustically tagged individuals.

Behavioural rhythms are present at all levels of ecological organization, i.e. from individuals to populations, species and communities, with relevant effects on levels of perceived biodiversity with temporally scattered sampling procedures (Aguzzi et al., 2015). In the present study, for the first time, we monitored the movement behaviour of several individuals concurrently, at a high frequency, in deep-water areas. We observed maximum movement activity in daylight, confirming field and laboratory experiments (Aguzzi et al., 2003; Sbragaglia et al., 2015). The temporal tracked pattern we obtained is fully related to locomotion and detectability, which includes animals engaged in 'door-keeping' behaviour (i.e. animals waiting at their burrow entrance) (Aguzzi et al., 2003). Norway lobsters from deep-water habitats present diurnal burrow emergence during light hours, in contrast to equivalent individuals from northern regions, which inhabit shallower depths with an emergence peak of activity at night (Aguzzi et al., 2003; Chiesa et al., 2010).

A potential management measure to recover overfished marine populations is the implementation of no-take reserves on fisheries grounds (Goñi et al., 2010; Di Lorenzo et al., 2016), which could be applied to highly exploited Norway lobsters. Among the different aspects to be considered, the size of the no-take marine areas is fundamental to ensure that the target species have enough area to meet their vital requirements (Edgar et al., 2014). Based on the spatial movements of the Norway lobsters, we found that the approximate home range area used by settled individuals ranged from 17.75 to 736.25 m^2. Considering the 10 km^2 no-take reserve, we suggest that this area can cover and protect a large number of Norway lobsters.

Our analyses have provided the first insights into the spatial ecology of Norway lobsters after only 2 yr of the establishment of the no-take marine reserve. This species may present fluctuations in density or biomass on spatiotemporal scales, thereby changing their activity patterns and behaviour (Merder et al., 2020). It is therefore important to encourage and promote long-term monitoring projects and programmes to assess whether the observed patterns described in this study are maintained over time. Aside from increasing the number of acoustically tracked individuals inside the no-take marine reserve, another challenging future step in this research should be to include the connectivity factor including more no-take marine reserves generating a network, taking in account the larval dispersal and recruitment (Smith and Jensen, 2008).

2.3.5. Conclusions

The present study provides useful information on the spatial ecology of Norway lobsters. We found acoustic telemetry suitable for acquiring in situ high frequency data on the spatial ecology of Norway lobsters, as baseline ecological knowledge for the design of no-take reserves. The study confirms that a no-take area of 10 km^2 should be sufficient to protect Norway lobster populations. It is possible to recover the stock of Norway lobsters by designing small MPAs, as most individuals would remain inside the protected area, thereby avoiding fisheries. To specify the minimum adequate MPA size, we propose performing this experiment in shallower habitats. If the interest is to incorporate other species, we suggest conducting a similar spatial ecology study to understand their spatial behaviour to protect these target species and then determine the adequate MPA size. Long-term monitoring programmes are encouraged to assess changes over time of the spatial patterns of Norway lobsters identified in the present study. Further studies will benefit from increasing the number of acoustically tracked individuals inside the no-take marine reserve and assessing larval connectivity indicators among a no-take marine reserve network.

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2.4. Before-after control-impact (BACI) assessment of the effects of a deep-water no-take reserve on overfished Norway lobster (*Nephrops norvegicus*) population and their coexisting demersal megafauna

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Abstract

One of the main drivers of marine ecosystem change is fishing activity, bottom trawling being the most intensive fishing practice affecting benthic ecosystems worldwide. In the western Mediterranean Sea, Norway lobster stocks present signs of overexploitation due to trawling pressure, as its biomass and abundance have decreased abruptly during the last years. No-take fishery reserves, a type of marine protected area where fishing is prohibited, could be efficient management measures to recover Norway lobster overexploited populations and coexisting demersal megafauna. Adopting a BACI (before–after control–impact) approach, we performed experimental fishing surveys before and after 4 years of the implementation of a deep-sea no-take reserve in the northwestern Mediterranean. After 4 years of closure, the Norway lobster population increased in abundance, biomass, body size, and trophic level in the no-take reserve. Our approach also revealed an increase in Norway lobster biomass beyond its boundaries, suggesting a spillover effect. Other demersal fish species also increased in biomass and abundance in the no-take reserve. Based on the results of this study, we suggest that no-take reserves might be an effective measure for recovering the Norway lobster stock and some species present in the same habitat.

Keywords: BACI, closed areas, experimental surveys, fisheries, marine protected areas, Norway lobster, no-take MPA.

2.4.1. Introduction

One of the main drivers of marine ecosystem change, beyond the potential effects of climate change, is fishing activity (Costanza et al., 2017; Rousseau et al., 2019). Since the 1960s, fisheries have spread followed by major declines in catch rates of several marine species (Pauly et al., 2002; Froese et al., 2018), impoverishing marine biodiversity and habitats (Puig et al., 2012; Díaz et al., 2019). Among the different types of fishing gear, bottom trawling is considered the most intensive and extended worldwide fishing practice, being a source of direct physical disturbance to the seabed and having great impact on demersal and benthic deep-water ecosystems (Tillin et al., 2006; Halpern et al., 2008; Olsgard et al., 2008). These impacts can lead to a decrease in diversity, productivity and biomass of the species found in the impacted habitat (Costanza et al., 2017; Díaz et al., 2019).

In the Mediterranean Sea, most stocks (close to 62.5%) are fished at their maximum sustainable levels or even above (Tsikliras et al., 2015; FAO, 2022). This sea is highly exploited by bottom trawlers which operate at depths between 50 and 800 m (Gorelli et al., 2011; Lucchetti et al., 2021). One of the main targets of bottom trawling is the Norway lobster (*Nephrops norvegicus*), which is distributed on muddy bottoms along the Mediterranean Sea and the northeast Atlantic Ocean (Bell et al., 2006; Aguzzi and Sardà, 2008; Ungfors et al., 2013). This benthic crustacean has been the focus of many studies due to its ecological and economical value as one of the most important target species of commercial European fisheries (Issifu et al., 2022; Aguzzi et al., 2023). The Norway lobster stocks in the western Mediterranean Sea are experiencing signs of overexploitation due to high trawling pressure (Fig. 2.4.1; Sardà, 1998a; Rotllant et al., 2005). This crustacean is a burrowing species whose galleries provide habitat structures for other demersal species (Roberge and Angelstam, 2004; Aguzzi and Sardà 2008). Although these galleries may offer some protection from trawling, the severe impacts trawling generates on the seabed make Norway lobsters highly vulnerable to this fishing activity (Campbell et al., 2009).

By restricting fisheries and other extractive activities, marine protected areas (MPAs) have been useful tools in restoring populations of overexploited species, including the Norway lobster, benefiting both fisheries management and marine conservation (Halpern, 2003; Ban et al., 2017; Vigo et al., 2023). MPAs have been used not only for conservation, but also for fishing management (Follesa et al., 2011; Moland et al., 2013; Vigo et al., 2023). No-take fishery reserves (NTRs) are one category of MPAs where all fisheries and extractions are strictly prohibited (Category 1a by the International Union for Conservation of Nature). NTRs have shown direct increases in the population density, biomass, and individual size of the most overexploited populations (Lenihan et al., 2021; Vigo et al., 2023). Moreover, these benefits are not only observed inside the NTR but also in the surrounding area (Sala and Giakoumi, 2018), due to a spillover of individuals that benefits nearby fisheries (Goñi et al., 2010; Kerwath et al., 2013).

However, different studies have revealed that not all MPAs are truly effective in achieving their conservation targets (Bennett and Dearden, 2014; Chaigneau and Brown, 2016), due to many factors such as the inadequate size of the protected area or poor management and enforcement (Halpern, 2003; Clements and Hay, 2017; Pendleton et al., 2018). It is therefore crucial to evaluate the MPAs management continuously to enhance its effectiveness in achieving the goals and objectives set for the protected area (Hockings et al., 2000; Pomeroy et al., 2005; Vigo et al., 2021). Assessment via a BACI (before–after control–impact) design is a powerful tool in environmental impact assessment (Jones et al., 1992) and the most rigorous design for assessing MPA effectiveness (Ojeda-Martínez et al., 2011; Sciberras et al., 2013). By implementing BACI approaches, ecological variables and population metrics can be studied before and after protection measures are implemented. This should contribute to novel insights into the accurate effects of management measures (Pitcher et al., 2009; Sørdalen et al., 2018, 2020). To evaluate the effectiveness of the MPA, population indicators are measured, abundance and biomass being the most representative (Moland et al., 2013; Rife et al., 2013; Smokorowski and Randall, 2017), although other variables such as trophic status can determine indirect effects and changes in the trophic structure and relationships of marine communities (Smith et al., 2011; Pinnegar et al., 2017).

In this study, we adopted a BACI approach to assess the effect of a pilot deep-water no-take fishery reserve (hereafter called NTR) implemented in the northwestern Mediterranean Sea on the Norway lobster population and its coexisting demersal megafauna. We conducted standardized experimental fishing surveys before the establishment of this NTR (in 2017) and 4 years after the closure (in 2021) in the NTR and a control (fished) area (hereafter called CA) to analyse the effects of the fishing cease on three key population parameters (abundance, biomass, and body size) of Norway lobster and the demersal megafauna community present in this habitat. We also examined the effect of the NTR on the trophic niche (stable isotopic markers) of Norway lobsters before and after closure in both the NTR and CA. Moreover, we examined whether the NTR generated Norway lobster spillover to the surrounding fishing grounds. After only 4 years of protection, we expect evidence of recovery in Norway lobsters, such as higher abundances, larger individuals inside the NTR, changes in trophic niche, and biomass exportation towards the boundaries of the reserve.

Additionally, certain coexisting demersal megafauna species may also exhibit signs of recovery depending on their specific characteristics and life traits. Species with limited mobility and small, well-defined home ranges within the NTR are expected to respond more positively to the protection measures compared to migratory or highly mobile species that spend only a brief period within the reserve (Claudet et al., 2008; Game et al., 2009). Furthermore, species with an r-selected strategy, characterized by a high reproductive output and shorter lifespans, are likely to demonstrate a more rapid response to protection, exhibiting higher densities inside the NTR compared to the CA, benefiting from the absence of fishing pressure and the presence of larger individuals with increased fecundity rates (Dayton et al., 2000; Micheli et al., 2004; Claudet et al., 2010). We examined trajectories of change over time and space and relate them to the species life history characteristics to better understand their response to the NTR. Considering potential predators of Norway lobsters, we do not expect particularly high densities to threaten Norway lobster populations. Finally, it is anticipated that the most exploited species will exhibit higher recovery rates, as previous studies have demonstrated that signs of recovery are more rapidly observed in depleted stocks (Micheli et al., 2004; Claudet et al., 2006).

2.4.2. Material and Methods

Study area and surveying procedures

This study was conducted in an NTR and in a fished CA, each spanning an area of 10 km^2, at 351–475 m in the northwestern Mediterranean Sea (Catalan Sea, Spain; Fig. 2.4.1A-B). Due to the declining situation of Norway lobster stocks in recent years (Fig. 2.4.1C), fishing activity in the NTR ceased in September 2017 through an agreement between the two local fishery associations (Roses and Palamós), and it was designated MPA in 2020 by the Spanish Government (Order APA/753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753To). The CA was ecologically and geomorphologically equivalent to the NTR, but bottom trawling activity was permitted. The NTR and the CA were established on the northern flank of the Palamós canyon, where bottom trawling targeting Norway lobster stocks has been carried out for around a century (Sardà, 1998b; Puig et al., 2012). The sediment in the study area is compact slit and clay mud, suitable for the burrowing behavior of Norway lobsters (Maynou and Sardà, 1997; Vigo et al., 2023).

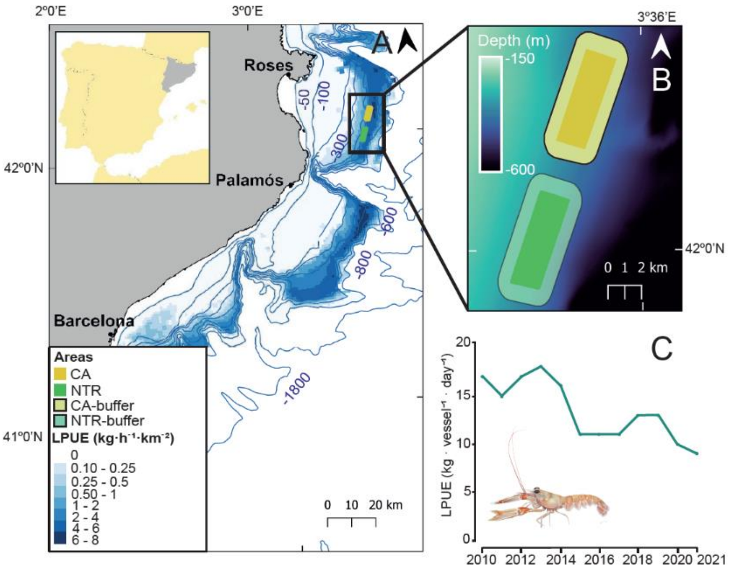

Figure 2.4.1. The study area showing the A) spatial distribution of the annual averaged LPUE (Landings Per Unit Effort) of Norway lobster from 2016 to 2021 (European Commission 2022), and locations of the no-take reserve (NTR) and the control area (CA). B) Fine bathymetry of the no-take reserve, the control area, and their respective buffer areas, NTR-buffer and CA-buffer. C) Annual LPUE of Norway lobsters represented as biomass in kg landed per day and per vessel in LPUE from Catalan trawler vessels. Norway lobster illustration by Joan Mir-Arguimbau.

To evaluate the recovery of Norway lobster population and the coexisting demersal megafauna in terms of changes in abundance, biomass, and body size in the NTR, we established the baseline situation (BASELINE) of the NTR by conducting standardized experimental trawl surveys before the closure (August 2017) and 4 years later (August 2021). Specifically, to establish the BASELINE, we conducted four fishing surveys in the NTR, and two in the CA, and after 4 years (August 2021), we conducted six surveys in the NTR and six in the CA. Experimental trawling surveys were selected randomly within each sampling area, resulting in different trawl stations at different depths (see Table S2.4.1 in the Supplementary Material section). Bathymetry differs slightly between trawl stations, although these differences were not found to be significant concerning the community assemblages nor the Norway lobster distribution and abundance. All experimental fishing surveys were performed with the same vessel (*FV Solraig*), using an otter bottom trawl net of a square mesh size of 40 mm with a cover net of 12 mm mesh size. We performed 1-hour hauls at an average speed of 2.5 knots. The swept area (km^2) of hauls was estimated based on vessel speed (*S*, in knots), average horizontal opening of the net (*BT*, in m), and haul duration (*H*, in h) between the initial and final position of the gear on the bottom (Sparre and Venema, 1998). The value 1852 was used as the conversion factor for nautical miles to meters (1 nm = 1852 m), and the value 10^6 was used to convert m^2 to km^2.

$$Swept\ area = BT \cdot S \cdot H \cdot 1852/10^6 \qquad (1)$$

All individuals caught by the hauls were identified at species level, classified taxonomically, counted, weighed, and measured (total length TL for fish, in cm; preanal length AL for filiform shape fish species as macrourids, in cm; cephalothorax length CL for crustaceans, in mm; and mantel length ML for cephalopods, in cm).

Since the number of fishing surveys conducted to establish the BASELINE in the NTR (four) and CA (two) was very low, and because the abundance and biomass of Norway lobster did not differ between both areas (PERMANOVA tests; abundance, Pseudo-F = 2.11, p = 0.07; biomass, Pseudo-F = 0.57, p = 0.73), we decided to group the surveys conducted in the CA and in the NTR (named BASELINE). Thus, we compared the population metrics on Norway lobster and the other megafauna collected during the fishing surveys between the BASELINE situation, the NTR 4-years after the closure (NTR) and the CA 4-years posterior to the closure (CA).

Abundance and biomass of Norway lobster

We estimated the abundance ($N \cdot km^{-2}$; N = number of individuals) and biomass ($kg \cdot km^{-2}$) of all recorded species in each fishing survey, standardized by the swept area (see Table S2.4.1 in the Supplementary Material section). We compared the abundance and biomass of each species between BASELINE, NTR and CA by applying PERMANOVA tests (Anderson, 2001) based on the Bray-Curtis similarity matrix.

Length-frequency distribution and sex-based differences of Norway lobster

The mean size and sex ratio of Norway lobsters at each sampling station (BASELINE, NTR, and CA) were determined based on the average estimated from the mean values obtained from each trawl haul, which served as the sampling units. By calculating the mean values from multiple trawl hauls, we aimed to obtain a representative estimate of the size and sex ratio for each sampling station. We compared the length-frequency of Norway lobsters among BASELINE, NTR and CA by using non-parametric Kruskal-Wallis tests (as normality and homogeneity of variances were not met) and post-hoc Dunn tests ("dunn.test" package). To test the length-frequency distribution variation among

BASELINE, NTR and CA, we performed Kolmogorov-Smirnov tests using the function *ks.test* from the package "stats". All calculations were obtained in R software version 4.1.2 (R Core Team, 2021).

We performed two-way ANOVA tests to determine if there was a difference in body size between the sexes and between BASELINE, NTR, and CA. In order to evaluate the sex ratio, we conducted non-parametric Scheirer-Ray-Hare tests to test for differences in abundance between males and females among BASELINE, NTR and CA. We also calculated the abundance proportions of each sex according to the total population for BASELINE, NTR and CA, separately. Pairwise Kolmogorov-Smirnov tests were conducted to examine for differences in body size distribution between both sexes and among BASELINE, NTR and CA. The proportion of berried females according to class range size among BASELINE, NTR, and CA was tested using non-parametric Kruskal-Wallis and Dunn tests.

Trophic niche of Norway lobster

To examine the effect of the closure on the trophic niche of Norway lobster, we compared the stable isotope values of $\delta^{15}N$ and $\delta^{13}C$ in the muscle of 40 individuals collected in the NTR and CA during the BASELINE (20 individuals collected in the CA and 20 individuals collected in the NTR) and of 30 individuals collected after the closure (15 individuals collected in the NTR and 15 individuals collected in the CA) (see Table S2.4.2 in the Supplementary Material section). Individuals were randomly selected from each trawl haul at each sampling station (BASELINE, NTR, and CA), sampling individuals with a carapace length (CL) >25 mm. This size threshold was chosen based on previous studies (Sardà, 1991) to ensure that the selected individuals were predominantly sexually mature. By using this size criterion, we aimed to focus on individuals that have reached sexual maturity, which is an important factor when studying population dynamics and assessing the impact of fisheries. The random selection process within the specified size range helped ensure a representative sample of sexually mature individuals from each sampling station. To do this, we extracted white muscle samples from all the individuals after their capture during the experimental surveys. Muscle samples were freeze-dried and powdered, and 0.28–0.33 mg of each sample was packed into capsules and sent to the Laboratory of Stable Isotopes of the Estación Biológica de Doñana CSIC (www.ebd.csic.es/lie/index.html) where stable isotopic analyses were performed (see Vigo et al., 2022 for a detailed description of the stable isotope procedures).

In order to compare the stable isotope values between BASELINE, NTR, and CA, we used Kruskal-Wallis and Wilcoxon post-hoc tests. We also calculated the isotopic niche of Norway lobster during BASELINE, and after 4 years in NTR and CA. To do this, we used kernel utilization density (KUD) estimators to characterize the 50% of the isotopic data (core) using the "adehabitatHR" package (Calange, 2014) in R version 4.1.2 (R Core Team, 2021). The KUD method estimates areas of high use across a regular network of equally spaced points, with the grid extent larger than that of the observations (Venables and Ripley, 2002; Eckrich et al., 2020). Interpolation was carried out by fitting contour lines from the Euclidean distances of each observation to the centroid in bivariate space (Robinson, 2022). The overlap among KUDs was calculated using the Utilization Distribution Overlap Index (UDOI; Hurlbert, 1978), in whose values range from 0 (complete spatial segregation of KUDs, no overlap) to 1 (uniform distribution with 100% overlap between pairs of KUDs). We used the “rKIN” package (Albeke, 2017) in R version 4.1.2 (R Core Team, 2021) to calculate the overlap between KUDs.

Spillover of Norway lobsters in the surroundings of the no-take reserve

To investigate the effect of the NTR on the biomass spillover of Norway lobster outside the reserve, we examined the landings per unit effort (LPUE, $kg \cdot h^{-1} \cdot km^{-2}$), the biomass landed (kg), the annual revenues (in €), and the fishing effort (time of fishing activity, h) accumulated inside two areas of 22 km^2 with a range distance of about ~1100 m from the border of the NTR and the CA (hereafter called buffer-NTR and buffer-CA, respectively; see Fig 2.4.1B). This distance falls within the range where MPAs spillover effect is potentially detected (Halpern et al., 2009). The biomass of Norway lobster in these two buffer areas was obtained by crossing the annual VMS (Vessel Monitoring System) data and LPUE from all trawlers fishing in the study area from 2016 to 2021.

Community diversity metrics

We calculated three diversity metrics from the experimental fishing surveys: the species richness (*S*), the Shannon’s diversity index (*H’*) (Shannon and Weaver, 1948), and the Chao estimator, which indicates the species richness controlled by the sampling effort (Chao, 2006) between BASELINE, NTR and CA. These diversity indices were calculated by considering all detected species grouped into four taxonomic categories (teleost, elasmobranchs, cephalopods, and crustaceans).

Population changes in demersal megafauna

We used multivariate analyses to examine the similarity of species assemblages between BASELINE, NTR and CA. Abundance and biomass data were square-root transformed to reduce the negative effect of weighting the most abundant species. As for Norway lobsters, we compared the abundance and biomass of the demersal community between BASELINE, NTR and CA with PERMANOVA tests (Anderson, 2001). When significant differences ($p < 0.05$) between BASELINE, NTR, and CA were detected, we used pairwise multilevel comparisons with Bonferroni-based adjusted p-values (Martinez Arvizu, 2020).

For the species that showed significant differences in abundance or biomass between BASELINE, NTR, and CA, we tested for differences in body size using non-parametric Kruskal-Wallis tests (as normality and homogeneity of variances were not met). To perform statistical testing on body size, we utilized the mean size at each sampling station (BASELINE, NTR, and CA), which was derived from the average of the mean sizes estimated at each sampling unit (trawl haul). This approach allowed us to obtain representative mean size measurements for each sampling station by considering the average values derived from multiple trawl hauls. By conducting statistical tests on these mean size measurements, we aimed to assess and compare potential differences in body size among the sampling stations. The species that showed significant differences ($p < 0.05$) were later analyzed with the Dunn test. To compare length-frequency distributions between BASELINE, NTR and CA, we performed two-sample Kolmogorov-Smirnov tests. We categorized the species into three groups based on the fluctuations observed in their abundance, biomass, or size structure across the sampling stations. This categorization helped us better understand these fluctuations: “fluctuations generated by the NTR”, species in this group showed consistent values between the BASELINE and CA sampling stations, while their values within the NTR differed significantly; “fluctuations in time”, species in this group exhibited similar values between the CA and NTR sampling stations, but these values differed from the BASELINE, suggesting that the observed fluctuations were driven by temporal variations in environmental conditions or fishing pressure; “fluctuations in time and generated by the NTR”, species in this group displayed variations in their values across all sampling stations, including both the CA and NTR, indicating complex dynamics that are influenced by multiple factors, including the closure of the NTR and other environmental or ecological processes. All potential predator species were identified (P) to observe their specific response in time and inside the NTR. These predators were identified following Vigo et al. (2022), which identified that the predators of Norway lobsters were different cephalopods such as *Sepietta oweniana*, *Abralia veranyi*, *Eledone cirrhosa*, or *Rossia macrosoma*; teleosts such as *Lophius budegassa*, *Merluccius merluccius*, or *Conger conger*; and the demersal shark *Scyliorhinus canicula*.

2.4.3. Results

Norway lobster population changes

Norway lobster abundance and biomass differed significantly between BASELINE, NTR, and CA (abundance, Pseudo-F = 77.34, p = 0.001; biomass, Pseudo-F = 93.5, p = 0.001). Specifically, the abundance and biomass of Norway lobster were higher in the NTR compared to the CA (abundance, Pseudo-F = 101.62, p = 0.006; biomass, Pseudo-F = 101.62, p = 0.006) and the BASELINE (abundance, Pseudo-F = 82.55, p = 0.009; biomass, Pseudo-F = 82.55, p = 0.012). At the CA, Norway lobster abundance and biomass were lower than in the BASELINE (abundance, Pseudo-F = 101.62, p = 0.006; biomass, Pseudo-F = 54.61, p = 0.006) (Fig. 2.4.2A). The abundance and biomass of Norway lobster increased by 60% between the BASELINE and the NTR, and decreased by 80% between the BASELINE and the CA.

Body length measurements revealed that most Norway lobsters in the BASELINE and CA ranged between 20 and 40 mm of CL, whereas those in the NTR ranged between 30 and 50 mm of CL (see Table 2.4.1, Fig. 2.4.2B). The sex ratio of Norway lobsters was similar between BASELINE, NTR, and CA ($H_{1,35}$ = 0.81, p = 0.88). In comparing BASELINE, NTR, and CA, the presence of berried females differed significantly between BASELINE, NTR and CA (χ^2 = 20.19, p < 0.0001). There were more berried females in the NTR (about 28.78% of the total females caught) than in CA (approximately 3.88% of the total females caught; p < 0.01), and BASELINE (p = 0.002) (see Table 2.4.1).

The body size of males and females showed significant differences between BASELINE, NTR, and CA (Table 2.4.2; Fig. 2.4.2B; $\chi^2 = 1598.4$, $p > 0.0001$). In particular, in the BASELINEs, both sexes showed the smallest body sizes (mean and standard deviation; males=29.10 ± 3.99 mm; females=27.31 ± 3.25 mm), followed by the CA (males=31.81 ± 4.85 mm; females=30.44 ± 3.93 mm), and the NTR (males=36.02 ± 5.21 mm; females 33.49 ± 3.89 mm) (Table 2.4.2).

Trophic metric indicators of Norway lobster

The δ^{15}N values in the Norway lobsters collected in the NTR were higher than those in individuals sampled in the BASELINE and CA (Fig. 2.4.2C; $F_{2,49}$= 17.59, $p < 0.001$; Table S2.4.2 in Supplementary Material section). The KUD estimator showed a clear segregation between the Norway lobsters from the NTR and the individuals sampled in the CA and the BASELINE, which showed a high overlap (Fig. 2.4.2C).

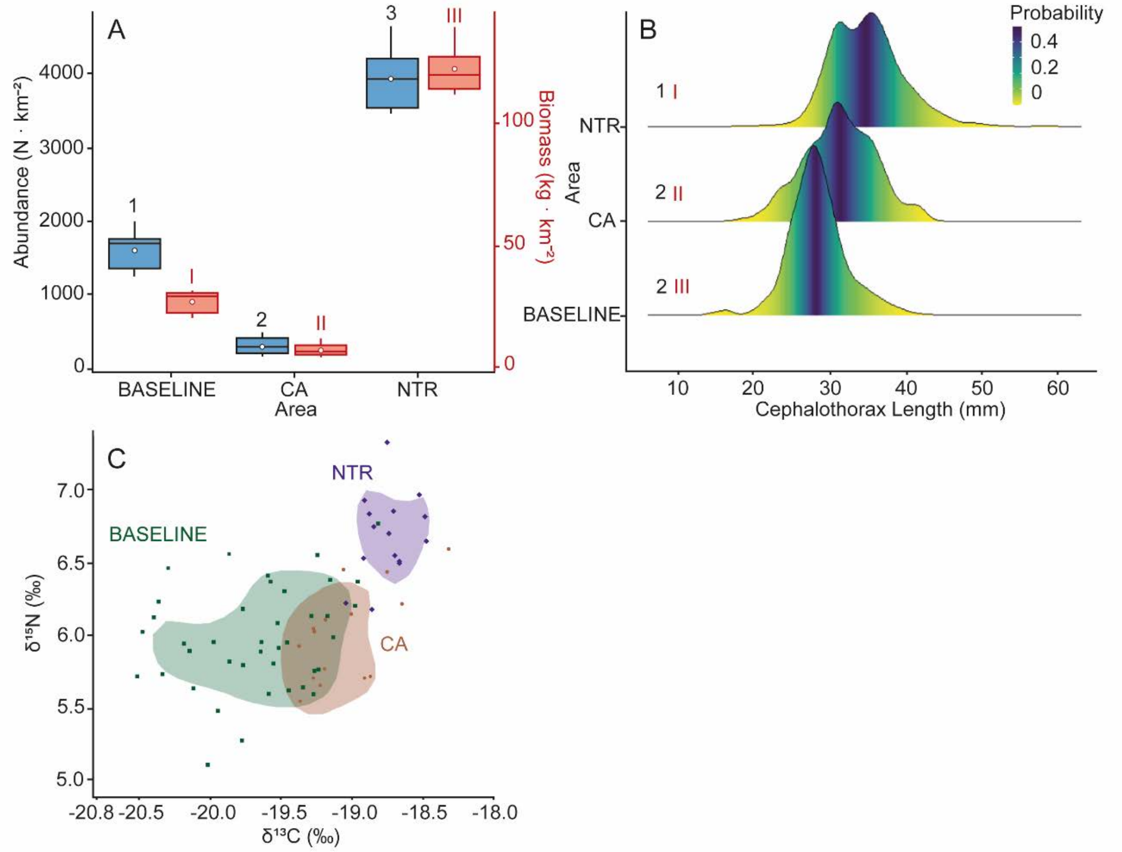

Figure 2.4.2. Effects of the no-take reserve on Norway lobsters. A) Abundance (in blue) and biomass (in red) of Norway lobster in the control area (CA) and the no-take reserve (NTR) at the initial baseline state and 4 years later. Different Arabic numbers for abundance and roman numbers for biomass indicate statistically significant differences. B) Length-frequency distribution of Norway lobster before the closure (BASELINE) and after 4 years in the control area (CA) and no-take reserve (NTR), indicating statistically significant differences in mean sizes with Arabic numbers, and differences in size distribution with roman numbers. According to colour degradation, the most probable size to coincide with the mean size (CL, mm) is dark blue. C) Isotopic niche size and overlap estimates of Norway lobsters generated for 50% contour levels kernel utilization density.

Table 2.4.1. Sex ratio of Norway lobsters by range of size class in CL (mm) before the closure (BASELINE) and after 4 years in the control area (CA) and the no-take reserve (NTR). The number of individuals (N·km^{-2}), the number of males M (% of the total), and females F (% of the total). The number of berried females (Berried-F) identified are also indicated (% in the total females identified at each range of size class).

Area	Range	Sex Ratio			Berried-F (%)
		N	M (%)	F (%)	
BASELINE	0-10	0	0	0	0
	10-20	26 ± 27	9 ± 23 (0.56)	17 ± 23 (1.05)	0
	20-30	1,134 ± 234	624 ± 127 (38.81)	509 ± 137 (31.65)	2 ± 6 (0.39)
	30-40	440 ± 125	346 ± 92 (21.52)	95 ± 44 (5.90)	8 ± 8 (8.42)
	40-50	7 ± 7	7 ± 7 (0.44)	0	0
	50-60	1 ± 3	1 ± 3 (0.07)	0	0
	T	1,608 ± 300	988 ± 191 (61.40)	621 ± 169 (38.60)	10 ± 10 (1.61)
CA	0-10	0	0	0	0
	10-20	1 ± 3	0	1 ± 3 (0.62)	0
	20-30	114 ± 55	62 ± 32 (19.68)	51 ± 26 (16.19)	1 ± 3 (1.96)
	30-40	189 ± 55	113 ± 40 (35.88)	76 ± 50 (24.14)	4 ± 4 (5.26)
	40-50	11 ± 4	11 ± 4 (3.49)	0	0
	50-60	0	0	0	0
	T	315 ± 127	186 ± 61 (59.05)	129 ± 72 (40.95)	5 ± 4 (3.88)
NTR	0-10	0	0	0	0
	10-20	2 ± 6	1 ± 3 (0.03)	1 ± 3 (0.03)	0
	20-30	487 ± 112	209 ± 103 (5.31)	278 ± 49 (7.06)	9 ± 11 (3.24)
	30-40	2 958 ± 464	1,327 ± 166 (33.69)	1,631 ± 361 (41.42)	526 ± 185 (32.25)
	40-50	473 ± 123	443 ± 115 (11.25)	30 ± 29 (0.76)	25 ± 33 (83.33)
	50-60	17 ± 12	16 ± 11 (0.42)	1 ± 2 (0.03)	0
	T	3,938 ± 474	1,997 ± 238 (50.70)	1,942 ± 363 (49.30)	559 ± 195 (28.78)

Table 2.4.2. Results obtained from the two-way ANOVA test, to test for differences in mean size in Norway lobster between sexes (F-F: females; M-M: males; F-M: females and males) before the closure (BASELINE) and after 4 years in the control area (CA) and the no-take reserve (NTR). N indicates the number of individuals expresses in mean and standard deviation, CL indicates the Cephalothorax Length expresses in mean and standard deviation (in mm), and Comparison indicates the differences based on the two-way ANOVA tests. The F-M relation indicates the differences in abundance between sex in the same area) before the closure (BEF) and after 4 years in the CA and the NTR.

	BASELINE		CA		NTR		
Sex	N	CL	N	CL	N	CL	Comp.
F	621 ± 169	27.31 ± 3.25	129 ± 72	30.44 ± 3.92	1,942 ± 363	33.49 ± 3.39	BASELINE < CA < NTR
M	988 ± 191	29.10 ± 3.99	11 ± 4	31.81 ± 4.85	1,997 ± 238	36.02 ± 5.21	BASELINE < CA < NTR
F-M	1,608 ± 300	28.39 ± 3.81	315 ± 127	31.25 ± 4.54	3938 ± 474	34.77 ± 4.58	BASELINE: F < M; NTR: F < M; CA: F < M

Spillover effect of Norway lobster

The LPUE of Norway lobster exhibited a similar spatial distribution among years (Fig. 2.4.3A-B) but decreased between 2016 and 2021 (Fig. 2.4.3C). The transition over time between accumulated LPUE (kg · h^{-1} ·km^{-2}) inside the buffers around the CA and the NTR showed the same pattern (Fig. 2.4.3C). The LPUE and annual revenue followed a similar trend, with a maximum in 2018 followed by a negative trend since then to 2021. In 2021, both LPUE and total revenues were higher in the buffer zone around the NTR than in the buffer zone around the CA. Regarding the percentage reduction from 2016 to 2021 (Fig. 2.4.3C-D; see Supplementary Material section, Table S2.4.4), we observed that in the buffer of the CA, the decrease of LPUE, biomass landed, and annual revenues declined almost half of the initial LPUE in 2016 (49.96, 59.92 and 41.02% of the decrease, respectively) (Fig. 2.4.3D). The fishing effort diminished similarly in both areas, with effort declining by 21.48% in the buffer of the CA and 29.9% in that of the NTR. In contrast, the LPUE and annual revenue declined to a much lesser extent in the buffer area of the NTR (35.6 and 32.4%, respectively).

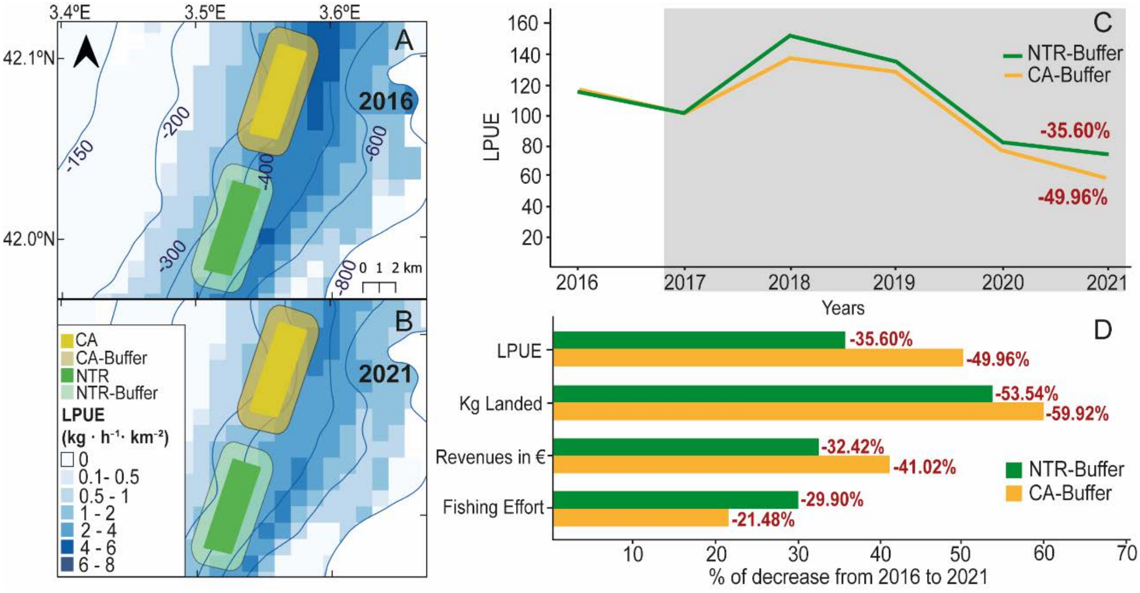

Figure 2.4.3. Spillover of Norway lobsters to the buffer area (22 km^2) around the no-take reserve (NTR) and the control area (CA). A) Spatial distribution of Norway lobster LPUE (kg·h^{-1}·km^{-2}) in 2016, B) and 2021, around the NTR and the CA and their buffers. C) Annual LPUE of Norway lobster between 2016 and 2021 inside the buffer areas of the NTR (NTR-Buffer) and the CA (CA-Buffer). The light grey area indicates the temporal closure. D) % of decrease from 2016 to 2021 in the NTR-Buffer and CA-Buffer in the annual LPUE, annual kg Landed, annual revenues in €, and the total annual fishing effort (time of fishing activity, h).

Community diversity metrics

The species richness was similar between BASELINE, NTR, and CA (Table 2.4.3). The taxonomic group presenting the highest species diversity was the teleost (S = 26–31), followed by crustaceans (S = 10–12). Shannon diversity values were slightly higher in the BASELINE (H' = 2.64) than in the NTR (H' = 2.38). However, the Chao estimator indicated that species richness was higher (97.33 ±21.86 species) in the NTR than in the CA and in BASELINE (76.63 ±11.02 and 69 ±4.65 species, respectively).

Table 2.4.3. Total number of species, total abundance (Ab, $N \cdot \mathrm{km}^{-2}$),Shannon diversity (H) and Chao index (mean and standard deviation) of megafauna species observed before the closure (BASELINE) and after 4 years in the control area (CA) and the no-take reserve (NTR).

		Total	Teleost	Echinoderm	Cephalopod	Elasmobranch	Crustacea
BASELINE	**Species**	63	26	2	10	2	23
	Ab	15,294	5,066	22	3,081	1,201	5,924
	H	2.64	2.19	0.69	0.61	0.03	1.87
	Chao	69 ±4.65					
CA	**Species**	61	28	2	10	2	19
	Ab	7351	4,313	1	488	152	2,397
	H	2.09	1.33	0.69	0.37	0.01	1.12
	Chao	76.63 ±11.02					
NTR	**Species**	64	31	1	12	1	19
	Ab	8,619	4,375	1	705	202	3,336
	H	2.38	1.59	0	0.54	0	1.65
	Chao	97.33 ±21.86					

Abundance, biomass, and length-frequency of coexisting demersal species

The assemblages were composed of teleosts, elasmobranchs, cephalopods, crustaceans, and echinoderms. The abundance and biomass of the demersal community differed significantly between BASELINE, NTR, and CA (abundance, Pseudo-$F_{2,97}$ = 11.47, adjusted-p = 0.001; biomass, Pseudo-$F_{2,97}$ = 16.29, adjusted-p = 0.001). For each species, PERMANOVA tests indicated that for abundance and biomass, 6 teleosts, 1 cephalopod and 3 crustaceans differed among BASELINE, NTR, and CA (Fig. 2.4.4; see Table S2.4.5 in the Supplementary Material section). The species that only presented fluctuations in the NTR were the teleost *Helicolenus dactylopterus* for both abundance and biomass, and the demersal shark *S. canicula* only for biomass (Fig. 2.4.4A-B). Species that showed fluctuations in time were the teleost *Argentina sphyraena*, *Gadiculus argenteus*, *Molva macrophtalma* (Fig. 2.4.4C-E), and the crustaceans *Chlorotocus crassicornis* and *Plesionika heterocarpus* (Fig. 2.4.4F-G). There were species that presented differences in time and inside the NTR, these were the teleosts *Coelorinchus caelorhincus*, *Phycis blennoides*, the cephalopod *A. veranyi* and the crustacean *Parapenaeus longirostris* (Fig. 2.4.4H-K).

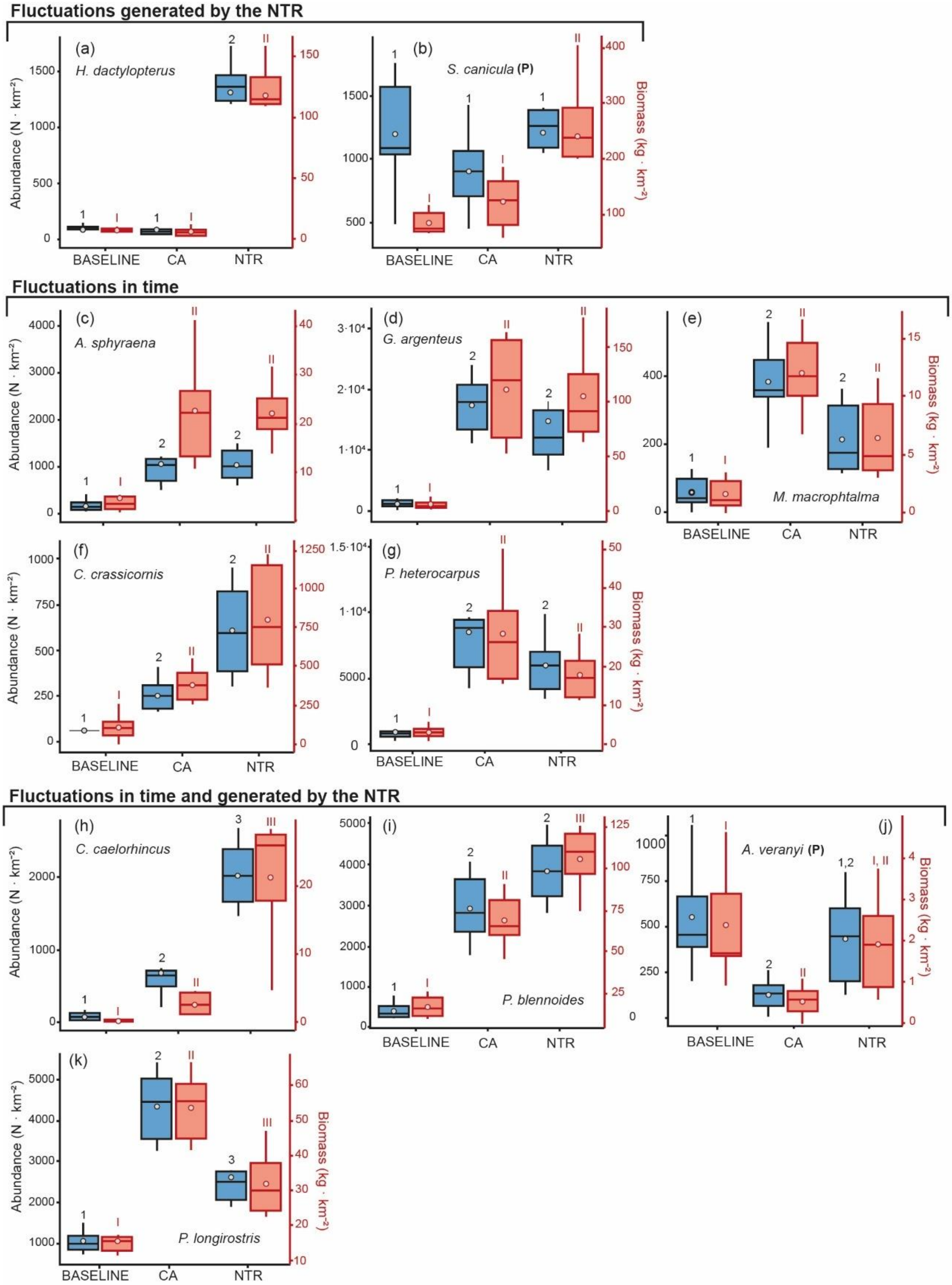

Figure 2.4.4. Coexistent species classified according to the effects observed differences among control area (CA), no-take reserve (NTR) and before the closure (BASELINE). Abundance (in blue) and biomass (in red) of Norway lobsters and the statistically significant differences indicated in Arabic numbers for abundance and roman for biomass. Predator species indicated with (P).

Regarding body size, we found that some species presented differences in the mean body size and size distribution patterns among the NTR, the CA, and the BASELINE (Fig. 2.4.5, Table S2.4.6 in the Supplementary Material section). Regarding differences in mean sizes, the species with fluctuations generated by the NTR were the teleost *C. caelorhincus* and *H. dactylopterus* (Fig. 2.4.5A-B). Fluctuations in time were observed in the teleost *Trigla lyra,* and the cephalopod *A. veranyi* (Fig. 2.4.5C-D). Species that differed in size over time and inside the NTR were the teleosts *A. sphyraena, G. argenteus, Micromessistius potassou, M. macrophtalma*, *P. blennoides* (Fig. 2.4.5E-I), the shark *S. canicula* (Fig. 2.4.5J), and the crustaceans *C. crassicornis*, *P. longirostris*, and *P. heterocarpus* (Fig. 2.4.5K-M). As for shifts in body size distribution patterns, tested by Kolmogorov-Smirnov tests, the species that showed significant differences in distribution among BASELINE, NTR, and CA were the teleosts *G. argenteus*, *M. macrophtalma*, and *P. blennoides*, the cephalopod *A. veranyi*, the elasmobranch *S. canicula*, and the crustaceans *C. crassicornis, P. longirostris*, and *P. heterocarpus* (Fig. 2.4.5).

Regarding the potential predators of Norway lobster (Vigo et al., 2022), the demersal shark *S. canicula* and the cephalopod *A. veranyi* were the species that showed significant fluctuations over time inside the no-take reserve.

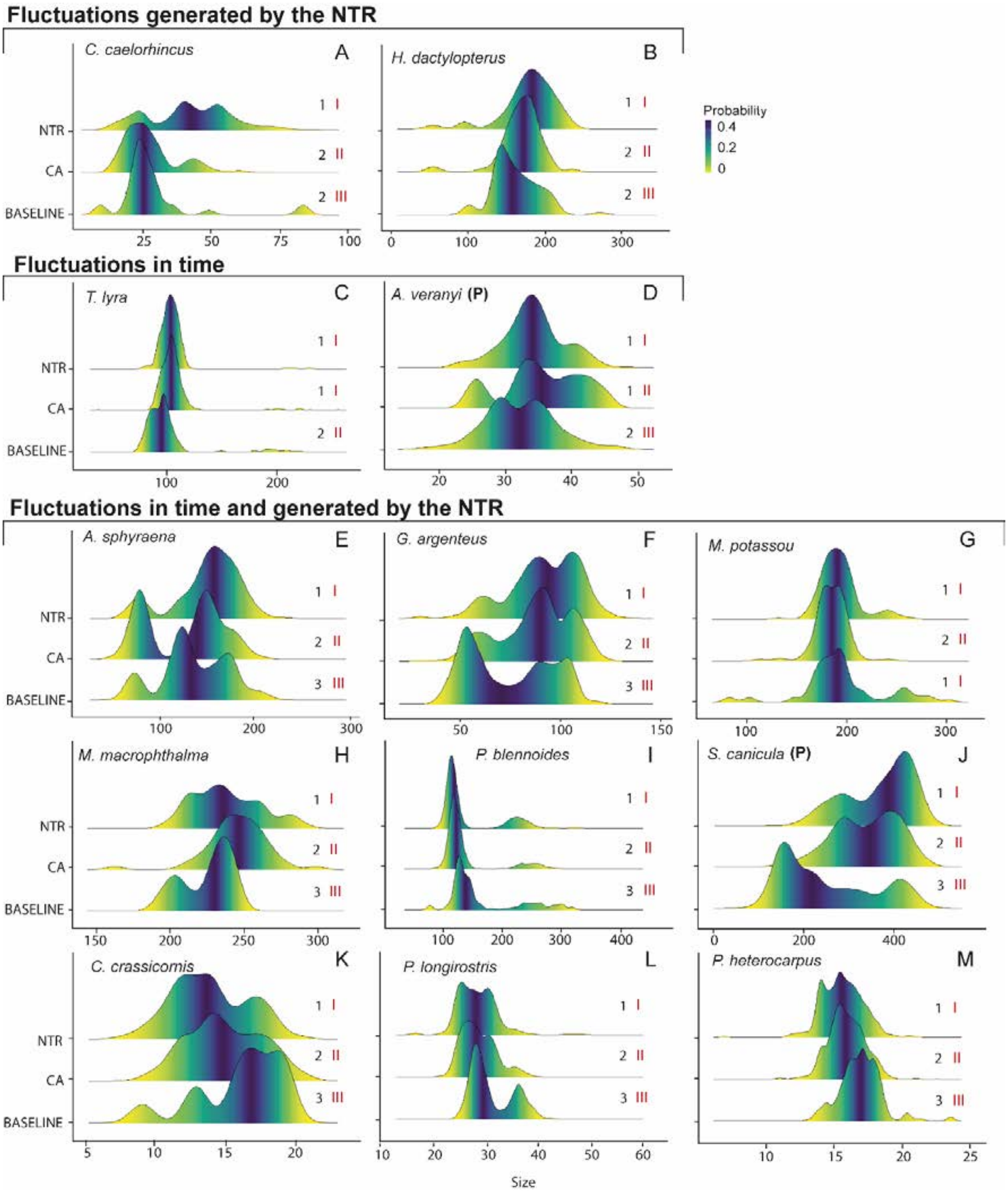

Figure 2.4.5. The length-frequency distribution of body length of Norway lobsters coexisting species that showed differences among control area (CA), no-take reserve (NTR) and before the closure (BASELINE) classified in three categories. According to colour degradation, the most probable size to coincide with mean size (CL for crustaceans, TL and AL for teleosts, and ML for cephalopods, in mm) is dark blue. Different Arabic numbers and roman numbers indicate statistically significant differences on mean sizes and size distributions, respectively. Predator species indicated with (P).

2.4.4. Discussion

Using a BACI approach, we assessed the effect of a NTR in the Mediterranean deep-water on three population parameters (abundance, biomass, and size structure) of Norway lobster and coexisting demersal megafauna after four years of protection. Our findings revealed that the Norway lobster showed signs of recovery, showing higher abundance, biomass, and larger individual body size inside the NTR compared to a control (fished) area and the initial baseline state. We also found higher biomasses around the NTR borders than in the surroundings of the CA indicating a positive spillover effect of the NTR. The protection also increased the trophic level and shifted the trophic niche of Norway lobster inside the NTR after four years. At the community level, although community metrics indicated similar diversity and species richness, we found an increase in the population descriptors of three fish species (*C. caelorhincus*, *H. dactylopterus*, and *P. blennoides*) and one elasmobranch (*S. canicula*) that were more abundant and showed higher biomass in the NTR than in the control area and the initial baseline state.

The ceasing of fishing in a deep-water area that was overfished has proven to be an effective management tool to restore the abundance and biomass of Norway lobster. These results corroborate a previous evaluation conducted 2.5 years after the closure using ROV video surveys in both the NTR and the CA (Vigo et al., 2023). Here, we report that the Norway lobster population increased by 60% compared to the baseline state before the closure. Moreover, we observed a decrease in abundance and biomass in the CA during the study period, amounting to about 80% relative to the baseline state, four years before the closure of the NTR.

The NTR also generated a recovery of size-structure, achieving large individuals for both males and females in the NTR. Individuals may respond to shifts in size-selective mortality inside the NTR due to fisheries-induced selection (Baskett and Barnett, 2015; Moland et al., 2021). Other lobster species have shown patterns of size-assortative mating more pronounced inside MPAs, such as claw size as a sexually selected trait (Sørdalen et al., 2018, 2020; Moland et al., 2019). The sex ratio was similar between the NTR, CA, and the baseline state, with more males than females before and 4 years later. This can be explained by the activity pattern behavior of Norway lobster females that hide inside their galleries after the spawning period (Aguzzi et al., 2007). During the spawning season, berried females hide inside their burrows for a long period, which confer them some protection from trawling, and consequently, more males are caught between September-February by fisheries. However, we found a higher abundance of berried females in the NTR that could increase the potential recruitment, more individuals added to the local population (Agnalt et al., 2007; Di Salvatore et al., 2021), and more potential spillover of eggs and larvae. The combination of higher abundance and large-size females could result in a high reproductive output, producing more off-spring of better condition (Hixon et al., 2014; Dick et al., 2017). The female population in the NTR may not only provide good recruitment for the local population, but also benefit fishers in promoting spillover, exporting more larvae to other habitats where fisheries are still undergoing (McClanahan and Mangi, 2000; Planes et al., 2009; Huserbråten et al., 2013). The export of adults from

MPAs to areas adjacent to the reserve has been proven, in many cases, to provide significant benefits to fisheries despite the loss of the MPA's area as a fishery ground (Follesa et al., 2011; Di Lorenzo et al., 2016; Lenihan et al., 2021). According to the biomass fished (LPUE and kg data) around the NTR and the CA, the Norway lobster population has clearly decreased in the recent years. However, we found a mitigation effect around the NTR, probably associated with a spillover of adult individuals from the NTR to the surroundings. The LPUE, although lower than in 2016, was higher at the NTR borders than in the CA. It is important to note that revenues showed a decrease in both areas compared to 2016, with the decreases being more pronounced in the buffer of the CA. Despite the possible higher abundance of Norway lobsters in the buffer of the NTR, it is worth considering the possibility that larger individuals are being also exported outside the reserve, thereby increasing the commercial value of the landings as observed with other lobster stocks (Moland et al., 2013). We suggest that the larger individuals, which potentially fetch higher prices in the market, may be contributing to revenues outside the NTR. Protected areas can hold larger and older fish, and in this sense, some studies have even reported that protected areas exported world-record fish catches, supplying trophy-size fish to recreational fisheries (Bohnsack, 1996; Roberts et al., 2001). Indeed, considering the distribution of fishing effort and the behavior of fishers around the boundaries of the NTR is crucial to understanding the dynamics and fluctuations in the catch per unit effort (CPUE) or LPUE (Smith and Jensen, 2008; Lenihan et al., 2023). The increase in LPUE can be influenced by factors such as a net export of individuals from the NTR (Goñi et al., 2006; 2010) or lower fishing effort within the reserve area. This has been observed in other Mediterranean reserves with other lobster stocks (Follesa et al., 2011; Kleiven et al., 2019). In this study, a general decrease in fishing effort was observed in both areas, with slightly higher reductions observed around the NTR. While continued monitoring of the fishing effort distribution is necessary, based on the available data, we suggest that the increase in LPUE of Norway lobsters around the NTR is primarily due to a net export of individuals rather than solely a result of lower fishing effort within the reserve area. Acknowledging the complexity of factors influencing LPUE, including fishing effort distribution and fisher behavior, allows for a more comprehensive understanding of the observed changes in catch rates. It is essential to continue monitoring these dynamics and further investigate the contribution of different factors to the observed patterns in LPUE around the NTR. Closing an area to fisheries involves possible shifts not only in single targeted species but also in habitat and ecosystem status (Bourlat et al., 2021; Vigo et al. 2023). Analysing carbon and nitrogen isotope ratios, we observed a trophic niche shift in Norway lobsters inside the NTR after four years of closure. Prey availability and abundance may change the trophic niche and cause diet differences (Vizzini and Mazzola, 2009). Specifically, carbon ratios provide information about the primary energy source (e.g. benthic or pelagic photosynthesis), while nitrogen allows us to distinguish trophic levels and determine the trophic position of consumers (O'Reilly et al., 2002). Our study found that Norway lobsters in the NTR had higher nitrogen stable isotope values after four years of closure, indicating that these individuals consumed trophic resources placed in a higher position in the food web than those in the CA and before closure. The results suggest that the NTR affects not only the abundance and size structure of species, but also the diet composition and trophic biology of individuals (Dell et al., 2015). Norway lobster's diet consists basically of other decapods, other crustaceans (euphausiids and peracarids), and fish (Cristo, 1998; Cristo and Cartes, 1998). In many cases, however, suspended particulate organic matter constitutes a significant part of its diet, particularly among small and medium-sized and berried female Norway lobsters (Santana et al., 2020). Greater food availability and the presence of larger individuals in the NTR may have generated this trophic shift inside the NTR. Future studies could shed light on Norway lobster feeding ecology inside the NTR and examine seasonal variations using stomach contents and stable isotope analyses.

BACI results also revealed that protection did not increase biodiversity inside the NTR, with similar megafauna assemblages found in both evaluated areas over time. However, the species cumulative curves and the Chao estimator allowed us to compare the species diversity at each area, suggesting that with more sampling effort we could have achieved a greater composition of species in the no-take area, indicating a potential higher diversity (Moreno and Halffter, 2000). After 4 years, community metrics (e.g. diversity and species richness) showed similarity of species composition between areas, but we detected significant differences in abundance, biomass, and size structure at species level due to the closure. We have already mentioned the significant changes observed in Norway lobsters inside the reserve attributed to the closure of the area. Observing the different responses among all species, only three teleosts (*C. caelorhincus*, *H. dactylopterus*, and *P. blennoides*) showed an increase in abundance, biomass, or size structure following fishing cessation. These species are commonly fished in the multispecies trawl fishery targeting Norway lobsters in the study area (Sardà, 1998b). As the most widely commercialized scorpionfish species, *H. dactylopterus* may resist fishing pressure due to the dispersal of young individuals to northern areas and the effective reproductive strategy in which viviparity confers high fecundity and enhanced survival for embryos and larvae (Muñoz and Casadevall, 2002; Ribas et al., 2006). The teleosts *H. dactylopterus* and *C. caelorhincus* were the species that better responded in all the parameters (abundance, biomass, larger body sizes). In addition to the direct effect of fishery protection on these species, higher densities are usually found in areas with greater food availability, which may be an indirect driver of the increase in density in the NTR (Massutí et al., 1996; García-Ruiz et al., 2020).

However, it is important to note that many other species experienced shifts in density, biomass, and size structure that cannot be solely attributed to the protection provided by the reserve. Population abundance, biomass, and size of some species may have changed over time due to factors such as oceanographic conditions, which may show a great inter-annual variability (Bonaduce et al., 2021) and can have significant impacts on marine ecosystems, influencing primary production, species composition, reproductive cycles, and overall health of marine organisms (Bellard et al., 2012; Bernardello et al., 2012; Bruno et al., 2018). The distribution and abundance of some species can be strongly correlated to sea temperature, such as cold-water species (*C. caelorhincus*, *A. sphyraena*, *G. argenteus*, and *M. macrophtalma*) that suffer physiological stress associated to variations in temperature (Perry et al., 2005; Sabatés et al., 2012). In this study, we did not compare the fluctuations of environmental factors with the response of species over time, though it is a fact that climate change is continuously increasing water temperatures (Van Vuuren et al., 2008). However, we observed greater abundances and biomass of cold-water species in time. This could be due to the fact that temperature can regulate the condition and reproductive strategies of some cold-water species, which produce a higher number of eggs, but of poorer quality, when temperature increases (Dutil and Lambert, 2000; Serrat et al., 2018). The proximity of the Gulf of Lions, one of the coldest areas of the Mediterranean Sea, and the presence of deep cold waters sinking from the surface can indeed act as a climatic refuge for many cold species (Petrenko, 2003; Ben Rais Lasram et al., 2010). These environmental conditions provide a sanctuary from the warming effects of the surrounding Mediterranean waters, offering favorable temperatures and habitat for cold-adapted species. Other species, as is the case with some deep-sea shrimps, may present fluctuations due to changes in their feeding assemblages or some other specificities related to the habitat (Carbonell et al., 2003). Another unexpected response was found with *P. longirostris*, a valuable and highly exploited crustacean that is a short-life species with high reproduction rate (Ribeiro-Cascalho and Arrobas, 1987; Abelló et al., 2002). This crustacean intensively increased in time in the CA, suggesting a general increase of the population due to external factors, possibly temperature (Colloca et al., 2014; Quattrocchi et al., 2020), while in the NTR it decreased with respect to the control. We suggest that limited resources or competitive interactions with other species may have affected the population of *P. longirostris* inside the NTR (Carr, 2000).

The recovery of the Norway lobster population within the NTR did not appear to be affected by predator species (Vigo et al., 2022). The increased abundance of Norway lobsters within the reserve may have implications for the population structure of their predator species. The protection provided by the NTR can result in an increase in predators' density due to the higher abundance of prey or food availability (Coll et al., 2006; Daskalov et al., 2007). This increase in prey availability can also benefit the population growth of Norway lobsters, as they primarily feed on other decapod crustaceans, euphausiids, peracarids, and even fish that can also benefit from the protection provided by the reserve (Cristo and Cartes, 1998; Zacchetti et al., 2022). However, in this study, we observed an increase in the Norway lobster population despite the increase in abundance, biomass, or size structure of two of their predator species (*A. veranyi* and *S. canicula*). These two species showed fluctuations in time with shifts in the mean body size and lower densities in the CA, while higher densities and larger individuals were found within the NTR. Considering that these species are highly mobile, their rapid increase over a period of only four years suggests that marine reserves may have more of a benefit for those types of species than would have been expected. It is plausible to suggest that more individuals, including larger individuals, remain within the NTR due to the higher availability of food resources (Laptikhovsky, 1999; Barría et al., 2018; Serrat et al., 2018; Guerra-Marrero et al., 2020). The protection provided by the reserve may contribute to enhanced foraging opportunities and increased food availability, attracting these species and promoting their growth and abundance within the reserve. It is important to note that these dynamics may change over time, and further monitoring is necessary to evaluate the long-term effects on predator-prey interactions within the NTR.

All the factors mentioned have the potential to affect the recovery and resilience of species (Andrello et al., 2015). Furthermore, it is crucial to acknowledge that species' response and adaptation to closure measures can vary, and a 4-year closure period is relatively short to observe clearer signs of recovery for some species. Many species did not present any effect, maybe due to other factors such as their life-history traits or shifts in species relationships that were not controlled in this study, such as predation and competition. Long-lived species, such as elasmobranchs, also influenced by their commercial and exploitable value, may require longer periods of protection to adequately respond due to their relatively low growth rate, late maturity rate, and low fertility rate (Cailliet et al., 2005; Claudet et al., 2006; Kaplan et al., 2019), while other species may respond quickly to protection due to their high fecundity rate such as some crustaceans and teleosts observed in this study (Coll et al., 2011; García-Rubies et al., 2013). It is worth noting that highly mobile species may not be significantly impacted by small- to medium-sized protected areas (Game et al., 2009; Grüss et al., 2011; Pittman et al., 2014; Di Franco et al., 2018), such as the reserve examined in this study. Given these complexities, a comprehensive approach is necessary when assessing the effectiveness of marine reserves. To fully comprehend the observed changes in the species dynamics, factors beyond the closure itself, such as environmental changes and species-specific characteristics, should be considered (Magris et al., 2014).

In conclusion, after only 4 years of protection, this deep-water NTR has proved to be a strong effective management measure for restoring the Norway lobster population as indicated by larger individuals and almost four times the biomass observed in the control even if MPA size was only about 10 km^2 (see first description of this MPA in Vigo et al., 2021). This NTR was a pilot closure evaluated to prove that it was an effective measure to recover Norway lobster population. On the basis of our results, we propose establishing a network of small NTRs focused on recovering Norway lobster stocks as an effective management tool for fishery conservation (Gaines et al., 2010; Grorud-Colvert et al., 2014), obtaining relatively rapid gains over the cost of closing fished areas. The NTR could also serve as a planning unit in terms of size and shape for developing spatial conservation planning methods (e.g. Ball et al., 2009). Long-term monitoring is crucial for evaluating the effects of this NTR on Norway lobster and the co-existing megafauna, as its effects could fluctuate over time (Vandeperre et al., 2011; Merder et al., 2020).

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with good animal practice as defined by the current Spanish, Catalonian, and European legislation.

Conflict of interest

The authors have no conflicts of interest to declare.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

Author contributions

Maria Vigo (Data collection, Methodology, Formal analyis, Investigation, Writing), Joan Navarro (Conceptualization, Data collection, Investigation, Validation, Writing), Guiomar Rotllant (Data collection, Review & editing), Nixon Bahamón (Data collection, Review & editing), Marta Carretón (Data curation, Review&editing), Marta Carretón (Data curation, Review & editing), Juliana Quevedo (Data collection, Review & editing), Alba Rojas (Data collection, Review & editing), and Joan B. Company (Conceptualization, Data collection, Investigation, Validation, Writing)

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2.5. ROV-based monitoring of passive ecological recovery in a deep-sea no-take fishery reserve.

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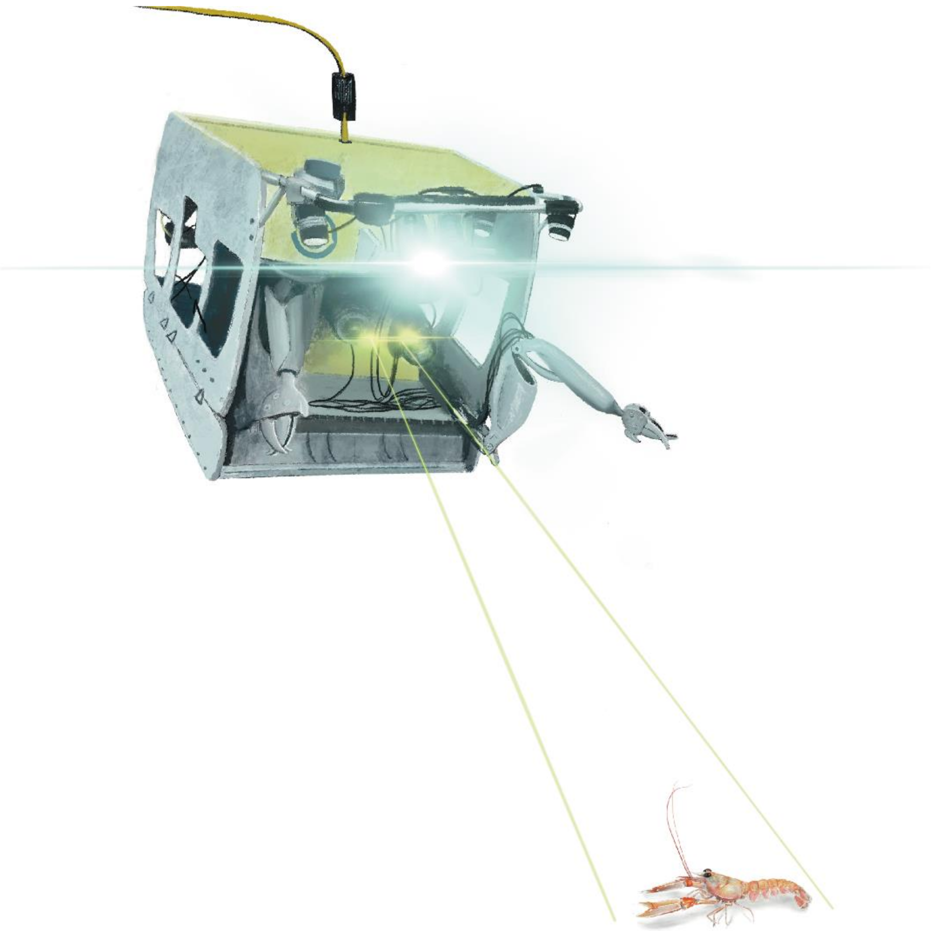

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Abstract

In the context of marine conservation, trawl fishing activity is the most important ecosystem stressor in demersal Mediterranean waters. Limited management measures in bottom trawling have caused deep-sea stocks of the iconic Norway lobster *Nephrops norvegicus* to decrease over the last decade. This crustacean acts as an umbrella species for co-existing megafauna. Here, we used non-invasive Remote Operated Vehicle (ROV) video-surveys to investigate the status of a pilot deep-sea no-take reserve implemented in the northwestern Mediterranean by quantifying demographic indicators of Norway lobsters and the co-existing benthic community, seafloor restoration, and the presence of marine litter. The results revealed that in the no-take reserve the Norway lobster stock showed higher abundance and biomass, and slightly larger body sizes than in the control area without fishing prohibition. Some taxa, such as the fishes *Helicolenus dactylopterus* and *Trigla lyra* and anemones of the family Cerianthidae, increased in abundance. We also observed that all trawling marks were smoothed and most of the seafloor was intact, clear indicators of the recovery of the muddy seafloor. The accumulation of marine debris and terrestrial vegetation was similar in the no-take reserve and the fished area. On the basis of the results of this study, we suggest that the use of no-take reserves might be an effective measure for recovering the Norway lobster stock, its co-existing megafauna community, and the surrounding demersal habitat. We also suggest that ROV video-survey might be a useful, and non-invasive method to monitor megafauna and seafloor status in protected deep-sea environments.

Keywords: deep sea, habitat restoration, Marine Protected Area, *Nephrops norvegicus*, trawling, video-monitoring.

2.5.1. Introduction

The Mediterranean Sea is a biodiversity hotspot, constituting <1% of the global ocean surface, but comprising up to 18% of the world's marine species, 25–30% of them being endemic (Bianchi and Morri, 2000; Coll et al., 2010; Regato, 2008). Fishing activity is one of the most important ecosystem stressors in Mediterranean waters, altering biodiversity and habitats (IOC-UNESCO, 2021). Fisheries play an important economic and social role in local and regional economies, representing nearly 20% by weight and 35 % by value of European fishery production (Papaconstantinou and Farrugio, 2000). Although in 2019 the European Commission implemented a global management strategy for the whole western Mediterranean (WestMED initiative, European Commission, 2017a, 2017b), each country independently legislates its own fisheries, applying diverse management measures linked to the reduction of effort, such as a decrease in the number or fishing capacity of vessels, governing bottom otter trawl (trawling, hereafter), or restricting fishing activity seasonally or in particular areas (Papaconstantinou and Farrugio, 2000; Aristegui-Ezquibela et al., 2021).

Beyond the potential effects of global change on marine biodiversity and functioning (Denman, 2008; Levin and Le Bris, 2015; Trindade-Santos et al., 2020), the high-impact bottom trawling that has been used by Mediterranean Sea fisheries for >80 years (Palanques et al., 2006; Puig et al., 2012) is one of the main drivers of ecosystem change in deepsea Mediterranean demersal communities (Danovaro et al., 2017). The main concern about applying management measures for fishery sustainability in the Mediterranean is related to the multi-specificity of fisheries preventing bottom trawl fleets from catching just the target species, rather than a relatively large number of unwanted species that are discarded (i.e., wasted), which may represent, on average, 25% of the total catches (Sánchez et al., 2004; Gorelli et al., 2016; Blanco et al., 2023). Bottom trawling is a poorly selective fishing method with a great impact on demersal communities and deep-sea ecosystems. Consequently, most Mediterranean stocks (ca. 62.5%) are being fished at their maximum sustainable yield or above their maximum reaching unsustainable levels (Papaconstantinou and Farrugio, 2000; Tsikliras et al., 2015; FAO, 2022). Moreover, bottom trawlers disturb and destroy seafloor habitats in their path, including seagrasses, coral reefs, or rock gardens, considered key habitats for multiple species (Reed et al., 2007; Stiles et al., 2010). Bottom trawling can also strongly modify seafloor morphology because of the resuspension and removal of a large amount of sediment by the action of wires, otter doors, sweeps, and nets (Palanques et al., 2006; Puig et al., 2012). As a result, historically intense commercial trawling has acted as a geological force flattening the surface of the continental shelf and slope margins in the Mediterranean, exposing its hardened substrate (Puig et al., 2012).

In the western Mediterranean Sea, the trawl fleet operates at a depth of between 50 and 800 m (Gorelli et al., 2011) targeting Norway lobster *Nephrops norvegicus* at a 300–500 m depth (Sardà, 1998a). This demersal decapod is one of the most important demersal stocks for European fisheries, distributed on muddy bottoms along the northeast Atlantic Ocean and the Mediterranean Sea (Bell et al., 2006; Aguzzi and Sardà, 2008; Ungfors et al., 2013; Aguzzi et al., 2023). Nevertheless, due to high fishing pressure and ineffective management measures for the sustainable exploitation of the species, the catches of this iconic European crustacean have been decreasing over the last several years (from 2008 to 2016 there has been a decrease of 19% in catches in the EU, EUMOFA, 2019; Letschert et al., 2021; Lolas and Vafidis, 2021). The species' dependency upon fragile silt and clay mud habitats, in which Norway lobsters dig their burrows, makes it highly vulnerable to trawling impacts (Campbell et al., 2009). Also, as a marine ecosystem engineer, the Norway lobster's burrowing behaviour increases habitat heterogeneity and provides structures for other co-existing megafauna, acting as an umbrella species (i.e., a key conservation target to protect the whole benthic community; Roberge and Angelstam, 2004).

The establishment of marine protected areas (MPAs), such as legally recognized no-take reserves where fishery activity is prohibited, could be a useful management measure for not only recovering the over-exploited Norway lobster stock, in terms of density and body size, but also promoting the co-existing benthic community (Melaku Canu et al., 2020; Vigo et al., 2022, 2021) and enhancing seabed quality and overall demersal richness (Sala and Giakoumi, 2018; Cabral et al., 2020; Sala-Coromina et al., 2021). The benefits obtained from MPAs could also be observed in adjacent areas, as a result of the spillover of adults and juveniles from the protected area (Lenihan et al., 2021; Sala-Coromina et al., 2021). Management evaluations within no-take fishery reserves have already been carried out on crustacean species, such as the European lobster *Homarus gammarus* and the spiny lobster *Palinurus elephas* (Goñi et al., 2010; Follesa et al., 2011; Wiig et al., 2013; Padilla et al., 2022). In the Mediterranean Sea, there are very few assessments of the use of no-take reserves for the recovery of Norway lobster populations, except for the Pomo Pit area in the Adriatic (Bastardie et al., 2017; Melaku Canu et al., 2020) and a no-take fishery reserve located at a deeper depth (375–400 m) in the northwestern Mediterranean (APA/753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753To; Vigo et al., 2021).

Monitoring strategies for the evaluation of the efficacy of no-take reserves for the recovery of Norway lobster stocks are a priority (Lester et al., 2009). Unfortunately, compared to shallow areas (e.g., Lloret et al., 2006; Linares et al., 2012), the monitoring of deep-sea stocks is a technological and operational challenge (Aguzzi et al., 2020). Experimental trawling remains the most common tool to quantify the abundance and biomass of deep-sea stocks (e.g., Fiorentini, 1999; Sánchez et al., 2007; Tuset et al., 2021). However, its use in an MPA is not desirable due to its intrinsic impact on benthic communities and habitats. As an alternative strategy to assess the status of demersal and benthic communities, visual monitoring through the use of Remotely Operated Vehicles (ROVs), Autonomous Underwater Vehicles (AUVs), and other systems is increasingly employed (Huvene et al., 2016; Chimienti et al., 2018; Benoist et al., 2019). In fact, there are regular underwater television (UWTV) surveys that are conducted to provide abundance estimates for Norway lobsters on the functional units (FUs) in the North Atlantic to assess their stocks (Dobby et al., 2021). Video-surveys can provide habitat assessments evaluating anthropogenic impacts at the level of seabed sediment integrity or the presence of marine litter (Bo et al., 2014; Mecho et al., 2020) defined as any persistent, manufactured or processed solid material discarded, disposed, or abandoned (definition by the United Nations Environment Programme; UNEP).

In this study, we used ROV video-surveys to investigate the ecological and morphological status of a pilot no-take reserve implemented in a deep-sea northwestern Mediterranean area 2.5 years after its establishment as well as the situation of a nearby control (fished) area. We followed an ecosystem-based approach, i.e., by quantifying the demographic indicators of abundance, biomass, and body size of Norway lobsters and other co-occurring benthic megafauna, including the main predators of Norway lobsters. We also examined the status of seafloor recovery as a metric for passive recovery from trawling impacts and the presence of marine litter and terrestrial vegetation in the reserve.

2.5.2. Material and Methods

Study area and ROV surveying procedures

This study was conducted in a deep-sea no-take fishery reserve with an area of 10 km^2 (hereafter referred to as no-take reserve), located along the continental margin from 351 to 475 m depth in the northwestern Mediterranean Sea (Fig. 2.5.1A). This no-take reserve was established on the northern flank of the Palamós canyon, where deep-sea trawling has taken place for around a century (Puig et al., 2012). In the whole slope region, the sediment is compact silt and clay mud suitable for the excavation of burrows by Norway lobsters (Maynou and Sardà, 1997). This reserve was created in 2020 by the Spanish Government (Order APA/753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753To) with the main objective of recovering the stock of Norway lobster in this Mediterranean area. However, before the designation as an MPA, fishing activity inside the no-take reserve was ceased in September 2017 through an agreement, i.e., not officially enforced, between two local fishermen's associations (Roses and Palamós). We used, for comparative purposes, an adjacent control area (i.e., ecologically, geomorphologically and bathymetrically equivalent) where bottom trawling was permitted, having the same dimensions as the no-take zone (Fig. 2.5.1B). The no-take reserve has a bathymetric range of 310–475 m and the control area has a range of 290–440 m depth (Fig. 2.5.1C).

Just prior to the cessation of fishing in the no-take reserve (August 2017), we conducted 4 experimental fishing surveys in the no-take area and 2 in the control area, using an otter bottom trawl net of a square mesh size of 12 mm. All hauls were of 1 h of duration, with an average speed of 2.5 knots. The swept area (km^2) of all hauls was estimated based on vessel speed (S, in knots), average horizontal opening of the net (BT, in m) and haul duration (H, in h) between the initial and final position of the gear on the bottom (Sparre and Venema, 1998). The preliminary results of these experimental trawling surveys (see Fig. 2.5.2) indicated that abundance (control area; mean = 1584.31; SD = 925.89 No.·km^{-2}; no-take reserve; mean = 2789.56; SD = 1446.37 No.·km^{-2}), biomass (control area; mean = 24.65; SD = 12.54 kg·km^{-2}; no-take reserve; mean = 42.16; SD = 20.79 kg·km^{-2}), and size distribution (control area; mean = 23.37; SD = 4.97 mm CL; no-take reserve; mean = 27.30; SD = 4.81 mm) of Norway lobster did not differ between both control area and no-take reserve (Abundance; $F_{1,5} = 0.31$, $p = 0.61$; Biomass; $\chi^2 = 0.86$; $p = 0.35$; mean size distribution; ($\chi^2 = 0.05$, $p = 0.48$).

To monitor Norway lobster (Fig. 2.5.1D) abundance and biomass in a non-invasive way, ROV video-surveys were performed in both the no-take zone and adjacent control area in February 2020, 2.5 years after the implementation of the no-take reserve. In particular, we conducted six ROV video-survey transects in the no-take reserve (341–376 m depth) and six in the control area (327–424 m depth) (Fig. Fig. 2.5.1C, see Supplementary Material section Table S2.5.1). These surveys were performed on board the R/V Sarmiento de Gamboa with ROV Liropus 2000, a Super-Mohawk ROV. The ROV was equipped with a forward-facing video camera (HD Kongsberg OE14-502) positioned below four Halogen 250 W Deep Sea Power & Light (DSPL) lights. The ROV also had two parallel lasers with 10 cm separation, to provide a reference scale for animal sizing within the camera field of view. Underwater ROV positioning was measured by a High Precision Acoustic Positioning system (HiPAP; 350 P Simrad) with a spatial accuracy of 0.3% and an error of range of detection <20 cm. This was linked to the Differential Global Positioning System of the R/V.

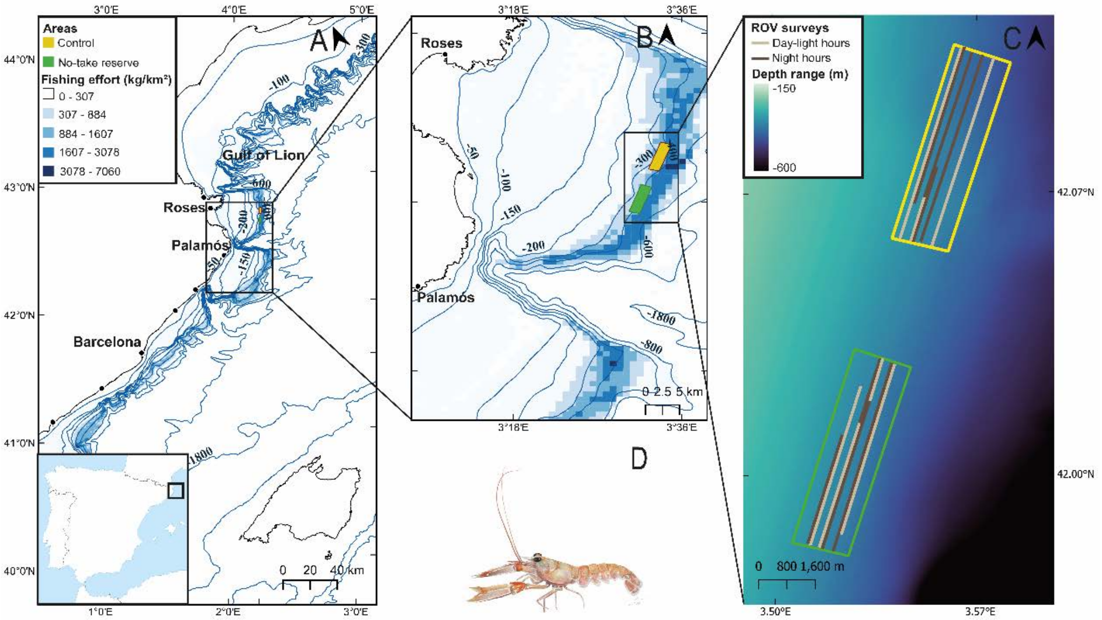

Figure. 2.5.1. The study area showing A) the spatial distribution of Norway lobster catches, B) the location of the no-take reserve and the control area, and C) the position of the ROV video-surveys. The spatial distribution of Norway lobster catches accumulated was obtained by combining vessel monitoring system information and official daily landing data in the time period 2005–2018 (European Commission, 2022). D) Norway lobster illustration by Joan Mir-Arguimbau.

The ROV video-surveys were continuously recorded and conducted during consecutive 24 h cycles close to the bottom (50–100 cm of altitude above the seabed) at a constant speed of 0.6 $m \cdot s^{-1}$ (Ayma et al., 2016; Mecho et al., 2018, 2020; Grinyó et al., 2022). The video-swept area was calculated from the ROV instantaneous velocity each second, multiplied by the width of the image as measured by the laser pointer (approximately 1.5 m width at a constant height of 1.8–2 m). Despite possible bathymetric and swept area differences between surveys, each ROV video-survey conducted was considered a replicate within each. We standardized by adjusting the resulting parameters according to the swept area. We also quantified the presence of other co-occurring megafauna species, marine litter, organic debris such as terrestrial vegetation, and the status and recovery of the seabed by categorizing the trawling impact marks (see below for a more detailed explanation).

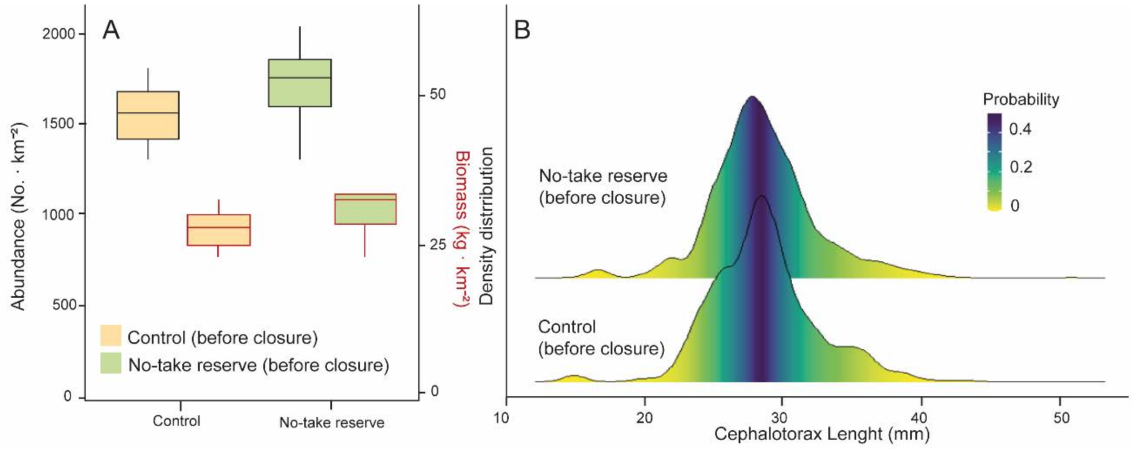

Figure 2.5.2. A) Abundance and biomass of the Norway lobster in the no-take reserve and in the control area in August 2017 as determined by experimental trawl fishing. B) Body size density distribution determined by experimental trawl fishing in August 2017. Based on the color degradation, dark blue indicates the highest likelihood of sizes (CL, mm) coinciding with the mean size.

Norway lobster evaluation

To estimate the abundance and biomass of Norway lobsters in the no-take reserve and in the control area, we conducted two complementary approaches: “burrow-system counting” and “animal counting”. In the burrow-system approach, we followed the assessment protocols of the Working Group on *Nephrops* Surveys (ICES, 2016; Dobby et al., 2021), counting all burrow-systems in the control area and the no-take reserve. Burrows of Norway lobster present characteristic features related to the shape and appearance of burrow openings that occasionally number two or three in a system, and are easily identified (e.g., Chapman, 1980; Tuck et al., 1994; Froglia et al., 1997; Supplementary Material section Fig. S2.5.2). To standardize the counting of burrows from each video-transect, their abundance was standardized by the unit of video-swept seabed surface, obtaining a density estimate as the number of burrow-systems per km^2. We assumed that one burrow-system contained only one Norway lobster as this species is highly territorial and usually only one adult occupies the burrow-system (Johnson et al., 2008; Sbragaglia et al., 2017; Vigo et al., 2021). We also considered that all burrow-systems were occupied, as unoccupied burrows rapidly degrade and collapse (Marrs et al., 1996).

In the animal counting approach, we standardized the number of individuals counted in ROV transects per unit of video-swept area during 24 h cycles. The video-swept area was calculated in m^2 for each minute of video recording (given the constancy of cruising; see above), and then converted into km^2. Therefore, the data were presented as the number of individuals per km^2 (i.e., density). Only in the animal counting approach, we tested for differences considering the abundance of Norway lobsters during daylight hours and then during nighttime hours (considering sunrise at 8 am and sunset at 6 pm).

To test the differences between Norway lobster counting approaches, burrow-system and animal counting, between the control area and the no-take reserve, two-way ANOVA tests were conducted. The test allowed assessing the variance of the abundance of Norway lobsters with two fixed factors (“Area” for the control and no-take reserve, and “Activity” for presence in daylight hours and in nighttime hours). For burrow abundance, we conducted non-parametric Kruskal-Wallis tests in the R software version 4.1.2 (R Core Team, 2021) using the function *kruskal.test*. Statistical analyses were carried out beforehand to test for normality and homogeneity of variances for each variable using the functions *shapiro.test* and *bartlett.test* respectively of the package “stats”.

On the basis of the frames recorded in the ROV surveys, we measured the body size of Norway lobsters based on their cephalothorax length (Carapace Length = CL, in mm) using the software ImageJ V. 1.53q (Abràmoff et al., 2004) measuring individuals aligned within the field of view (i.e., whose cephalothorax was seen next to the two laser beams). We estimated the body size of each individual by averaging five repeated measures to minimize measurement bias. Then, a class-size frequency distribution was constructed (using the averaged CL measure for each individual) for both the control area and no-take reserve. We applied one-way ANOVA tests to compare body size between the control area and the no-take reserve.

The body mass (in g) of Norway lobsters was estimated from a length-weight relationship for the species, using a standard allometric model. We averaged the allometric coefficients from 1995 reported by Sardà et al. (1998), in the same area of this study (GSA06), between female and male coefficients for obtaining combined sexes coefficients (Sardà et al., 1998):

$$W = 0.00045\ CL^{3.10} \tag{1}$$

where W is body weight in grams and CL is cephalothorax length (see above). The constants 0.00047 and 3.14 are the coefficients a and b of the allometric model. Weight was calculated from each measure of CL computed for both the control area and no-take reserve, and the average and standard deviation were also estimated. Subsequently, we estimated the biomasses along each video-transect in the no-take and control areas. For this, we converted the previously obtained weight into biomass ($kg \cdot km^{-2}$) with the following formula (Froglia et al., 1997; Morello et al., 2007):

$$B = \overline{W} \cdot A / 1000 \tag{2}$$

where B is the biomass ($kg \cdot km^{-2}$), W is the mean individual weight (g) from all the individuals that were possible to measure with ImageJ (we were only able to measure individuals aligned within the field of view), and A is the total abundance corrected by swept area ($No. \cdot km^{-2}$). We calculated a total of four biomasses depending on the A source: for the two areas, control zone and no-take reserve, and the two approaches, burrow-system and animal counting.

A non-parametric statistical approach was used to determine significant differences between groups for cases in which normality and homogeneity of variance were not met. The Kruskal-Wallis non-parametric test was used to compare estimated biomasses in the control area and the no-take reserve, and between burrow-system counting and animal counting of Norway lobster. To compare estimated biomasses from burrow-systems in different areas, we conducted parametric one-way ANOVA tests.

Community megafauna taxa evaluation

Taxonomic identification and counting of the co-existing megafauna taxa were performed for each ROV video-survey analyzing the recorded video frames. A video-catalog of best images of the detected taxa that appeared in the area was built as a reference for their classification (Supplementary Material section Figs. From S2.5.3 to S2.5.9). All these individuals were then classified at the lowest possible taxonomic level according to identification guides (Lloris, 2015; Froese and Pauly, 2022; Grinyó et al., 2022; Fricke et al., 2022; WoRMS Editorial Board, 2022) and by taxonomic specialists from the Institut de Ciències del Mar (ICM-CSIC). Due to the difficulty of correctly assigning cephalopods to particular species, we classified them into three larger taxonomic groups: Superorder Decapodiformes, Order Octopoda, and Order Sepiida. The community (dis)similarity of all co-occurring taxa was calculated via the video-swept area method (see previous section). We also identified the main predators of Norway lobster based on Vigo et al. (2022).

To examine the differences between the control area and the no-take reserve in the composition and abundance of taxa, we generated a nonmetric Multi-Dimensional Scaling (nMDS) ordination analysis in the R software version 4.1.2 (R Core Team, 2021) using the function *metaMDS* of the package “vegan”. The abundances were previously square-root transformed to achieve normality, and a Bray-Curtis similarity matrix was calculated. Once we visualized the grouping, we conducted a one-way permutational multivariate analyses with *adonis* from the package “vegan” (PERMANOVA tests; Anderson, 2001) using one fixed factor (‘area’, with two levels) to test for differences in community (dis)similarity between transects from the control area and the no-take reserve. As for Norway lobsters, we compared all taxa abundances between the control area and the no-take reserve with PERMANOVA and a pairwise multilevel comparison with Bonferroni-based adjusted p-values by using the package “pairwiseAdonis” and pairwise.adonis (Martinez Arbizu, 2020). Moreover, Shannon's diversity index (H′, log 10 base) (Shannon and Weaver, 1948) was calculated to measure species diversity in each community (control area and no-take reserve). To test for differences between areas, one-way ANOVA tests were performed for each biodiversity index.

We constructed two taxa accumulation curves (Thompson and Withers, 2003; Ugland et al., 2003) to record the cumulative number of species in each study area (control and no-take reserve) as a function of the cumulative effort expended searching for them (hours of video recorded by ROV surveys). The taxa accumulation curves allowed us to assess and compare diversity across the two areas and to evaluate the adequacy of the ROV video-surveys in representing the benthic and demersal fauna in each area. We also calculated the Chao estimator in the R software version 4.1.2 (R Core Team, 2021) using *specpool* from the package “vegan” for assessing species richness in the two communities, the control area and the no-take reserve. This estimator indicates how many species or different taxa would be registered if the effort sampling was increased or how many species we did not record with our effort (Chao, 2006; Béguinot, 2016).

Marine litter and terrestrial vegetation

We classified marine litter as plastic, metal, glass, and the remains of fishing nets (Ramirez-Llodra et al., 2011; Mecho et al., 2020; GESAMP, 2021). We also counted terrestrial vegetation items (such as tree branches) to analyze all organic inputs coming from terrestrial sources (Galimany et al., 2019). The abundance of the different types of litter and terrestrial debris were also standardized by the swept area (km^2). The differences in the abundance of anthropogenic debris between the control area and the no-take reserve were tested using two-way ANOVA tests with two fixed factors (‘area’ with two levels for the control and no-take reserve, and ‘type of debris’ with five levels). The difference in the abundance of terrestrial debris between the control area and the no-take reserve was also tested with non-parametric Kruskal-Wallis tests in the R software version 4.1.2 (R Core Team, 2021) using the function *kruskal.test*.

Seafloor integrity and recovery

We examined seafloor integrity in the control area and the no-take reserve by assessing the perturbations of trawling marks (by bottom trawl metal doors and trawl nets). We classified them into six different categories according to the degree of alteration (see description in Table 2.5.1, Fig. 2.5.3).

We recorded the duration of their appearance in each ROV video-survey, classifying them as stated in Table 2.5.1, and then a percentage was calculated considering the total time recorded at each transect. Finally, we estimated the overall average and standard deviation of the control area and the no-take reserve.

We tested for differences in the variance of presence of each category of alteration between areas and also among all six categories defined in Table 2.5.1 We conducted the non-parametric test of Scheirer Ray Hare in the R software version 4.1.2 (R Core Team, 2021) using the function *scheirerRayHare* of the package “rcompanion”. The post-hoc tests were performed using multiple comparisons with Dunn's Test using the function *dunn.test* from the package “dunn.test” and “FSA”.

Table 2.5.1. Categories of seafloor impact due to trawling.

Categories	Description
1	Seafloor with no perturbations. No signs of trawling effects.
2	Perceptible trawling marks, probably old trawling marks in recovery.
3	Smoothed door mark from the trawling gear.
4	Flattened seafloor due to the net of the trawling gear.
5	Flattened seafloor with door marks and berming of the muddy sediment.
6	Deeply altered seafloor due to a profound door mark of the trawling gear.

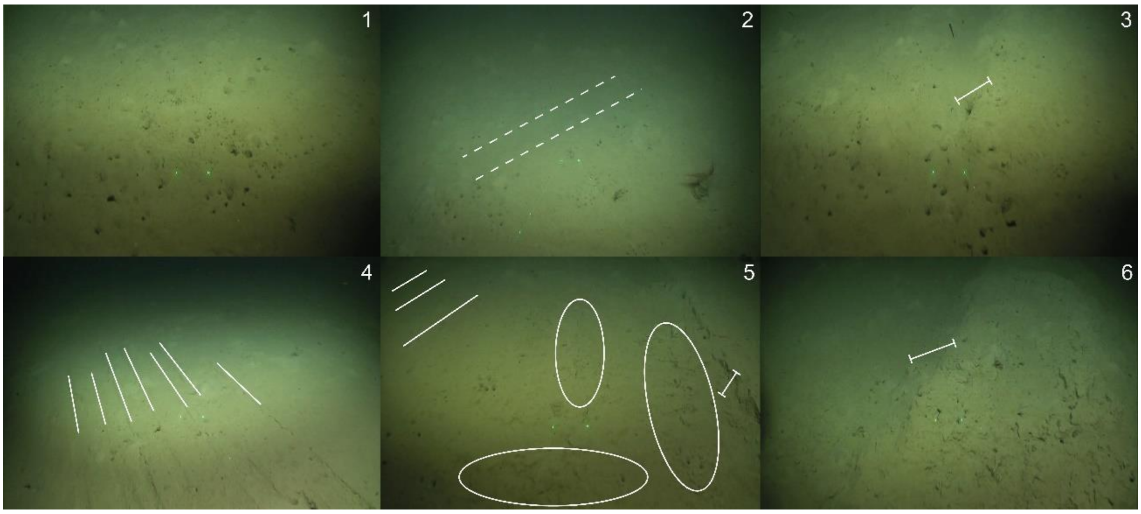

Figure 2.5.3. Trawl mark categories used to evaluate the seafloor state following the descriptions in Table 2.5.1. 1: No signs of trawling effects, 2: perceptible trawling marks, 3: smoothed door marks from trawling gear, 4: flattened seafloor due to the trawling gear net, 5: flattened seafloor with door marks and the berming of muddy sediment, 6: deeply altered seafloor due to deep door marks from trawling gear.

2.5.3. Results

In total, we recorded 72 h in all the ROV surveys, corresponding to a total swept area of 83.82 km^2 (Supplementary Material section Table S2.5.1). We covered a similar time and area in the control area (time = 32 h; area = 40.18 km^2) and the no-take reserve (time = 39 h; area = 43.64 km^2).

Norway lobster evaluation

ROV surveys showed significantly higher numbers of Norway lobsters in the no-take reserve than in the control area, independent of the approach used (burrow-system or animal counting; Figs. 2.5.4–2.5.5). Regarding the abundance of Norway lobster based on burrow-system counting, although the average number of burrows in the no-take reserve (mean = 7513; SD = 2951 No.·km^{-2}) was higher than in the control area (mean = 4411; SD = 3203 No.·km^{-2}), the difference was not statistically significant ($\chi^2 = 3.10$; p = 0.07). With the animal counting approach, during nighttime, we found a similar (Fig. 2.5.4A; $F_{1,6} = 23.22$, p = 0.95) abundance of Norway lobster in both areas (control area; mean = 1022.94; SD = 954.9 No.·km^{-2}; no-take reserve; mean = 1658.47; SD = 1529.01 No.·km^{-2}). In contrast, during daylight hours, we found that the abundance of Norway lobster in the no-take reserve was significantly higher than in the control area (Fig. 2.5.4A; $F_{1,6} = 11.59$, p = 0.002).

In relation to the body size of Norway lobsters, we measured 169 out of a total of 299 individuals detected. Testing for differences in body size (CL in mm), we found that individuals from the no-take reserve were significantly larger than the ones from the control area (Fig. 2.5.4B; control area; mode = 19, SD = 6 mm; no-take reserve; mode = 23, SD = 8 mm; $F_{1,166} = 14.44$, $p < 0.01$). Moreover, larger-sized individuals were found in the no-take reserve (maximum body size of 51 CL in mm) compared to the control area (maximum body size of 35 mm) (Fig. 2.5.4B).

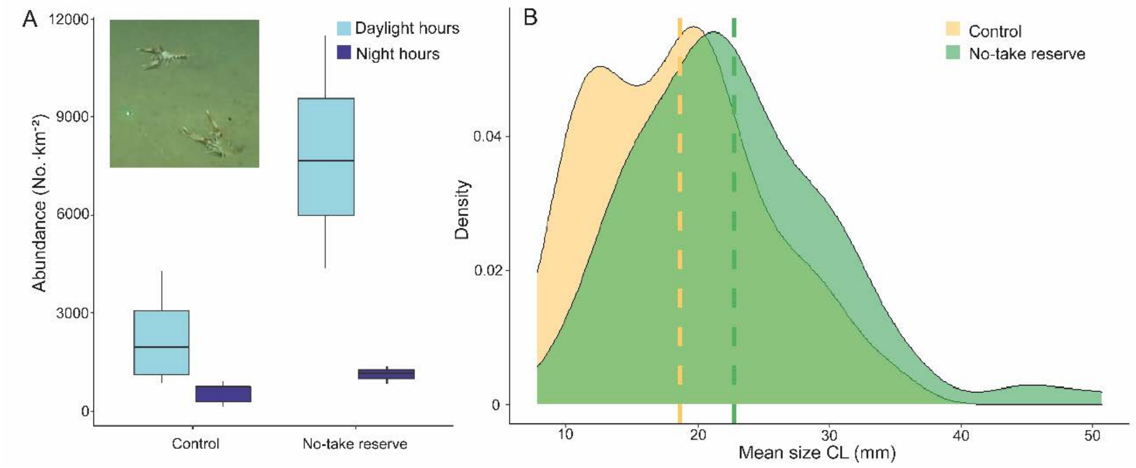

Figure 2.5.4. A) Abundance (animal counting in each transect corrected per the swept area covered) of Norway lobster in the control area and the no-take reserve during daytime and nighttime hours by ROV surveys. The picture shows two individuals of Norway lobster, one outside a burrow and the other inside with only the cephalothorax visible. Box length represents interquartile range, bar length represents range and horizontal lines represent median values. B) Body size distribution of Norway lobsters for the control area and the no-take reserve by ROV surveys. The dashed line represents the individual mean size for each compared area.

The estimated body mass (g) considering all individuals counted in the two areas was lower in the control area (body mass = 5.51 ± 5.76 g) than in the no-take reserve (body mass = 10.21 ± 12.78 g) (Table 2.5.2). Both the burrow-system counting and animal counting approaches showed a higher biomass of Norway lobster in the no-take reserve than in the control area (burrow-system method: $F_{1,11} = 16.88$, $p < 0.01$; animal counting method: $F_{1,18} = 5.14$, $p = 0.03$; Fig. 2.5.5). Nevertheless, we found significant differences between the burrow-system and animal counting methodologies. By using the burrow-system approach, the biomass of Norway lobster in both the control area and the no-take reserve was higher than the biomass estimated with the animal counting approach ($\chi^2_{1,30} = 4.23$, $p = 0.04$; Fig. 2.5.5A). In contrast, the abundance of Norway lobsters did not differ significantly between burrow counting and animal counting approaches ($\chi^2_{1,30} = 3.95$, $p = 0.05$; Fig. 2.5.5B).

Table 2.5.2. Population parameters of Norway lobster in the control area and the no-take reserve based on ROV surveys. Biomass was obtained from the total density and the mean weight of individuals calculated from an allometric model, which considered the mean size (CL) of individuals. Body mass was calculated from the mean body size of each area of study.

	Control	**No-take reserve**
Burrow-systems abundance (No.·km^{-2})	4,411 ± 3,203	7,513 ± 2,951
Individual abundance (No.·km^{-2})	2,227 ± 1,849	4,518 ± 4,248
Body size (CL length, in mm)	19 ± 6	23 ± 8
Body mass (g)	5.51 ± 5.76	10.21 ± 12.78
Biomass from burrow-systems abundance (kg·km^{-2})	28.81± 20.92	91.82 ± 36.06
Biomass from animal abundance (kg·km^{-2})	12.27 ± 9.71	46.13 ± 43.37

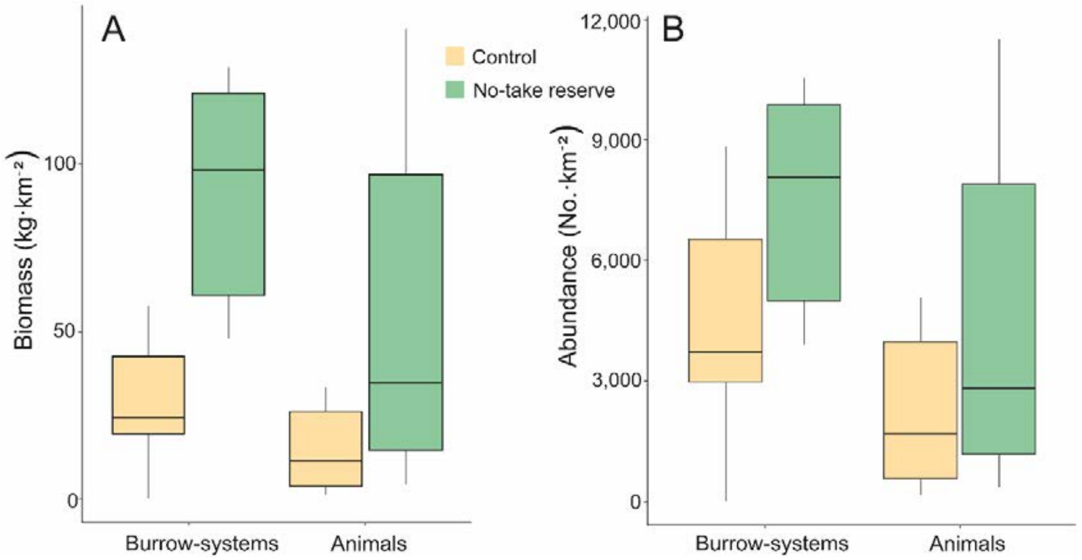

Figure 2.5.5. A) Abundance (counts in each transect corrected per the swept area covered) and B) biomass of Norway lobster calculated with both methodologies (burrow-system counting and animal counting referred in the Figure as "Burrow-systems" and "Animals" respectively) in the no-take reserve and in the control area. Upper and lower 95 % confidence limits are represented by the extent of the vertical bars in the boxplots, indicating the quantiles and the median.

Community megafauna taxa evaluation

We identified a total of 43 taxa from seven major taxa groups: Cephalopoda, Cnidaria, Crustacea, Echinodermata, Elasmobranchii, Porifera, and Teleostei (see Figs. from S2.5.3 to S2.5.9 and Table S2.5.10 of the Supplementary Material section). Diversity indexes showed a similar composition of taxa between the benthic community found in the control area and in the no-take reserve, with Teleostei being the most diverse taxon group in the benthic community followed by Crustacea (Fig. 2.5.6A). The Bray-Curtis matrix of distances obtained from the abundances of the demersal community was represented in a nMDS (Fig. 2.5.6B). The ordination had a relatively low stress value (0.13) and showed no obvious separation of transects between areas, as was corroborated with a PERMANOVA test (pseudo$F_{1,18}$ = 1.61, p = 0.06).

After comparing the abundance of all identified taxa between the control area and the no-take reserve, we found that only the fishes *Helicolenus dactylopterus* and *Trigla lyra*, and the anemones of the Family Cerianthidae, showed higher abundances in the no-take reserve than in the control area (Table 2.5.3; Fig. 2.5.6C). The other recorded taxa did not differ in abundance between the control area and the no-take reserve (Table 2.5.3). In relation to the predators of Norway lobster, we found that their abundance was similar between the control area and the no-take reserve (Table 2.5.3). We did not observe an increase in predators in terms of abundance as a result of the protection provided by the no-take reserve.

The taxa accumulation curves indicated that nearly all taxa were recorded in both areas suggesting a good sampling effort. In the control area, we recorded a total of 40 different taxa, while the Chao estimator was 43, only three more taxa compared with our observations. Similarly, in the no-take reserve, we recorded a total of 43 taxa, while the

Chao estimator was 47. In both cases, the saturation curve was reached at approximately 15–20 h of time effort and the estimator indicated that only 3–4 taxa were unrecorded (Fig. 2.5.6D).

Table 2.5.3. Mean (±SD) of the abundance (No.·km^{-2}) of the megafauna species observed in the control area and the no-take reserve based on ROV surveys. Results of PERMANOVA statistical tests performed are also indicated with the Bonferroni-based adjusted p-values. The predators of Norway lobster based on Vigo et al. (2022) are indicated with a (P). The species that showed significant differences in statistical results are in bold.

Species	Control	No-take reserve	Statistical results
TELEOSTEI			
Arctozenus risso	442 ± 202	487 ± 1	Pseudo-F=0.54 adjusted-p=0.59
Coelorinchus caelorhincus	597 ± 231	397 ± 236	Pseudo-F=1.08 adjusted-p=0.30
Conger conger (P)	837 ± 453	927 ± 425	Pseudo-F=1.19 adjusted-p=0.28
Gadiculus argenteus	456 ± 200	718 ± 520	Pseudo-F=0.06 adjusted-p=0.81
Helicolenus dactylopterus	**280 ± 1**	**2,157 ± 2,954**	**Pseudo-F=23.36 adjusted-p=0.002**
Lepidopus caudatus	407 ± 121	995 ± 834	Pseudo-F=1.49 adjusted-p=0.28
Lepidorhombus boscii	4059 ± 4,040	4,277 ± 1,763	Pseudo-F=1.102 adjusted-p=0.31
Lophius spp. (P)	346 ± 148	241 ± 120	Pseudo-F=2.20 adjusted-p=0.16
Merluccius merluccius (P)	496 ± 628	281 ± 192	Pseudo-F=0.22 adjusted-p=0.86
Micromesistius poutassou	177 ± 56	0	Pseudo-F=2.66 adjusted-p=0.22
Molva macrophthalma	252 ± 80	199 ± 69	Pseudo-F=2.26 adjusted-p=0.17
Family Myctophidae	964 ± 776	538 ± 668	Pseudo-F=1.27 adjusted-p=0.19
Ophichthus rufus	0	138 ± 1	Pseudo-F=1.40 adjusted-p=0.42
Ophisurus serpens	0	166 ± 59	Pseudo-F=3.25 adjusted-p=0.17
Phycis blennoides	2,183 ± 4,144	1,786 ± 929	Pseudo-F=1.25 adjusted-p=0.26
Symphurus nigrescens	272 ± 148	142 ± 4	Pseudo-F=0.12 adjusted-p=0.85
Trigla lyra	**212 ± 78**	**772 ± 427**	Pseudo-F=**5.65** adjusted-**p=0.017**
Trisopterus capelanus	388 ± 290	255 ± 155	Pseudo-F=0.02 adjusted-p=0.83
Unclassified	705 ± 244	386 ± 285	Pseudo-F=0.67 adjusted-p=0.38
ECHINODERMATA			
Astropecten sp.	410 ± 228	363 ± 154	Pseudo-F=0.31 adjusted-p=0.60
Brissopsis lyrifera	391 ± 1	253 ± 166	Pseudo-F=4.31 adjusted-p=0.10
Holothuroidea spp.	1,683 ± 3,097	440 ± 252	Pseudo-F=0.57 adjusted-p=0.54
ELASMOBRANCHS			
Raja spp.	251 ± 1	138 ± 1	Pseudo-F=0.05 adjusted-p=1.00
Scyliorhinus canicula (P)	4,901 ± 3,069	5,678 ± 2,408	Pseudo-F=1.57 adjusted-p=0.23
CEPHALOPODS			
Decapodiformes (P)	342 ± 217	226 ± 165	Pseudo-F=0.92 adjusted-p=0.93
Octopoda (P)	1,496 ± 2,811	365 ± 256	Pseudo-F=0.08 adjusted-p=0.90
Sepiidae (P)	475 ± 435	249 ± 106	Pseudo-F=0.81 adjusted-p=0.52
CNIDARIA			
Arachnanthus oligopodus	16,294 ± 14,046	14,391 ± 10,927	Pseudo-F=1.62 adjusted-p=0.21
Family Cerianthidae	**34,982 ± 23,279**	**63,745 ± 30,532**	**Pseudo-F=4.30** adjusted-**p=0.02**
Funiculina quadrangularis	933 ± 874	1,059 ± 884	Pseudo-F=1.27 adjusted-p=0.22
CRUSTACEA			
Dardanus arrosor	666 ± 163	1,034 ± 755	Pseudo-F=0.05 adjusted-p=0.76
Goneplax rhomboides	731 ± 342	377 ± 247	Pseudo-F=0.39 adjusted-p=0.66
Brachyura	15,206 ± 13,986	12,155 ± 13,639	Pseudo-F=1.01 adjusted-p=0.36
Monodaeus couchii	21,471 ±18,809	13,065 ± 10,831	Pseudo-F=0.72 adjusted-p=0.44
Munida sp.	1,036 ± 754	647 ± 248	Pseudo-F=0.63 adjusted-p=0.38
Family Pandalidae	4,025 ± 3,924	2,921 ± 2,525	Pseudo-F=0.89 adjusted-p=0.91
Parapenaeus longirostris	238 ± 1	317 ± 229	Pseudo-F=4.27 adjusted-p=0.0
Plesionika heterocarpus	2,279 ± 2,047	3,824 ± 2,642	Pseudo-F=1.51 adjusted-p=0.16
Processa sp.	2,642 ± 1,961	2,424 ± 2,079	Pseudo-F=0.07 adjusted-p=0.89
Solenocera membranacea	1,797 ± 2,037	1,023 ± 1,076	Pseudo-F=0.43 adjusted-p=0.65
PORIFERA			
Polymastia spp.	2,023 ± 2,177	2,287 ± 1,838	Pseudo-F=1.59 adjusted-p=0.23

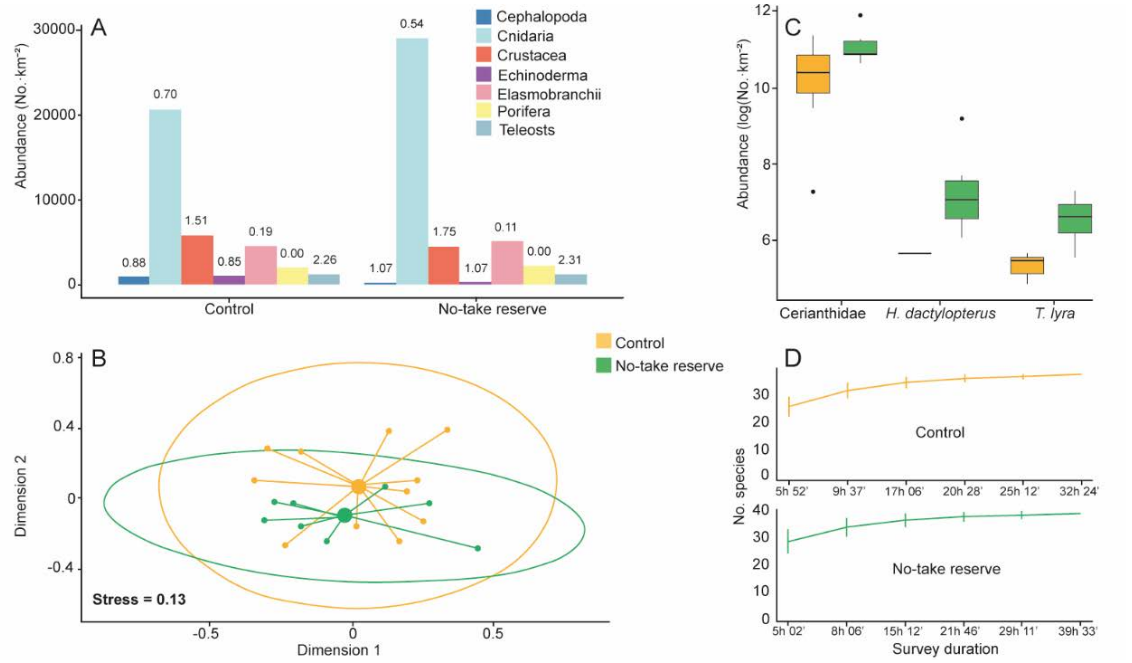

Figure 2.5.6. A) Abundance of all megafauna taxa observed separated into six groups (Cephalopoda, Cnidaria, Crustacea, Echinoderma, Elasmobranchii, Porifera, and Teleostei) indicating the Shannon diversity values from each group in both the no-take reserve and the control area. B) Non-metric multidimensional scaling representation which indicates the similarities in terms of abundance and species composition (counts of all species corrected per the swept area covered in each transect) between the no-take reserve and the control area by overlapping both areas. Ordination ellipses represent 95% confidence, and spiders connect the species composition variability with the centroid of each area, control area (in yellow) and no-take reserve (in green). C) Violin plots representing the densities of Family Cerianthidae, *Helicolenus dactylopterus*, and *Trigla lyra* individuals in the control area (in yellow) and in the no-take reserve (in green). D) Species accumulation curves for the no-take reserve and the control area, the hours accumulated for each transect are also specified. The error bars represent the standard deviation of the accumulation curve.

Marine litter and terrestrial vegetation

The abundance of anthropogenic debris and terrestrial vegetation debris were similar between the control area and the no-take reserve (Fig. 2.5.7A). We did not find significant differences between the control area and the no-take reserve concerning the abundance of anthropogenic debris, ($F_{1,14} = 0.45$, $p = 0.52$), among types of different debris ($F_{3,14} = 0.72$, $p = 0.57$), or the abundance of terrestrial vegetation ($\chi^2 = 0.04$; $p = 0.84$). The diversity of anthropogenic debris was higher in the control area (fishing net, glass, metal, and plastic) than in the no-take reserve (plastic and metal) (Fig. 2.5.7B).

Trawl marks

All ROV video-surveys conducted in the control area showed high percentages of seafloor impacted (Fig. 2.5.8A). In the no-take reserve, more intact patches (Category 1) showed the highest average percentage (97.24 ± 3.61 %), with the rest of the perturbations being < 0.05; $H_{5,72} = 28.27$, $p < 0.05$; $H_{11,72} = 22.29$, $p < 0.05$), indicating the presence of more intact patches (Category 1) in the latter and more deeply ploughed patches

(Category 6) in the former. The only categories of impact that appeared in the no-take reserve were smoothed door marks (1 ± 1.12) and slightly perceptible trawl marks (1.52 ± 2.62) (Fig. 2.5.8).

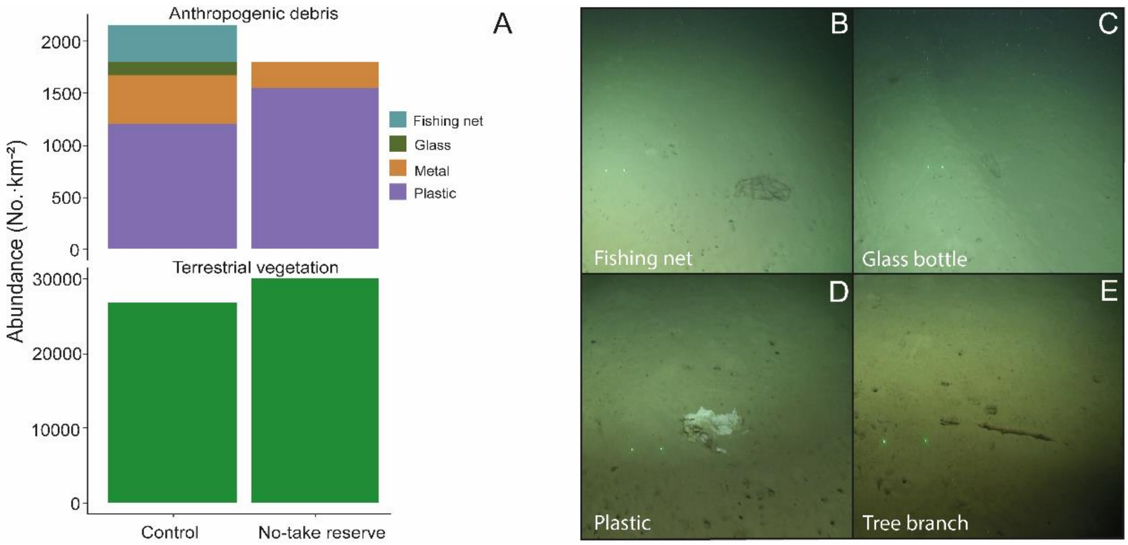

Figure 2.5.7. A) Anthropogenic litter classified as fishing net, glass, plastic, or metal and quantified in both the no-take reserve and the control area; terrestrial vegetation quantified in the control area and the no-take reserve; the plot shows the density of debris from terrestrial vegetation, plastic, and other debris (metal and undefined); examples of B) fishing net, C) glass bottle, D) soft white plastic, and E) tree branch.

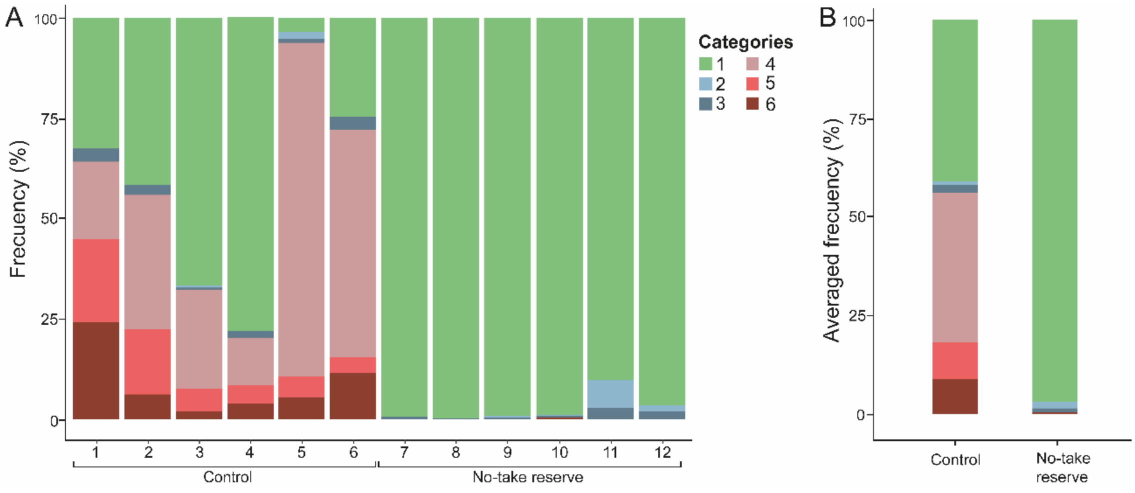

Figure 2.5.8. A) Percentage of trawl mark categories observed via ROV video-survey; B) averaged frequency (%) of trawl mark categories in the control area and the no-take reserve.

2.5.4. Discussion

Here, we investigated the effects of passive ecological recovery of a deep-sea no-take reserve from the western Mediterranean Sea using noninvasive ROV video-surveys. We examined the recovery state of the overexploited Norway lobster stock and assessed how their densities and biomasses differed in this no-take reserve compared to an adjacent control area in which bottom trawl fisheries operate. The results revealed that in a relatively short period of time (2.5 years) after ceasing trawling activity, the Norway lobster population showed higher abundance, biomass, and larger mean individual size in the no-take area than in the control area. Moreover, we also found that some community species, such as the Teleostei *H. dactylopterus* and *T. lyra* and sessile marine species from the family Cerianthidae, were more abundant in number inside the no-take reserve. We also observed how trawling marks on the seafloor in the no-take reserve were nearly absent.

Norway lobster recovery

The recovery of overexploited stocks of Norway lobster has been suggested to take between four to six years (Sardà et al., 1998) and some habitats may require at least 10 years to detect signals of recovery (McClanahan and Mangi, 2000). Here, after only 2.5 years, we found that the population of this crustacean in the no-take reserve was recovered in comparison with the control trawled area. This result suggests that MPAs may offer quick benefits in locations near fishing grounds where fishing mortality is elevated and stocks are below sustainable fishing levels (Halpern, 2003; Hart, 2006), corroborating the fact that the Norway lobster stock is being highly overexploited in the study area (Sardà, 1998; Field et al., 2006). The recovery rate of this species depends upon the rate of successful recruitment (Sardà, 1998a). Since small juvenile Norway lobsters remain hidden inside burrows during the first year of life (Powell and Eriksson, 2013; Tuck et al., 1994), the present study refers to the population after their first year of life, or those individuals that already exhibit burrow emergence behaviour.

In the last few decades, UWTV surveys have become the primary assessment method used by the WGNEPS focusing on burrow counting, as they are static and relatively constant (Sardà and Aguzzi, 2012; Bell et al., 2018). However, the burrow counting method has uncertainties such as the persistence of empty burrows or exclusion from tunnel occupation by other fish and crustacean species that maintain its structural integrity (Aguzzi et al., 2021). To address this issue, we foresaw an opportunity to improve current stock assessment methods by applying two different approaches to estimate stock abundance and biomass, namely “burrow-system counting” and “animal counting”, which showed contrasting results. With the burrow-system approach, we observed similar abundances in the control area and the no-take reserve. Therefore, similar counts in both areas demonstrate that burrows can resist trawling, indicating equivalent numbers/densities of remaining individuals that rebuild the burrow systems after trawling disturbance, assuming that all are occupied only by Norway lobsters, as other species may opportunistically occupy and maintain Norway lobster tunnels (reviewed by Sardà and Aguzzi, 2012). Considering that juveniles initially occupy burrows linked to those of adults (Chapman, 1980; Tuck et al., 1994), the maintenance of high burrow densities could indicate a suitable habitat for good recruitment (Chapman and Howard, 1988; Johnson et al., 2013). Nonetheless, tunnel counts present several levels of uncertainty. Burrows can offer some protection from trawling; however, intense impacts on burrows destroy system integrity (Hiddink et al., 2006; Tillin et al., 2006). We did not measure the size and shape of burrow systems, although we generally noticed that burrow systems from the control area were more flattened and without the muddy mounds characteristic of well-structured systems in the no-take reserve (Supplementary Material section, Fig. S2.5.2). In addition, the stability of burrow systems per se also depends on the composition of the sediment in relation to currents (Campbell et al., 2009). In our case, differences in both habitat variables were not studied (as currents were not measured), since both surveyed areas are just small parcels of a much larger and homogenous slope area (Send et al., 1999; Palanques et al., 2005). In this scenario, we did not observe species other than Norway lobster close to tunnel system entrances in either area. Norway lobster juveniles usually occupy burrows already created by adults to avoid predation (Chapman, 1980).

Here, we suggest a complementary and more reliable approach to counting all individuals of Norway lobster, classifying them according to their activity, as an alternative method of ICES stock assessment by UWTV surveys (Bell et al., 2018). This approach expanded on the results of animal density in relation to behavioral rhythms obtained through UWTV surveys in shallower areas of the Atlantic Ocean (Aguzzi et al., 2021). In regard to the day-night activity of Norway lobsters in deep-sea waters, we observed the limited presence of visible individuals during the night, corroborating how the locomotor activity of Norway lobsters that inhabit deep ecosystems below 300 m in depth is predominant during daylight hours (Aguzzi et al., 2003; Vigo et al., 2021). This result confirms that any video-based fishery-independent assessment of species along the continental slope should be carefully centered on daytime hours to better capture visible animals and to perform their count for calibration with counting burrow systems (Aguzzi et al., 2021).

The abundance of Norway lobster was higher in the no-take reserve compared to the control area. However, we only noticed this significant increase during daylight hours, whereas at night the abundance of Norway lobster was similar: very scarce in both the control area and the no-take reserve. This fact can be explained by their burrowing behaviour, which indicates that the demographic indicators of this species should be evaluated according to their activity patterns which depend on optimum environmental light conditions (Chapman and Rice, 1971). The class-size distribution of the no-take reserve showed a higher mode size with larger sizes absent in the control area. We expect that the ranges of body size distribution and mode will increase in the no-take reserve, proportionally to the years of protection at a relatively fast pace (Babcock et al., 2007; Lester et al., 2009; Moland et al., 2013). It is important to highlight that before the closure, the body size distribution of Norway lobster was similar in both no-take reserve and control area (Fig. 2.5.2). However, a long-term monitoring for demographic assessment is crucial to observe these beneficial size shifts in the no-take reserve in comparison to adjacent areas.

Total biomass reflects both size and abundance, resulting in a robust measure for MPA protection (Lester et al., 2009; Soykan and Lewison, 2015). In some cases, MPAs have only a detectable biomass response, and not an abundance response, due to the low pre-MPA harvest of some species or high variability in recruitment (Kaplan et al., 2019). Biomass can increase much more quickly than abundance as a result of the low mortality of older and larger-sized individuals. On the other hand, if biomass is low, but abundance is still high, an increase in recruitment into the area could be indicated (Nalepa et al., 2010). Estimating this demographic variable through mean body size as calculated in the two approaches (i.e., burrow-system and animal counts) indicates how in both cases biomass was higher in the no-take reserve. All the evaluated variables (i.e., abundance, mean body size, and biomass) reflected the positive effects of passive restoration in the no-take reserve. We found the species in the no-take area showed a rapid response to protection from fishing and that it may asymptotically increase until reaching carrying capacity over the years as long as this protection measure lasts. Comparing both counting methods, burrow-system and animal counts, we recommend the second approach as it provides more accurate information.

Community megafauna taxa recovery

The number of megafauna taxa detected showed similar values in both areas, with a total of 43 and 40 taxa in the no-take reserve and control area, respectively. The ROV video-surveys may not have been able to detect all species of the benthic community, as many different behavioral reactions to ROV presence occur, from stillness to active avoidance (see behavioral classifications in Lorance and Trenkel, 2006; Ayma et al., 2016). We found that two Teleostei species, *H. dactylopterus* and *T. lyra*, showed higher abundance in the no-take reserve than in the control area. These species are commercialized by Norway lobster fishers and therefore may also benefit Norway lobster fisheries outside the reserve. The anemones from the family Cerianthidae that can retract when the gear of bottom trawl fisheries approaches (Hall-Spencer, 1999) may still be vulnerable to trawling impacts (Kenchington et al., 2006). In our study, these species were abundant in both areas although they also showed a higher abundance in the no-take reserve than in the control area.

Sessile species increase the roughness of mud plains and thus can accelerate the restoration of seabed quality by trapping drifting sediment (Buhl-Mortensen et al., 2010; Grinyó et al., 2020). The anemones from the Cerianthidae family may act as a refuge for other species, such as demersal fishes and crustaceans (Shepard et al., 1986). In fact, we observed the copresence of *H. dactylopterus* and *Munida* spp. with these anemones, indicating higher abundances of both species within the family Cerianthidae patches as previously reported in other areas (Uzmann et al., 1977; Valentine et al., 1980; Auster et al., 2003). The greater abundance of anemones in the no-take reserve could offer more refuges against predation to other fish and decapod crustacean species, resulting in their increased abundance, as reported here for *H. dactylopterus* and also by Grinyó et al. (2020) in the Alboran Sea. Thus, *H. dactylopterus* and *T. lyra* could be defined as key indicators of the effectiveness of a no-take habitat established in Norway lobster grounds, as they are very sensitive to trawling, presenting significant increases in only a short time due to the protection of the no-take reserve. For the remaining species with depleted stocks due to fishing activity, we may likely observe benefits with additional protection (e.g., for species with low fecundity rates and high maturity ages) (Nickols et al., 2019). However, other species may not exhibit benefits because of the small size of the reserve that was designed for the Norway lobster, a crustacean that uses a reduced spatial area (Vigo et al., 2021).

Some MPA assessments consider the species interactions involved, such as predator-prey interactions, evaluating predator densities and biomasses. This approach is crucial even in small MPAs as an incremental shift in predator densities could halt the recovery of an overexploited species and even undermine it (Clements and Hay, 2017), while a lack of predators could also lead to permanent habitat regime shifts (Daskalov et al., 2007). The predators of Norway lobster (Vigo et al., 2022) observed in this study did not present an increase in abundance in the no-take reserve, apparently not influencing the dynamics of their prey, at least during these first years of protection. This result re-enforces the use of reserves as a tool to preserve Norway lobsters compared to the European spiny lobster (*Palinurus elephas*), where juveniles were highly predated by fishes in the MPA (Díaz et al., 2005). One of the success in recovery on Norway lobsters versus the European spiny lobster could be the different habitat, muddy versus rocky substrates. Establishing a network of small no-take reserves should be considered as an effective management tool for fishery conservation of Norway lobster stocks.

Accumulation curves indicate the effectiveness of the monitoring effort, here in terms of hours of video observation. To avoid taxa underrepresentation in video-based monitoring in NW Mediterranean, we suggest that the minimum ROV video recording time for continental slope, muddy bottom Norway lobster grounds should be 20 h, as indicated by the taxa accumulation curves in the present study. This monitoring indicator, estimated along with data collection during both the daytime and nighttime, could facilitate the monitoring of sessile and motile megafauna in MPAs under restoration.

Marine litter, terrestrial vegetation, and seafloor recovery

Marine litter and terrestrial vegetation are present in all marine habitats, even in the most remote habitats of the ocean (Pham et al., 2014). We found similar densities between the control area and the no-take reserve in both marine litter and terrestrial vegetation. Most of the marine litter found was plastic, the most abundant form of marine debris, rising globally and with documented impacts on marine ecosystems (Sheavly and Register, 2007; Mecho et al., 2021). In the control area, we also observed fishing nets likely due to recent fishing activities (Galgani et al., 2000; Vieira et al., 2015), which also constitute a major problem as they can cause high fish mortality as a result of “ghost fishing” (Brown and Macfadyen, 2007). Even if trawl fisheries contribute to the removal or displacement of marine litter and terrestrial vegetation, they continuously enter from terrestrial habitats, ships, and other installations at sea. Enclosed areas such as the Mediterranean Sea exhibit some of the highest densities of marine litter (Galgani et al., 2015). The absence of trawling in the no-take reserve did not lead to more accumulation of marine litter nor terrestrial vegetation, as all this debris is continuously distributed, due to hydrography and geomorphological factors of the ocean (Galgani et al., 2000; Barnes et al., 2009), to hotspots of litter accumulation that include shores and the deepest areas in submarine canyons (Corcoran et al., 2009; Pham et al., 2014).

Trawling exerted above the maximum sustainable yield (i.e., overfishing) not only causes stock depletion, but also generates seafloor morphological changes, nutrient cycle alterations, sediment resuspension, and increased bottom-water turbidity (Tillin et al., 2006; Puig et al., 2012; Pusceddu et al., 2014). Here, we reported how the establishment of a no-take reserve helped to recover nearly the full extent of the area from trawling marks in a relatively short time following the termination of this activity. All surveys performed in the no-take reserve indicated only 5% of the seafloor was altered by trawling marks, with smoother marks already in the process of recovery. In contrast, the control area exhibited >60% of the seafloor impacted, presenting all categories of trawl marks. The muddy grounds of Norway lobster seem to rapidly recover when trawling fishery activity is stopped. The high density of Norway lobster and other burrowing species such as *Munida* spp. and *Goneplax rhomboides* can produce high bioturbation activity that could also be responsible for surface sediment mixing (to 5–20 cm sediment depth), thereby contributing to the rapid erasure of trawl marks in the no-take reserve (Schwinghamer et al., 1998; Mengual et al., 2016; Mérillet et al., 2018). Nevertheless, although they were not measured in the present study, we believe that the main factors that may be involved in the fast recovery from trawling marks in this area are hydrodynamic parameters such as tidal currents, natural sedimentation, and the deposition of suspended sediments (Linnane et al., 2000; Friedlander et al., 1999). The seafloor state, as we defined it, is a good indicator for measuring the passive restoration of a habitat from trawling. Intermediate approaches to fish stock recovery such as seasonal closure areas may represent too short a time span for the recovery of seafloor habitats (Smith et al., 2000; Demestre et al., 2008).

2.5.5. Conclusions

The recovery of overexploited Norway lobster populations and habitats may benefit from applying a passive habitat restoration approach based on total closure of areas for fishing activities. No-take deep-sea reserves require prolonged monitoring that may help to identify potential density dependent effects on Norway lobster populations in the long-term, inducing an increase in the competition for space. On the basis of our results, we propose establishing a network of small no-take reserves focused on recovering Norway lobster stocks as an effective management tool for fishery conservation, obtaining relatively rapid gains over the cost of closing fished areas. We also suggest the use of ROVs for monitoring marine reserves as an innovative and non-invasive method for evaluating the ecology and seafloor status. Focusing on target species of commercial interest could make the present monitoring procedure feasible in other deep-sea no-take areas worldwide.

CRediT authorship contribution statement

Maria Vigo- data collection, methodology, formal analysis, investigation, writing. Joan Navarro- conceptualization, data collection, investigation, validation, writing. Jacopo Aguzzi- data collection, investigation, validation, writing. Nixon Bahamón- data collection, formal analysis, review & editing. José Antonio García- data collection, programming, review & editing. Guiomar Rotllant- data collection, review & editing. Laura Recasens- data collection, review & editing. Joan B. Company- conceptualization, data collection, investigation, validation, writing.

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Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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2.6. Dynamic marine spatial planning for conservation and fisheries benefits.

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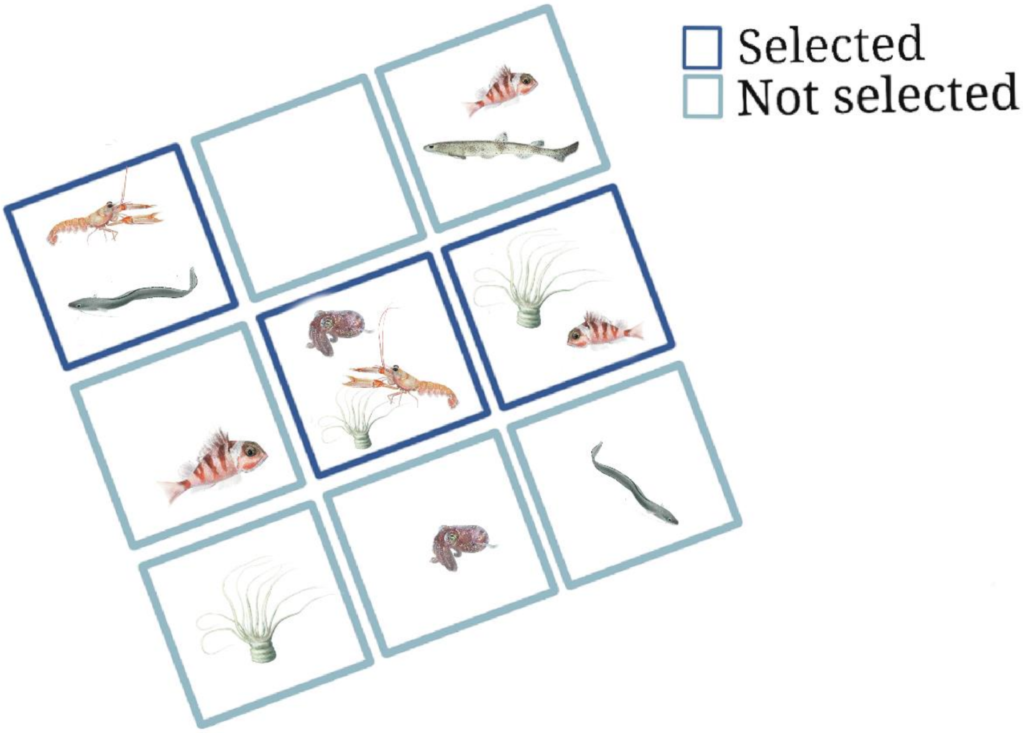

Under Review. Fish and Fisheries Journal.

Abstract

The increasing global demand for marine resources raises concerns about sustainable resource management and biodiversity preservation. Spatial closures, such as marine protected areas, can be useful tools for restoring and maintaining exploited populations. These spatial closures are usually static and do not consider factors like shifting patterns in species distributions, economic and social objectives, and changing environmental factors. Here, we used a conservation planning decision-support tool (the software *Marxan*) to compare the outputs of a static network of permanent no-take fishery reserves with other four dynamic scenarios, including both permanent and temporal closures that account for seasonal variations in species' populations. All scenarios prioritized the conservation of one of the most valuable European fishing stocks, the overexploited deep-sea populations of the Norway lobster (*Nephrops norvegicus*). Additionally, we considered another 12 species inhabiting the same ecosystem, that are also targeted by the Norway lobster fishery. To compare scenarios, we assessed retained biomass, area coverage, closure types (permanent and temporal), and opportunity costs within each no-take reserve network. We observed that all dynamic scenarios required a greater number of protected areas associated with a larger total area (corresponding to temporal and permanent closures) than the static scenario, but at a lower cost for fisheries and with a higher capacity for biodiversity conservation. We suggest that complementing the permanent closures with temporal closures could improve fisheries management benefiting both biodiversity conservation and fisheries. The novel dynamic planning method presented herein is transferable to various species, ecosystems and socio-economic contexts.

Keywords: dynamic planning, fisheries management, marine spatial planning, Marxan software, no-take marine reserves, temporal closures.

2.6.1. Introduction

The global consumption of marine resources has increased significantly in recent years. By 2020, it reached a record of 214 million tonnes and provided 20 kg per capita for human consumption, doubling the global consumption reported in the 1960s (FAO, 2022). While marine resources are so crucial for humans, fishing activity is one of the most damaging stressors for marine biodiversity, which, along with other human disturbances (e.g. pollution, introduction of invasive species), triggers the decline of populations and even the complete degradation of some marine species and habitats (Costanza et al., 2017; Díaz et al., 2019; Rousseau et al., 2019). Overfishing has also adversely affected ecosystem functions and the capacity of ecosystems to provide ecosystem services that are necessary for human well-being (Worm et al., 2006; Halpern et al., 2015; McQuatters-Gollop et al., 2022). Moreover, nowadays the fraction of fishing stocks within biologically unsustainable levels is increasing worldwide (FAO, 2022), raising concerns about the reversibility of overfishing effects and the effectiveness of fisheries management (Myers and Worm, 2003; Pauly, 2013).

As an important part of fishing management, technical regulations have been implemented to preserve fishery stocks, including catching limits, gear regulations, fishing selectivity improvements, local and regional co-management plans, as well as biological scientific advice to restrict some species to minimum conservation reference size (Sardà, 1998a; Sánchez Lizaso et al., 2020). Even though some fisheries have succeeded in achieving broad and sustainable fisheries (Beddington et al., 2007), many marine resources are still at overexploited levels (Cardinale et al., 2017). For some particular fisheries, such as multispecies fisheries, catch and effort limitations may be poor management tools as they land many species due to bycatch and discard many more (Hilborn et al., 2004). Inefficient fisheries management results from poor fishing regulations, weak enforcement, and lack of relevant biological knowledge (Beddington et al., 2007; Petter Johnsen and Eliasen, 2011). For this reason, there is an urgent need to identify effective management strategies to achieve sustainable fisheries that can protect marine biodiversity for both conservation and fisheries goals (Jupiter et al., 2017).

Spatial closures, such as marine protected areas (MPAs), have often proved to be an effective measure for restoring overexploited fishery stocks and for achieving a sustainable fishery and biodiversity conservation (Abesamis and Russ, 2005; Di Franco et al., 2016; Giakoumi et al., 2017). Empirical evidence shows that the density, biomass, and individual body size of overexploited species increase in well-enforced and effective MPAs, especially in no-take marine reserves where all extractive uses are banned (Linares et al., 2012; Sala and Giakoumi, 2018; Vigo et al., 2023). An example of the benefits of MPAs to fisheries occurs when the biomass enhanced inside the reserve is exported beyond the protected boundaries, achieved through the dispersal of adults, larvae, or eggs outward from the MPA (Manel et al., 2019; Marshall et al., 2019; Di Lorenzo et al., 2020). As a complement or alternative to existing MPAs, temporal closures (e.g. seasonal closures) can potentially preserve biodiversity and sustain fisheries in a similar way, and in some instances have even greater effects than permanent closures (Garcia, 1986;

Hilborn et al., 2004). The enforcement of temporal closures can reduce conflict with local users, especially fishers, compared to the enforcement of permanent closure areas. Moreover, temporal closures can be implemented at the appropriate time of the year for sensitive species in fisheries (e.g. to protect juveniles or reproductive individuals), addressing simultaneously ecological, economic, and social objectives (Hobday et al., 2013; Lewison et al., 2015).

Designing networks of effective MPAs while minimizing negative impacts on fisheries (e.g. through relocation of fishing activity) is a challenge. However, this can be achieved using systematic conservation planning approaches (Margules and Pressey 2000; Possingham et al., 2006) and optimization decision-support tools (e.g., Giakoumi et al. 2011; Giménez et al., 2020). Commonly, the planning solutions derived from spatial prioritization studies using optimization algorithms define closures that are static and considered permanent closures. According to some studies, dynamic management measures could address more efficiently the targets of fisheries and conservation, especially in dynamic marine environments such as pelagic ecosystems (Grantham et al., 2008; Dunn et al., 2016). In dynamic management approaches, fishing closures are adapted to actual biological, oceanographic, social, or economic conditions and the shifting nature of oceans and species (Maxwell et al., 2015).

In this study, we examined and compared different approaches for designing a network of permanent and temporal closures to achieve both conservation and a sustainable multi-specific deep-water fishery. Specifically, our primary target is one of the most valuable European fishing stocks, the Norway lobster (*Nephrops norvegicus*), whose population has been declining in the Mediterranean Sea, possibly due to overfishing (Vigo et al., 2023). Thus, we aimed to examine the biomass retained in the selected reserves, the coverage of the area and the types of closures selected (permanent and the temporal), the opportunity costs generated (i.e. fishing profits that are forgone when fishing is banned in an area) and trade-offs of these variables between different scenarios that depict alternative management options. These scenarios range from a more traditional no-take marine reserve planning approach based on permanent closures, to a combination of permanent marine reserves and priority areas for temporal closures. For this, we present different scenarios using different types of dynamic management measures that differ in temporal and spatial connectivity and follow a different set of conservation targets in accordance with the species' biological characteristics. Our results provide guidance to practitioners on how to address the management of multiple and conflicting objectives, such as biodiversity conservation and fishing stocks maintenance, in an optimal way in other marine environments or elsewhere, such as terrestrial and freshwater environments.

2.6.2. Material and Methods

Study area

This study was conducted in the northwestern Mediterranean Sea, along the Catalan coast (Balearic Sea) of Spain (GSA06; Fig. 2.6.1A). In this region, Norway lobster fishing grounds consists of muddy habitats mainly found between 300 to 500 m deep on the upper and middle slope of the continental margin, intersected by submarine canyons. The planning region - the spatial domain over which the planning process occurs - was delimited by bathymetric boundaries from 50 m to 800 m depth, covering the depth range at which commercial fisheries (e.g. bottom trawlers, longliners, purse-seiners) are allowed in the Mediterranean Sea (BOE No. 154, 28/06/2022). Approximately 11,720 km^2 were covered, and there were 1530 regular square gridded units referred to as planning units (PUs) (Fig. 2.6.1B). PUs were about 9 km^2 following the size design of a pilot no-take fishery reserve focused on restoring the Norway lobster population in the study area (Vigo et al., 2020; 2023).This no-take fishery reserve was established in 2020 by the Spanish Government (Order APA/753/2020; www.boe.es/eli/es/o/2020/07/31/apa753), but fishing activity had already ceased in 2017 through an agreement between the two local fishery associations (Roses and Palamós). To incorporate the existing permanent no-take fishery reserves in the area, which span approximately 500 km^2 of the Catalan Sea, we locked in the PUs in the grid that overlapped at least 25% of their area with a no-take fishery reserve. As a result, a total area of 748.61 km^2 within the planning region was designated already existing no-take fishery reserves (Fig. 2.6.1).

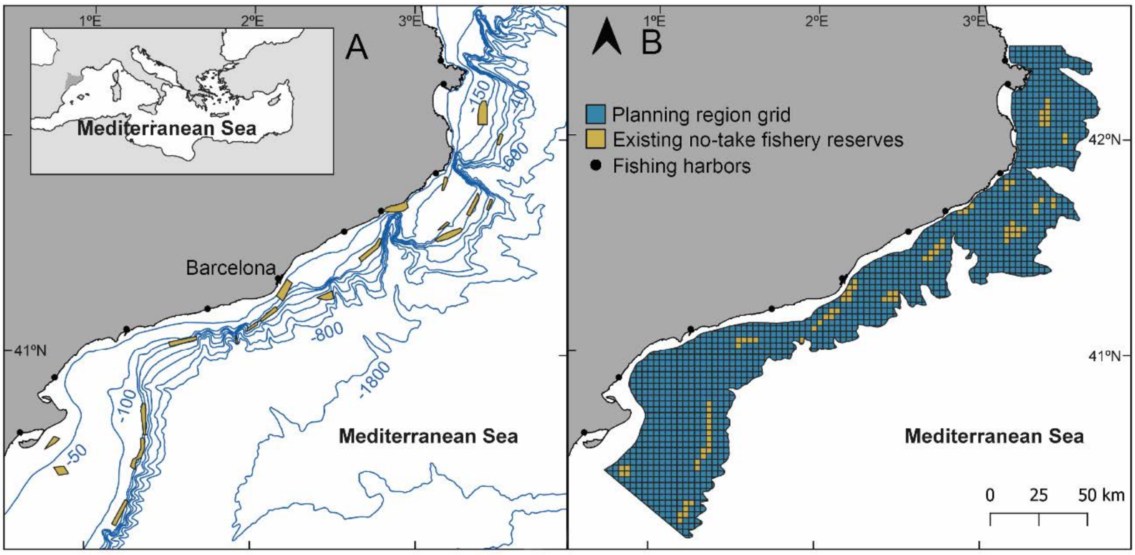

Figure 2.6.1. Study area in the northwestern Mediterranean Sea (north of the geographical region GSA06, established by the General Fisheries Commission for the Mediterranean). A) Bathymetry profile of the study area and the existing no-take fishery reserves (in yellow color). B) Planning region covering 11719 km^2, the grid consisting of 1530 planning units (PUs) of 9 km^2 (3 x 3 km) each one (in dark blue), and the already existing no-take fishery reserves (in sand color) that close around 748 km^2 of the planning region.

Biological data and opportunity costs

We combined trawling fleet Vessel Monitoring System (VMS) information and official daily landing data to estimate the monthly spatial distribution of the Norway lobster biomass and other 12 demersal species that inhabit on Norway lobster grounds and are also highly impacted by fisheries by-catch and discards from years 2017 to 2021. The 12 demersal species were the Teleostei argentine (*Argentinidae* spp.), blackbelly rosefish (*Helicolenus dactylopterus*), megrim (*Lepidorhombus* spp.), anglerfish (*Lophius* spp.), European hake (*Merluccius merluccius*), blue whiting (*Micromesistius potassou*), forkbeard (*Phycis* spp.), gunards (Triglidae spp.), the Cephalopoda horned octopus (*Eledone cirrhosa*), bobtails (*Sepietta* spp.), other variety of squids including species such as the European flying squid (*Todarodes saggitatus*), and the Crustacea deepwater pink shrimp (*Parapenaeus longirostris*). Landings were standardised by fishing effort (hours of fishing activity per area) and averaged yearly and seasonally to produce more robust planning solutions (see García-Barón et al., 2021).

The opportunity cost of selecting areas for protection was represented by the total fisheries income (in €) spatially distributed by combining VMS information and official daily landing data for all trawled and landed fish species per month and market prices from 2017 to 2021 in the planning region.

Spatial prioritization scenarios

We used the conservation planning software Marxan (Ball et al., 2009) to identify priority conservation and cost-effective areas to recover Norway lobster population and coexisting selected species while minimizing the impact of protection on fisheries (i.e. minimizing the forgone income from banning fishing in an area). Marxan uses a simulated annealing algorithm to find near optimal solutions to the minimum set. It includes some basic spatial properties of a protected area system such as geographic proximity or adjacency information (boundary) between every pair of PUs to help maximize clumping of a protected area system. Therefore, Marxan's mathematical formulation is as follows:

$$\text{minimize } \sum_{i}^{Ns} x_i c_i + b \sum_{i}^{Ns} \sum_{h}^{Ns} x_i (1 - x_h)\, cv_{ih} \tag{1}$$

where N is the number of PUs, x_i is a control variable which has the value of 1 for selected sites and 0 for unselected sites, c_i is the cost of the PU i, and cv_{ih} represents the length of the boundary between PU i and h, assuming that the larger the boundary shared by two PU, the stronger the connection between those PU. This parameter is weighted by b, the boundary length modifier (BLM). The previous formulation is subject to the constraint that all the representation targets are met:

$$\sum_{i}^{Nf} x_i r_{ij} \geq T_j \,\forall j \tag{2}$$

where r_{ij} is the amount of feature j in PU i and T_j are the conservation targets, which are the minimum amount or percentage of the conservation feature (e.g., species, habitat) within the planning region that must be included in the solution.

In this study, we compared a static scenario with permanent closures (hereafter scenario 1), in which the PUs selected by MARXAN are allocated similarly to MPAs, with other scenarios based on a dynamic management approach applying different strategies by prioritising the allocation of both permanent and temporal closures respectively (Fig. 2.6.2). All scenarios are planned to use the spatial distribution of the 13 taxa (conservation features) per month as well as the total fisheries income (opportunity cost) generated per month from 2017 to 2021.

For scenario 1, we summed up the monthly data to obtain an annual average from the period 2017-2021, and we translated the 13 taxa distribution and the fisheries income into our square gridded PUs. We also built a boundary file to include the connectivity between PUs and achieve spatially clumped solutions. Connections between PUs were measured as the boundary shared by contiguous PUs (3000 m in our case) as indicated in the previous equation with the parameter v. The BLM was calibrated for all scenarios with the value 0.2. We set different conservation targets (as a % of their biomass distribution) for each species: for the Norway lobster was 40%, while for the other co-existent megafauna species was 20%. The higher conservation target for Norway lobsters was formulated to reflect the priority of conserving this species, which is the principal species aimed at recovering from its overexploited status in the area. The 20% target for the other species was chosen as a representative percentage, as a baseline for including all species of equal importance within the conservation framework and aligning with recommendations from the 2002 Earth Summit (IUCN World Parks Congress, 2003; Morfin et al., 2016; Pasnin et al., 2016).

Scenario 2 simulates a more flexible regime of fisheries exploitation and closures, structured in four periods following seasonal variability in both opportunity cost and spatial biomass distribution of taxa. The main difference between scenarios 1 and 2 laid in that under scenario 1 we planned for a single time frame (whole year), while under scenario 2, we planned for each season individually. We summed up the data per season from 2017 to 2021 and we obtained the seasonal average of the 13 taxa distribution and the fisheries income. Therefore, in scenario 2, a decision on closing to fisheries a particular PU could be done for a particular season individually. To do this, we pseudo replicated each PU, so each original unit was split into four, one for each season, which resulted in 6,120 planning units (1,530 units x 4 seasons). We then translated all seasonal taxa distribution and fishery incomes for each of those seasons individually, so each original planning unit had four replicates of conservation features distributions (52 conservation features; 13 taxa per four seasons) and cost (four seasonal opportunity costs reflecting seasonal changes in opportunity cost at each PU). We set the same conservation targets as in scenario 1 for each season. To account for spatial-temporal connectivity, we adapted the boundary file described in scenario 1 to consider not only geographical proximity between planning units from the same season, but also temporal proximity among planning units from different seasons. For this, we replicated the spatial boundary file described above for each season individually. To account for seasonal connectivity, that is connectivity between seasonal pseudo replicates of each PU, we connected each PU to its temporal replicate. So finally, the spatial-temporal boundary file was a combination of the four individual spatial boundary files (one per season) and the temporal boundary file.

In scenario 3, we applied the same seasonal approach described for scenario 2 but also modifying the magnitude of the connectivity values between the most critical seasons for the Norway lobster, i.e. winter and summer. We prioritised these seasons according to the Norway lobster biology, winter becoming the hatching period in which berried females come out from their burrows releasing their eggs (Aguzzi et al., 2003), and summer where there is the spawning period (Rotllant et al., 2005). By doing this, we aimed to ensure adequate management during the most relevant seasons by closing the same spatially located PUs in both winter and summer. Conservation targets were constant values as the ones set in scenario 2.

Scenarios 4 and 5 were modifications of scenarios 2 and 3, respectively. However, in both scenarios, we changed conservation targets of the target species depending on the season. We adjusted the conservation target only for the Norway lobster, maintaining 40% target in the critical seasons of winter and summer, but reducing it to 20% in spring and autumn.

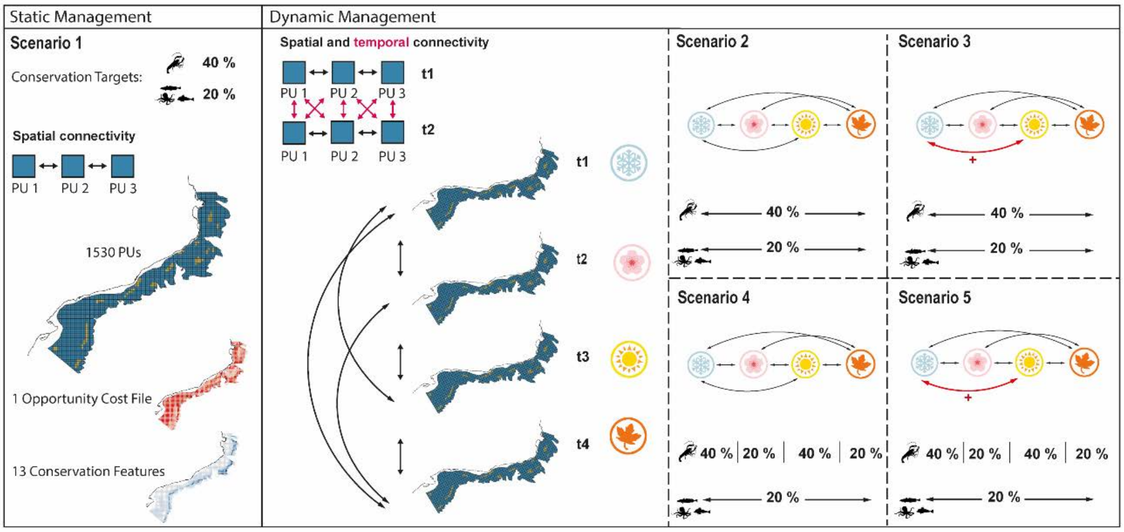

Figure 2.6.2. Scenarios of the different management strategies. The static Scenario, scenario 1, selects permanent no-take fishery reserves, using 1 opportunity cost file, 13 conservation features and 1530 planning units (PUs). Conservation targets are 0.40 for Norway lobsters, and 0.20 for the rest of the taxa. All dynamic management scenarios are split into 4 seasons, using 4 opportunity cost files, 13 conservation features per season, and 6120 PUs. There are 4 different dynamic scenarios: scenario 2, dynamic management selecting PUs seasonally; scenario 3, dynamic management selecting PUs seasonally increasing connectivity values between winter and summer; scenario 4, dynamic management selecting PUs seasonally modifying conservation targets for the Norway lobster over seasons; scenario 5, dynamic management selecting PUs seasonally modifying conservation targets for the Norway lobster and increasing connectivity values between winter and summer.

We run Marxan 100 times per scenario. We retained the best solution out of those 100 runs and the selection frequency of each planning for subsequent analyses, providing different information. The best solution is the solution with the lowest Marxan score (i.e., the most efficient solution), which is rather considered as a very good solution within a continuum of other options. The selection frequency represents the number of times a PU that was selected across the 100 Marxan solutions, and it is used as a proxy for PUs irreplaceability and to identify conservation priority areas (Stewart & Possingham, 2005). A high selection frequency for a PU designates it as a conservation priority area, while a low selection frequency suggests it is more replaceable, which is particularly useful when comparing differences between scenarios (e.g., Carwadine et al., 2008).

Spatial similarity among scenarios

To compare solutions among management scenarios, we calculated the extent of the area selected and the percentage of coverage over the total planning region. By using the best solution generated from each scenario, we were able to observe which of the scenarios had the greater extent at the least cost. We also calculated the area selected for each temporal closure (permanent, 3 seasons of closure, 2 seasons of closure, 1 season of closure).

We compared the similarity of the spatial distribution across scenarios. First, we tested the overlap of the PUs among scenarios best solutions using a pairwise statistic, the Cohen’s kappa coefficient (Landis and Koch, 1977). The values of this statistic range from -1 to +1, though usually is between 0 and 1, where -1 indicates complete disagreement, 0 indicates agreement no better than expected by chance and +1 indicates complete agreement. We used the “irr” package (Gamer et al., 2019) in the R software version 4.2.1. Secondly, we evaluated the overlap of the selection frequency among scenarios by using Pearson´s correlation by using the “stats” package (R Core Team, 2023). Here, we used the selection frequency of PU in each solution to explore if PUs were selected with the same frequency across scenarios. The values of this correlation coefficient range from -1 to 1 indicating the direction and the strength of the relationship between 2 variables, being stronger closer to -1 or 1 and independent variables closer to 0.

Exploring trade-offs between scenarios and temporal closures

We calculated the global opportunity cost at closing areas to fishing, and the biomass covered under PUs selected for closure, either permanent or temporarily, from all 100 solutions outputs obtained at each scenario and for temporal closures. We explored the emergent trade-offs between the opportunity cost and the biomass covered at each scenario individually due to the extent of the PUs selected and the temporal closures applied in each approach. We calculated these three variables (i.e. area selected, biomass, and opportunity cost). We tested for differences on the mean values obtained between scenarios and temporal closures, by using the non-parametric test of Scheirer Ray-Hare and the post-hoc with Dunn tests in the R software version 4.1.2 (R Core Team, 2021) with two fixed factors, “Scenario” and “Closure”.

We explored the emergent trade-offs in the use of different temporal closures for different purposes in decision-making processes. This was accomplished by illustrating the results and developing a table of consequences between scenarios and temporal closures applied to the extent of area selected, the opportunity cost, and the biomass contained. Temporal closures were examined for its contribution to each variable.

Protection equality of conservation features

We used the best solutions to evaluate the proportional protection equality (PEP) metric between conservation features in each scenario (Chauvenet et al., 2017) to ensure that all taxa were protected in the same proportion at the planning region. We checked, on the other hand, all types of closures, temporal and permanent, and on the other only the protection equality of the permanent areas selected. By using the R package "ProtectEqual" (Chauvenet et al. 2017), we obtained the Protection Equality values that range from 0 to 1, where 0 indicates unequal conservation and 1 indicates an equal protection of the conservation features.

2.6.3. Results

Spatial similarity among scenarios

We found spatial differences in the set of PUs selected under each scenario for permanent and temporal closures (Fig. 2.6.3A-E). In scenario 1, 22.5% of PUs were selected to achieve the targets for all species, while in all the other scenarios, less than 20% (15.61-18.15%) was selected for permanent closures (Fig. 2.6.3F). However, when checking the total area selected in scenarios 2-3, including PUs selected for temporary closures at least in one season, a greater coverage was selected in these scenarios, summing up to 30-35% of the planning region. Even though different areas were selected as temporal closures in the different scenarios, in all scenarios most PUs was selected as permanent closures (Table 2.6.1). In scenario 2, planning solutions suggested that in the broader area should be implemented 1 season of closure, followed by 2 seasons, with the least chosen, 3 seasons of closure. In scenario 3, Marxan selected the largest area of all scenarios, followed by scenario 5. Since the boundary length increased in these scenarios, 2 and 3 seasons of temporal closure were prioritized. In scenario 4, where conservation targets were increased in individual seasons (winter and summer), most PUs were selected for single-season closures rather than longer temporal closures.

Regarding the spatial overlap of selected areas in the best solutions between scenarios, scenario 1 showed a moderate agreement with all the remaining scenarios, with Cohen´s kappa values ranging from 0.45 to 0.52 (see Table S2.6.1 in Supplementary Material). Moreover, the pairwise Pearson´s correlation coefficient of selection frequencies across scenarios showed that scenario 1 presented a positive moderated relationship with the other scenarios, ranging from 0.54 to 0.61 (see Table S2.6.2 in Supplementary Material). The correlation of selection frequencies between all dynamic scenarios was stronger ranging from 0.88 to 0.95.

Trade-offs among scenarios

The extent of area chosen was directly correlated with the biomass, meaning that a larger selected area corresponded to a greater amount of biomass within the no-take fishery reserves (Fig. 2.6.4, Table 2.6.1). The opportunity cost was positively related to both the extent of the area selected and biomass protected under closures banning fishing for all fisheries. All types of dynamic management examined herein reduced the opportunity cost and increased the biomass contained in the selected area compared to the static scenario 1. In scenario 2 and 3, the highest biomass was retained but with a higher opportunity cost, while in scenarios 4 and 5 a high biomass was protected but at a lower opportunity cost. In scenario 5, a high extent of area at the minimum opportunity cost was selected, protecting greater biomass than in scenario 1.

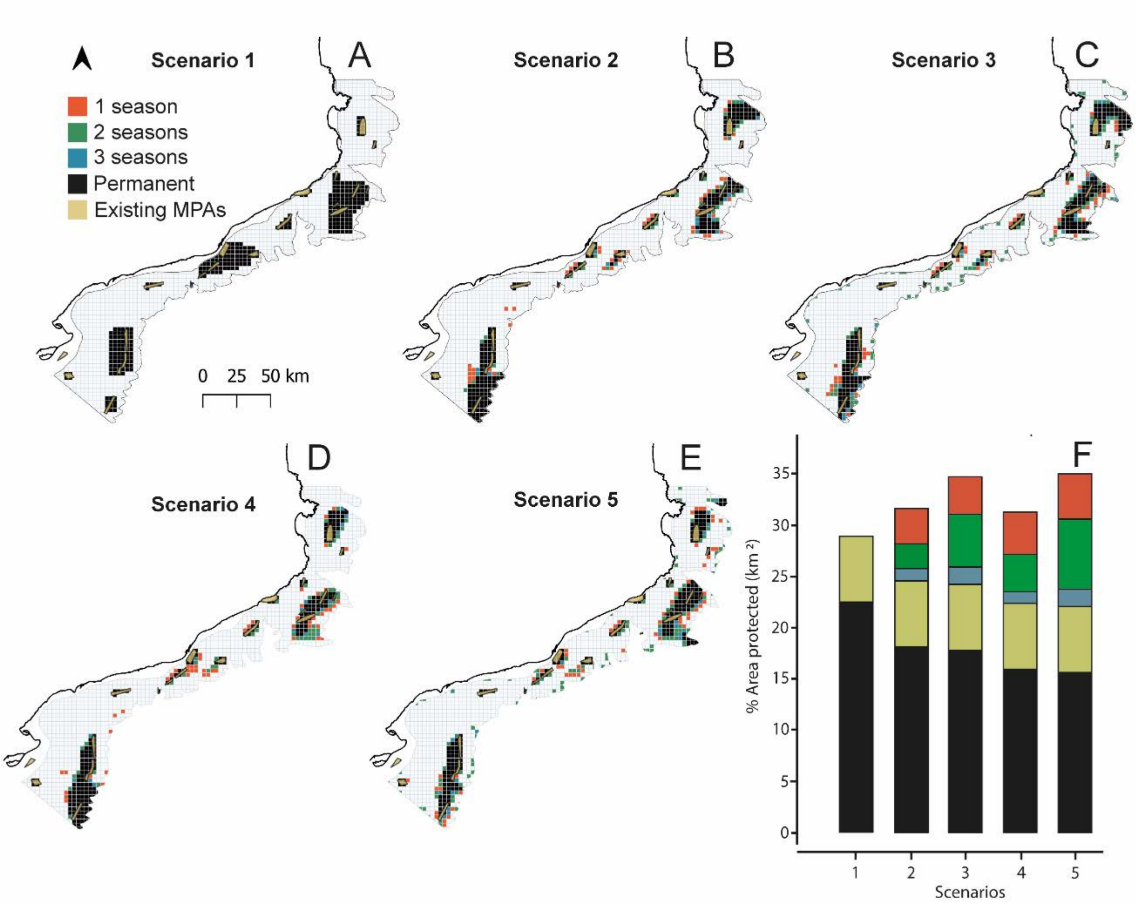

Figure 2.6.3. Network of permanent and temporal closures selected in the best solution of the different Scenarios. A) Scenario 1, as a static management with permanent no-take fishery reserves; B) Scenario 2, dynamic management selecting PUs seasonally; C) Scenario 3, dynamic management selecting PUs seasonally increasing connectivity values between winter and summer; D) Scenario 4, dynamic management selecting PUs seasonally modifying conservation targets for the Norway lobster; E) Scenario 5, dynamic management selecting PUs seasonally modifying conservation targets for the Norway lobster and increasing connectivity values between winter and summer; F) Coverage percentage of the areas selected in each scenario respect to the total area of the Planning Region. Colors represent the closure duration: black, permanent areas; blue, three seasons; green, 2 seasons including non-consecutive; and red, only one season of closure.

Testing for differences between the scenarios globally outputs, we found significant differences between variables (biomass: $H_{3,1699} = 25.07$, $p < 0.001$; opportunity cost: $H_{3,1699} = 36.50$, $p < 0.001$; area selected: $H_{3,1699} = 65.41$, $p < 0.001$) (Table 2.6.1; Fig. 2.6.4), as also between temporal closures (biomass: $H_{2,1699} = 1239.04$, $p < 0.001$; opportunity cost: $H_{2,1699} = 949.94$, $p < 0.001$; selected area: $H_{2,1699} = 1202.66$, $p < 0.001$). Permanent closures selected by dynamic strategies always differed from the static scenario 1 (Fig. 2.6.5). In all dynamic scenarios, a similar biomass retention was observed; in scenario 2 the highest values of 6813.98 ±305.37 kg was estimated, while in scenario 1, the lowest biomass was retained for protection. The global opportunity cost generated was lower in dynamic scenarios, being the scenario 3 the one with the lowest cost (Fig. 2.6.4).

Table 2.6.1. Consequence table of the extent of the area selected (km^2), the opportunity cost implied (M €), and the biomass retained in the no-take fishery reserves (kg) at each scenario (1-5) globally and per temporal closure (permanent, 3 seasons of closure, 2 seasons of closure, 1 season of closure). Values obtained from all 100 solutions generated at each scenario and represented in mean ± SD. The gradient of color indicates the highest value (the darkest color) to the lowest value (the lightest color) of the variables among scenarios: area selected in yellow, opportunity cost in red, and biomass in green.

	Scenarios				
	1	2	3	4	5
Global					
Area	2831.86 ±101.55	2989.66 ±127.05	3456.13 ±208.44	2955.03 ±169.88	3381.06 ±223.13
Cost	2.48 ±0.14	1.55 ±0.06	1.53 ±0.08	1.26 ±0.06	1.25 ±0.07
Biomass	5445.33 ±199.89	6813.98 ±305.37	6619.43 ±436.95	6483.52 ±465.00	6239.04 ±455.50
All year					
Area		2093.43 ±34.82	2045.10 ±61.41	1769.14 ±52.38	1792.40 ±66.03
Cost		1.32 ±0.02	1.26 ±0.03	1.02 ±0.02	1.01 ±0.03
Biomass		4978.29 ±76.67	4567.20 ±128.96	4163.08 ±158.90	4045.49 ±153.33
3seasons					
Area		148.84 ±25.82	215.25 ±36.02	180.99 ±34.24	206.16 ±39.12
Cost		0.07 ±0.01	0.10 ±0.02	0.09 ±0.02	0.09 ±0.02
Biomass		365.11 ±65.83	499.85 ±89.14	453.71 ±89.44	502.93 ±101.70
2seasons					
Area		352.33 ±28.99	794.97 ±55.92	433.41 ±35.72	856.59 ±62.18
Cost		0.11 ±0.01	0.11 ±0.01	0.06 ±0.01	0.07 ±0.01
Biomass		660.93 ±66.58	722.65 ±79.87	556.20 ±80.90	580.19 ±72.36
1season					
Area		395.06 ±37.42	400.81 ±55.09	571.49 ±47.55	525.89 ±55.50
Cost		0.05 ±0.06	0.05 ±0.01	0.07 ±0.01	0.07 ±0.01
Biomass		809.66 ±96.29	829.73 ±138.98	1310.53 ±135.76	1110.42 ±128.11

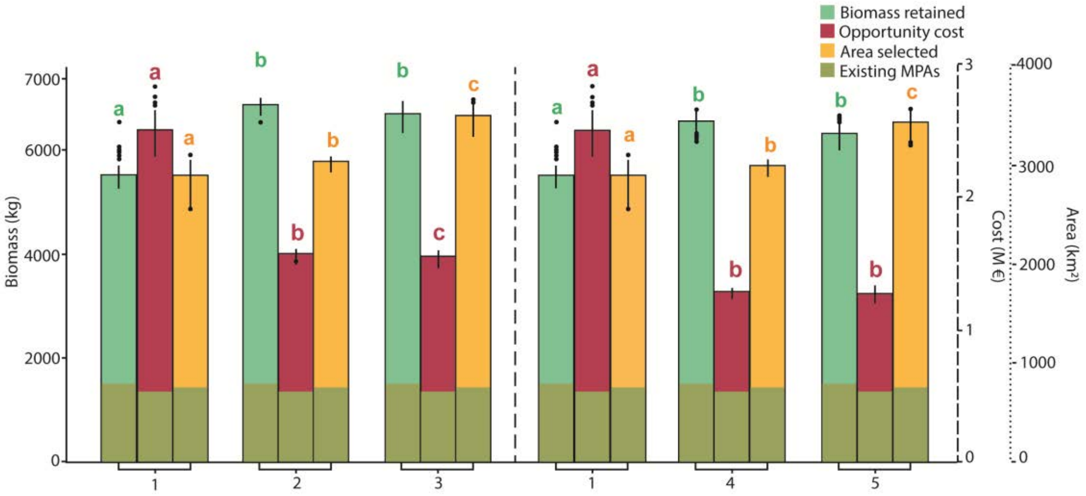

Figure 2.6.4. Trade-offs in each Scenario representing all 100 planning solutions computed. In each scenario there is the total biomass (kg, in green) gained, the opportunity cost (M€, in red) selecting the no-take fishery reserve network, and the total area selected (km^2, in yellow) to be both permanent and temporal closures. The outputs obtained from the already existing no-take fishery reserves (planning units blocked) are indicated in green olive. Error bars indicate the standard deviation.

Seasonally, we observed that the biomass of the 13 taxa was mostly retained in the permanent closure areas (Fig. 2.6.5A). Permanent closures also integrated the locked areas that represented the already existing no-take fishery reserves. These no-take fishery reserves, which covered 748.60 km^2, contained a 1482.97 kg at a 0.52 M €. Biomass contained by no-take fishery reserves consist of 27.23% from the total contained in scenario 1, and between the 29–37% of the permanent areas selected by dynamic strategies. Regarding opportunity cost, they represented the 20% in scenario 1, while in dynamic strategies represented between the 41–52% of the permanent areas selected. Opportunity cost from all fisheries were also mostly allocated under permanent closures, being most of it due to already existing no-take fishery reserves (Fig. 2.6.5B). In scenario 1, the PUs selected as permanent closures covered a larger area, with values averaging 2831.86 ±101.55 km^2, compared to the dynamic scenarios. Within the dynamic scenarios, scenario 2 had the highest value, reaching 2093.43 ±34.82 km^2, including the 748.61 km^2 of the already existing no-take fishery reserves (Fig. 2.6.5C).

Protection equality of conservation features

We found that the 40% and 20% conservation targets for the Norway lobster and all other species respectively were achieved in all scenarios and solutions. For most taxa, more than the 50% of their biomass (in the selected areas) was within the permanent closures (Table 2.6.2). In scenarios 4 and 5, in which conservation targets changed seasonally, the Norway lobster biomass was mostly preserved in the temporal closures (38.06 and 32.78 %, respectively, were only produced inside the temporal closures).

In all scenarios, permanent and temporal closures covered proportionally equal all conservation features in the resulting planning solutions indicating PE values between

0.81–0.85 (see Supplementary Material section Table S2.6.3). Permanent closures selected in each scenario keep representing all taxa with PE values ranging from 0.78 to 0.85.

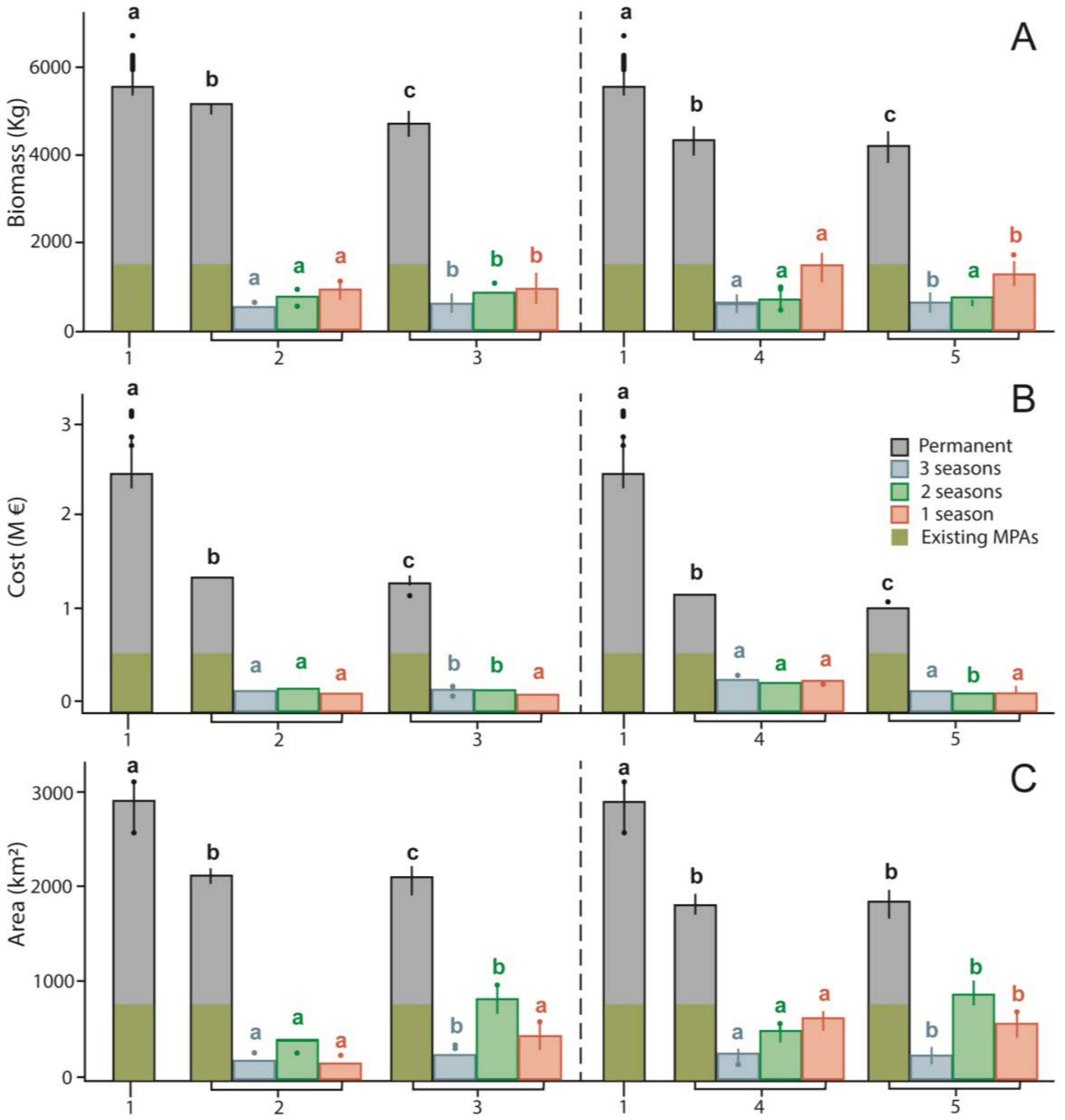

Figure 2.6.5. Trade-offs in each scenario representing all 100 solutions computed depending on the temporal closure: black, permanent closures; blue, three seasons; green; 2 seasons; red, 1 season of closure; green-olive, already existing no-take fishery reserves, planning units blocked. A) Total biomass gained (kg·km^{-2}·h^{-1}) in each scenario and temporal closure. B) Opportunity cost (M€) generated at selecting the no-take fishery reserve network in each scenario and temporal closure. C) Area selected (km^{2}) to implement the different types of temporal closures. Error bars indicate the standard deviation.

Table 2.6.2. Biomass retained (kg·h^{-1}·km^{-2}) at each scenario for each of the 13 taxa evaluated, and the percentage in brackets of the percentage of biomass retained only in the permanent closures. The value a_i indicates the area (in km^2) of a conservation feature *i* inside the planning region.

	Scenarios					
	1	2	3	4	5	a_i
TELEOSTEI						
Argentinidae spp.	256.70	382.08 (80.02)	403.39 (63.72)	388.14 (73.00)	347.31 (63.25)	2051.58
H. dactylopterus	120.14	245.60 (78.80)	257.97 (58.73)	234.18 (70.33)	219.30 (42.98)	1698.21
Lepidorhombus spp.	201.08	267.88 (76.60)	276.52 (70.62)	255.76 (68.25)	269.57 (63.39)	2107.09
Lophius spp.	577.00	781.64 (74.86)	808.39 (66.88)	762.20 (71.89)	791.74 (62.30)	8746.87
M. merluccius	1044.36	1464.13 (74.99)	1523.62 (67.61)	1448.29 (69.52)	1486.16 (61.74)	16771.03
M. potassou	630.46	946.56 (74.14)	1022.54 (57.87)	928.55 (53.52)	907.78 (44.29)	7096.71
Phycis spp.	15.00	19.73 (58.16)	20.63 (53.84)	20.47 (46.35)	7.98 (54.87)	243.76
Triglidae spp.	350.35	462.68 (75.19)	469.73 (69.42)	454.56 (74.56)	471.43 (68.25)	4942.32
CEPHALOPOD						
Eledone cirrhosa	449.06	556.41 (73.93)	585.28 (66.22)	546.41 (75.13)	560.00 (66.80)	8926.69
Sepietta spp.	12.02	10.06 (66.76)	10.19 (65.52)	9.94 (63.42)	11.06 (70.25)	114.58
Squids	650.99	695.46 (77.72)	721.75 (71.97)	705.31 (73.75)	709.46 (70.55)	9113.20
CRUSTACEA						
N. norvegicus	424.46	519.89 (65.20)	577.60 (53.55)	498.03 (38.06)	505.46 (32.78)	4218.59
P. longirostris	514.90	466.25 (68.65)	487.10 (61.54)	491.41 (56.24)	497.88 (52.30)	6644.02

2.6.4. Discussion

By comparing different dynamic management strategies with conventional static management, we found that dynamic management options required regulating a greater number of protected areas associated with a larger total area, most of which were temporal closures. However, these options incurred lower opportunity cost for fisheries while demonstrating a greater capacity for biomass conservation, thereby proving to be more effective conservation and fishery management strategies.

Dynamic management arose from the need to implement more effective management measures that consider the spatial dynamism associated with mobile species – such as migratory species or those with large home ranges – as well as environmentally induced range shifts (Dunn et al., 2016; Oestreich et al., 2020; Paradinas et al., 2023). Dynamic management has been applied in marine, freshwater, and terrestrial ecosystems to manage features that shift quickly in time and over spatial scales (Hermoso et al., 2011; Adams et al., 2014; Dunn et al., 2016). Most of the existing dynamic management strategies are often applied to a single target species (Howell et al., 2008), or rely on bycatch events before management actions are initiated (Dunn et al., 2016 Other studies solely focus on the changing environmental variables, such as temperature or currents, or on processes such as ecological, oceanographic, and atmospheric processes (Hazen et al., 2017; Ortuño Crespo et al., 2020). Here, we tested four dynamic management scenarios to account for the seasonal variations of several targeted species, fisheries landings and the total fishery income generated seasonally to ensure adequate conservation and a sustainable fishery while minimizing opportunity costs.

Dynamic management has been mainly proposed as a useful management tool for highly mobile pelagic species (Maxwell et al., 2015; Hazen et al., 2017). Our study contributes to a small number of studies demonstrating that dynamic management can more efficiently meet management targets for demersal species as well (Dunn et al., 2016). The Norway lobster is a territorial demersal crustacean that does not present large migratory movements (Sbragaglia et al., 2017; Vigo et al., 2021), it does show seasonal variations in landings, which are attributed to its biology and individual burrowing behaviour (Aguzzi et al., 2004; Vigo et al., 2023). This can be due to environmental factors such as the light-dependent activity behaviour, or due to the reproduction periods in which berried females hide inside burrows and are less represented in total landings (Aguzzi et al., 2007; 2021; 2023). The spatial patterns of Norway lobsters do not bathymetrically shift over seasons nor annually in this region (Vigo et al., 2023), which may explain why the permanent closures in all scenarios overlapped. Another possible explanation is that large part of this permanent closures overlap is imposed by the already existent MPAs. Our results show that dynamic approaches protected a larger biomass of Norway lobster and other species from fisheries by adapting fisheries management to the seasonal variations of the species than the constant and static strategy. These dynamic networks should be regularly monitored (e.g. yearly or biennal basis) to assess the effectiveness of these reserves and make any necessary adjustments. By monitoring these networks, changes in biomass and species abundance over time could be evaluated, including fluctuations in predator densities that could impact on the abundance of other species, as well as assess the ecological impact and effectiveness of the temporal closures (Pomeroy et al., 2005; Vigo et al., 2022). This information is essential for adapting management strategies and ensuring that spatial closures continue to meet their conservation and fisheries objectives.

The EU Biodiversity Strategy for 2030 aims to protect 30% of EU marine territories, with at least 10% being strictly protected, highlighting that healthy fish stocks are crucial for the long-term prosperity of fishers and the health of marine ecosystems and biodiversity (EC, 2020). The application of ecosystem-based management, supported by area-based conservation-management measures, can reduce the adverse impacts of fishing on the ecosystem while conserving fisheries resources. However, more effective conservation and management efforts are needed to achieve these goals, especially considering changing conditions, such as climate change, that present major challenges to biodiversity management (Rilov et al., 2020; Hermoso et al., 2022). Other Effective Area-based Conservation Measures (OECMs), defined by the Convention on Biological Diversity (CBD), can complement protected areas through sustained and positive conservation outcomes, even though they may be managed for other reasons (CBD, 2018). In the context of fisheries management and marine conservation, no-take fishery reserves called FRAs (Fishery Restricted Areas) are the most relevant OECMs (Petza et al. 2019). These are defined as areas in which specific fishing activities are permanently or temporarily restricted to recover exploited fishing stocks and habitats, as well as deep-sea ecosystems (Borrini-Feyerabend and Hill, 2015). However, there are concerns about the effectiveness of OECMs, as identifying and selecting suitable areas for conservation can be challenging (MacKinnon et al., 2015; Alves-Pinto et al., 2021). For example, when Shackell et al.

(2021) examined whether areas closed to fishing on the Scotian Shelf in Atlantic Canada could be managed as OECMs, they found that these closures failed to contribute to the recovery of groundfish and suggested that additional management measures should be adopted. In order to complement existing fisheries closures with additional permanent and temporal closures that will allow the recovery of marine biodiversity but also benefit fisheries, we suggest using planning decision-support tools, such as Marxan, which prioritizes areas that meet all conservation targets while minimizing impacts on socio-economic activities (Schram et al., 2019; Burns et al., 2023). The permanent closures proposed herein could be characterized as no-take marine reserves whereas the temporary closures could be considered as a type of FRAs that contribute to the conservation of Norway lobster (and other conservation features) while also promoting sustainable fisheries (GFCM, 2021; Chiarini et al., 2022).

The identified (potential) FRAs reinforced the protection of all species on that area reducing the opportunity cost of management by replacing permanent closures by temporal closures. Permanently closed areas, such as no-take reserves, are the closures that conserve more biomass and can preserve habitats (Goñi et al., 2010; Sala and Giakoumi, 2018). When replacing some permanent areas by FRAs, conservation targets were equally achieved at less opportunity cost. Another aspect to consider is that in the present study, we examined the biomass derived from landings data generated in already overexploited habitats. It is important to consider that the benefits of protected areas go beyond just conserving the existing biomass, as they also have the potential to increase the density and biomass of species and the exportation of biomass from the protected areas to surrounding overexploited areas (Di Lorenzo et al., 2020; Vigo et al., 2022; 2023). In addition to considering the biomass benefits derived from the 13 commercial species of the Norway trawl fishery, it is important to acknowledge the benefits of spatial closures for all species caught as bycatch and discards. It is worth noting that the discard ratio, in terms of weight, within the Catalan trawling fleet ranges from 12% to 26% in the upper slope (Blanco et al., 2023). Therefore, the designation of spatial closures can have significant positive impacts not only on the target commercial species but also on reducing the unintended catch and discards of non-target species within the fishery (Hilborn et al., 2004; Johnsen and Eliasen, 2011). Furthermore, it is important to protect critical periods in the life cycle of the species, such as juvenile stages, reproduction phases, and egg release, as these measures can significantly contribute to the recovery of fishery stocks over time and enhance fishing selectivity (Beets and Manuel, 2007; Dunn et al., 2011). In order to observe more comprehensive benefits from the no-take reserves, we recommend incorporating recruits and spawners modelled distribution data, in addition to relying solely on commercial species landing data. By incorporating key life cycle periods of key species, a more holistic understanding of the benefits of no-take reserves can be obtained, leading to better-informed management decisions (D'Aloia et al., 2017).

To conserve demersal stocks and ensure sustainable operations within the Western Mediterranean Sea, a multiannual plan has been implemented (West Med MAP, Regulation EU 2019/1022 of the European Parliament and Council of June 20; European

Commission, 2019). It extends along the northern Alboran Sea, Gulf of Lions, and Tyrrhenian Sea, covering the Balearic Archipelago, as well as Corsica and Sardinia, between France and Italy. This plan includes the regulation of the Norway lobster stock aiming to restore the maximum sustained yield (MSY) levels ensuring social and economic viability of the demersal stock by year 2025. To achieve this, the main solution is to reduce fishing effort (i.e. reducing fishing time by vessel or number of fishing vessels), though it has already been proved to be insufficient for recovering stocks (Sola et al., 2020). The combination of fishing effort reduction and spatial closures can help mitigate the potential negative effects of fishing effort redistribution (Hiddink et al., 2006). It is crucial to consider this factor because fishing effort redistribution can undermine both the retention of biomass and the fishing opportunity costs if fishers respond to spatial closures by intensifying their fishing efforts in other areas (Powers & Abeare, 2009; Lenihan et al., 2023). In some regions, such as the Catalan Sea continental margin (northern GSA06), trawlers associated to each of the different harbours are forced to cease all fishing activity for around 2.5 months at different periods without following any biological advice (BOE No.26, 31/01/2023). Recently, a fishery monitoring process has been initiated to gather high-quality data and establish a foundation for providing biological advice to fisheries (ICATMAR, 2021). By following the networks of permanent closures and OECMs (e.g. FRAs) selected with a spatial optimization tool, these forced banned periods could be assigned during the temporal closures. As a result, this could reduce even more the opportunity costs associated with closing areas in which fishing activities cannot be conducted if they are closed. The process of selecting and prioritizing areas is complex, but decision support tools, such as Marxan, can help marine planning processes and include many functionalities such as economic and trade-off analysis (Burns et al., 2023).

The results of our study were theoretical, as our aim was to present a methodological approach for the creation of dynamic plans using the most popular systematic conservation planning software, i.e. Marxan. These plans could be implemented for the conservation and sustainable fishery not only of the Norway lobster and its coexisting vulnerable species but also other species, regions, and even different temporal scales. We examined and simulated the outputs from different management strategies to evaluate the effectiveness of dynamic strategies over static ones in achieving the same conservation targets, without defining explicit socioeconomic targets or the present socioeconomic structures of the region. Notwithstanding, integrating ecological, social, and economic goals is crucial for successful marine conservation and management (Scholz et al., 2011; Markantonatou et al., 2021). We highlight the importance of integrating specific socioeconomic objectives in conservation practice to ensure equity among multiple groups of stakeholders and fishery associations in the planning region, as it can affect conservation outcomes and management efficiency and effectiveness (Halpern et al., 2013; Gurney et al., 2015; Klein et al., 2015). In this study area, where the Catalan fishery is divided among multiple fishery associations operating in different fishing grounds, it is indeed desirable to ensure that fishing limitations are distributed equitably. This approach aims to prevent any single fishing association or fishing ground from shouldering an unfair burden of the restrictions or experiencing disproportionate impacts. Incorporating socioeconomic and equity objectives, as well as a dynamic management approach, in the design of MPAs or other spatial closures is essential to guarantee the long-term success of both biodiversity conservation and fisheries goals and promote an equitable distribution of fishing limitations.

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2.7. Summary of results.

The previous six sections (from **2.1** to **2.6**) described the methodologies, results, and discussions related to the principal axes of this thesis. These sections begin by evaluating the status of an overexploited fishery resource, the Norway lobster, updating some of its biological parameters (**2.1**), followed by an ecological evaluation of the effectiveness of a pilot no-take fishery reserve on the passive recovery of ecosystem and community (from **2.2** to **2.5**) and conclude by developing and simulating a network of marine protected areas (**2.6**) based on the results of the thesis.

In **Chapter 2.1,** the Norway lobster stock of the northwestern Mediterranean Sea was evaluated by updating key biological parameters. We found clear signs of overexploitation of this species in the study area due to a reduction in size at first maturity and a negative trend in the biomass population over the years.

To predict how the Norway lobster population might fluctuate due to the predator population inside the no-take reserve, the potential predators of Norway lobsters were identified in **Chapter 2.2**. Then, to evaluate if the size of the no-take fishery reserve was adequate for Norway lobster recovery, in **Chapter 2.3** the spatial movements and behavior of Norway lobsters were investigated to examine their home range and activity patterns. The effectiveness of the no-take reserve in restoring Norway lobster populations and its coexistent demersal species was evaluated through two methodologies: experimental trawling surveys in **Chapter 2.4** and by using a non-invasive methodology, ROV (Remotely Operated Vehicles), in **Chapter 2.5**.

Finally, in **Chapter 2.6**, based on the results obtained with the experiments conducted in a pilot no-take fishery reserve, different scenarios of networks of no-take reserves were simulated, applying various dynamic management strategies. All scenarios focused on Norway lobster recovery and 12 coexisting species vulnerable to fishing activity. We compared a static scenario with four dynamic scenarios to examine which of them better achieved conservation and fisheries goals.

A summary of the major findings and results found in these chapters is provided below:

Chapter 2.1. An update of the population status of a commercially valuable European crustacean, the Norway lobster *Nephrops norvegicus*, in the highly exploited northwestern Mediterranean Sea.

This chapter provides updated information on **key biological parameters** of the Norway lobster population in the northwestern Mediterranean Sea. These parameters included **density**, **population structure**, **growth rate**, **reproduction**, and **fishery landings trends** and **spatial distribution**. The results obtained were compared with those from previous studies in the area as well as from other regions of the Mediterranean Sea.

From 1974 to 2021, Landings per Unit Effort (LPUE), which represents biomass corrected per fishing effort, exhibited a negative trend. Total landings decreased by 37.81% in 2021, amounting to 311,647 kg less than in 2000. However, despite this decrease, the population's spatial distribution, assessed using Cohen's Kappa and Spearman correlation coefficients, remained consistent within the same area from 2008 to 2021, with a moderate overlap. Similarity, the population maintained the same bathymetric range, with most biomass was found mainly between depths of 300–550 m.

Size distribution of individuals collected from 2019 to 2021, a total of 6698 individuals, ranged from 18 to 65.5 mm of cephalothorax length (CL) in males and 18 to 60.5 mm CL in females. Males were significantly larger than females, with mean CL of 36.45 ± 7.34 and 31.16 ± 5.16 mm, respectively. Males and females presented different size distributions according to the Kolmorov-Smirnov tests. Individuals mean size differed slightly from previous studies in the same area, but growth patterns were similar, indicating a positive allometric length-weight relationship for both males and females.

Landings per season reached their peak during spring and summer, with the highest catch densities recorded as 1191 (mean) ±711 (standard deviation) N km^{-2} and 1158 ± 598 N km^{-2}, respectively. In summer, specifically in July and August, females exhibited higher Gonadosomatic Indexes (GSIs) due to the reproductive season. Although females were present throughout the year, their numbers in total landings decreased from October to March. Consequently, sex ratios deviated from equilibrium (0.50) during autumn and winter. In late August, the brooding period already started, during which berried females became more abundant and sought shelter inside their burrows. This is the reason why the presence of females in total landings decreased during this time. A slight advancement in the brooding and spawning periods of approximately one month was observed. Based on GSI values, the estimated size at 50% maturity for females was 25.3 mm CL, which is lower than the measurement reported in previous studies conducted on the same population years ago, where the size at 50% maturity was documented as 30–31 mm CL.

Chapter 2.2. Using molecular and stable isotope markers to identify the main predators of *Nephrops norvegicus* in Mediterranean deep-water ecosystems.

This chapter identified the **main predators** of Norway lobster in the northwestern Mediterranean Sea by combining two methodologies: DNA identification of Norway lobster within the stomach contents of potential predators, and stable isotope analyses.

For this, 20 potential predators of Norway lobster, comprising cephalopods, teleost, and elasmobranch commonly found in Norway lobster grounds were collected from experimental fishing hauls. Muscle and stomach samples of a total of 249 individuals of these predators as well as muscle of 20 Norway lobsters. Subsequently, all stomach contents were examined for DNA identification of Norway lobster, by using a specific primer designed for this species to identify instances of predation on Norway lobster.

In the DNA identification analysis, Norway lobster DNA was primarily detected, accounting for more than 25%, in seven potential predators. Among the cephalopod species, the following percentages of Norway lobster DNA were found: *Todaropsis eblanae* (73.33%), *Abralia veranyi* (72.73%), *Seppietta* sp. (66.67%), *Todarodes sagittatus* (42.86%), and *Illex coindetti* (38.46%). Among the teleosts, the species were *Merluccius merluccius* (35.71%), and *Conger conger* (33.33%).

In terms of stable isotopic values, the Norway lobster exhibited complete segregation from all potential predator species based on $\delta^{15}N$ and $\delta^{13}C$ values. To simulate potential predators that exclusively consumed Norway lobster, an artificial predator was simulated for each species suspected of being a predator. Among the 20 potential predators, six showed an overlap of more than 25% in the real isotopic niches, estimated using Kernel Utilization Densities (KUDs) at 95%, with the artificial specialized predator. The cephalopod species that exhibited significant overlap were *Sepietta* sp. (58.1%), *S. oweniana* (55.9%), *Eledone cirrhosa* (34.5%), *A. veranyi* (30.3%), and *T. sagittatus* (25.9%). Additionally, the elasmobranch *Galeus melastomus* (64.3%) was one of the predators that overlapped the most with the specialized predator.

The genetic analyses of DNA provided insights into the short-term importance of predators, as direct detection of Norway lobster was observed in their stomach contents. On the other hand, the isotopic niches captured the long-term importance of predators by integrating and representing the dietary values of prey consumed several months ago. When considering both isotopic and genetic values, only the cephalopod species *Sepietta* sp. and T. *eblanae* exhibited high values for both parameters. This suggests that these cephalopods play a significant role in predation on Norway lobster based on both genetic and isotopic evidence.

A Predation Index (PI) was developed to encompass not only genetic and isotopic values but also the density of predator species within the study area. The most significant predators, ranked by higher PI values, were the cephalopods *S. oweniana*, *A. veranyi*, and *Sepietta* sp., followed by the demersal shark *Scyliorhinus canicula*, and the teleosts *M. merluccius*, *T. lyra*, and *C. conger*.

Chapter 2.3. Spatial ecology of Norway lobster (*Nephrops norvegicus*) in Mediterranean deep-water environments: implications for designing no-take marine reserves.

This chapter describes the home range and daily activity patterns of Norway lobsters within the pilot no-take fishery reserve. The study employed a combination of acoustic-tracking and tagging-recapture procedures. The primary objective was to evaluate the adequacy of the 10 km^2 size of the reserve in terms of restoring was the Norway lobster population, based on their movement patterns.

Out of the 19 acoustic-tagged individuals that exhibited activity, only 5 individuals remained within the monitored area, which covered approximately 0.28 km^2 with triangulated data, throughout four-month tracking period (May to September). By using only detection data, the area of detection increased to 0.6 km^2, revealing the presence of more individuals in the north-eastern and deeper regions of the no-take reserve. The estimation of home ranges using Kernel Utilization Densities (KUD) at 50% and 90% showed variations over the sampling period. In early June, the home ranges were larger (KUD50: mean = 2,476.32 m^2; KUD90: mean = 11,223.42 m^2; n=19) compared to the subsequent months of July (KUD50: mean = 18.4 m^2; KUD90: mean = 170.2 m^2; n=5), August (KUD50: mean = 305.6 m^2; KUD90: mean = 1,413.8 m^2; n=5), and September

(KUD50: mean = 278.4 m^2; KUD90: mean = 1341 m2; n=5). This suggests that individuals had smaller home areas as they sought locations to settle and build their burrows, indicating a process of final settlement. Overall, the findings suggest that within the monitored area inside the no-take reserve, a limited number of individuals maintained their presence, while the broader detection area revealed the movement of more individuals in specific regions. The observed changes in home ranges indicate the dynamic nature of Norway lobster behavior as they establish their preferred habitat for settlement.

During the initial phase of the tracking study, there was some slight overlap observed in the home ranges of the acoustic-tagged individuals. However, after some time, the home ranges of the individuals were segregated specially indicating that each individual had its own defined area of occupancy. Furthermore, the Coefficient of Association, which considers both spatial and temporal interactions, revealed that there was no spatial attraction observed between any of the acoustic-tagged individuals. This implies that the individuals did not display any significant tendency to interact or associate with one another in terms of their spatial distribution. Taken together, these results highlight the territorial nature of Norway lobsters and their preference for maintaining distinct home ranges without spatial attraction or overlap with other individuals within the monitored area.

Waveform analyses conducted by pooling together the movement data of all 19 individuals revealed that higher movement patterns were observed during the diel hours. Specifically, the major peak of activity occurred during the light hours between 8:00-17:00 GMT. This indicates that the Norway lobster individuals exhibited increased movement and activity levels during the daytime hours compared to the nighttime hours in deep-sea habitats.

During the capture-recapture experiments, a total of 216 Norway lobsters were tagged and released. However, only 5 individuals were subsequently caught by the fishery vessels that typically operate in the vicinity of the no-take reserve, accounting for a recapture rate of 2.32% of the total tagged individuals. This relatively low recapture rate, coupled with the observation of small home areas of approximately 30 m^2, suggests that no-take fishery reserves specifically targeting the restoration of Norway lobster populations do not necessarily require extensive areas to be effective. These findings imply that even relatively small-sized no-take reserves can provide suitable conditions and adequate protection for Norway lobsters to thrive and potentially contribute to population recovery.

Chapter 2.4. Before-after control-impact (BACI) assessment of the effects of a deep-water no-take reserve on overfished Norway lobster (*Nephrops norvegicus*) population and their coexisting demersal megafauna.

This chapter evaluates the effectiveness of the no-take reserve in recovering the Norway lobster stock, adopting a BACI (before–after control–impact) approach. The study design involves sampling through experimental fishing surveys conducted before the implementation of the reserve (referred to as the Baseline, in 2017) and four years after its establishment (in 2021). In addition to the study areas within the reserve, a control area where fishing activity is currently ongoing was included for comparison purposes.

The results of this chapter indicate positive signs of recovery for the Norway lobster stock within the no-take reserve. The abundance and biomass of the population were higher inside the reserve compared to both the control area and the baseline measurements. Additionally, the Norway lobsters inside the reserve exhibited larger body sizes, ranging from around 30–50 mm carapace length (CL), compared to the smaller sizes observed in the control and baseline areas (around 20–40 mm CL). The study also revealed a shift in the trophic niche of the Norway lobster population within the no-take reserve, as evidenced by higher values of $\delta^{15}N$ (a stable isotopic marker) compared to the control area and baseline measurements. By utilizing Kernel Utilization Densities (KUDs), the isotopic niche of Norway lobsters was examined. It was observed that individuals from the control area and baseline measurements overlapped, indicating a shared isotopic niche. In contrast, the Norway lobsters within the no-take reserve exhibited segregation, suggesting a potential change in their feeding habits or diet composition.

Furthermore, the analysis of Landing per Unit Effort (LPUE) data around the no-take reserve and the control area revealed a negative trend in the population, indicating a decline in abundance over the years. However, the loss of biomass around the no-take reserve appeared to be mitigated compared to the control area, with a total loss of 35.60% from 2016 to 2021, as opposed to approximately 49.96% in the control area. This suggests a potential spillover effect, where biomass from the no-take reserve may be exported to the surrounding area where nearby fisheries operate.

The analysis of coexistent demersal species in the habitat did not reveal significant differences in species richness and diversity indices between the control area, the no-take reserve, and the baseline measurements. However, certain species showed an increase in abundance and biomass within the no-take reserve compared to the control area. Among the species that exhibited higher abundance and biomass within the no-take reserve were the teleosts *Coelorinchus caelorhincus*, *Helicolenus dactylopterus*, and *Phycis blennoides*, as well as the demersal shark *Scyliorhinus canicula*. These species demonstrated a notable increase of biomass in the no-take reserve. Furthermore, when considering body size, the species that displayed larger individuals within the no-take reserve included the teleosts *Argentina sphyraena*, *Coelorinchus coelorhynchus, Molva macrophtalma*, and the elasmobranch *Scyliorhinus canicula*. This suggests that the no-take reserve may provide suitable conditions for the growth and development of these species, leading to the presence of larger individuals compared to the control area and baseline measurements.

Overall, these findings provide evidence of the positive effects of the no-take reserve in promoting the recovery and conservation of the Norway lobster stock, as indicated by increased abundance, biomass, larger body sizes, trophic niche shift, and potential spillover effects. The positive effects were also observed on certain coexistent demersal species, as evidenced by increased abundance, biomass, and larger body sizes within the reserve.

Chapter 2.5. ROV-based monitoring of passive ecological recovery in a deep-sea no-take fishery reserve.

This chapter evaluates the effectiveness of the no-take fishery reserve in recovering Norway lobster populations and coexistent megafauna species after 2.5 years of closure. To evaluate the recovery, non-invasive ROV (Remotely Operated Vehicles) video-surveys were conducted. Additionally, a control area where fishing activity was still ongoing was included for comparison purposes.

To assess the Norway lobster populations within the no-take fishery reserve and the control area two methods were employed: individual counting and burrow-system counting. Both approaches yielded consistent results, indicating that the Norway lobster populations within the no-take reserve had significantly higher abundances and biomasses compared to the control area. Furthermore, the relative body size of Norway lobsters was assessed in both areas. The measurements revealed that individuals within the no-take reserve exhibited larger body sizes, with a mean size of 22.76 ± 7.67 mm CL, compared to individuals in the control area, with a mean size of 18.65 ± 6.46 mm CL. This suggests that the no-take reserve not only supports higher abundances but also promotes the growth and development of larger individuals.

A total of 43 species and taxa were identified and classified into major taxonomic groups. The evaluation of coexistent megafauna species in the no-take fishery reserve and the control area revealed similar species compositions, as indicated by species richness and diversity indexes. However, despite the similarity in species compositions, there were notable differences in the abundance of certain megafauna species. Some species showed signs of recovery within the no-take reserve, indicating an increase in their abundance compared to the control area. These species included the teleosts *H. dactylopterus* and *Trigla lyra*, as well as the cnidarian species from the Family Cerianthidae.

The comparison of marine litter between the no-take fishery reserve and the control area revealed similar quantities in both locations. The types of marine litter identified included fishing nets, glass, metal, and plastic. The similarity in the amount of marine litter suggests that both areas may be subject to similar sources and inputs of litter.

In overall, the results of this chapter indicate that the seafloor in the no-take reserve has shown significant recovery from trawling impacts compared to the control area. In the no-take reserve, a high percentage (97.24%) of the recorded area was found to be intact, with only minor signs of old trawl marks that were already in the process of recovery. In contrast, the control area displayed a lower percentage of intact seafloor (41.17%), with a significant portion of the area showing alterations from net trawling marks (38.21%) to more intensive trawling marks (20%). These findings suggest that the absence of fishing activities in the no-take reserve has allowed for the natural regeneration and healing of the seafloor ecosystem.

Chapter 2.6. Dynamic marine spatial planning for conservation and fisheries benefits.

After evaluating the effectiveness of the pilot no-take reserve, this chapter aims to design a network of no-take fishery reserves based on the results of the thesis. Specifically, the main goal of this chapter was to use a systematic conservation tool (Marxan) to identify priority areas for the conservation of Norway lobster and 12 other species while minimizing the associated opportunity costs. The chapter compares dynamic approaches to static approaches using conventional permanent areas of closure.

The chapter compares the outputs from dynamic and static scenarios for designing a network of no-take fishery reserves. It notes that dynamic scenarios generally required larger areas to be managed compared to static scenarios. However, despite the larger spatial extent, that most of them were temporal closures, dynamic scenarios were found to incur lower costs for fisheries while having a higher capacity for conserving biomass. The selected areas for the reserves are directly linked to the biomass present within the chosen spatial closures. Additionally, the chapter notes that the opportunity cost associated with the establishment of reserves is positively related to both the biomass conserved and the selected spatial closures. This suggests that areas with higher conservation value in terms of biomass also tend to have higher associated costs, emphasizing the need to balance conservation objectives with the socio-economic considerations of fishing communities.

The spatial distribution of the scenarios obtained from each evaluated strategy is found to be similar along the Catalan coast. This spatial distribution is assessed using the Cohen Kappa coefficient, which measures the agreement between the selected areas. The coefficient indicates a moderate level of agreement, suggesting that both dynamic and static scenarios result in comparable conservation outcomes in terms of spatial distribution.

All conservation targets for all species were met in all scenarios. The permanent and temporal closures from each scenario covered conservation features proportionally, demonstrating Protection Equality values ranging from 0.81 to 0. The permanent closures selected in each scenario consistently represented all taxa, with Protection Equality values ranging from 0.78 to 0.85.

Chapter 3.
Summary of Discussions

The overall objective of this thesis was to evaluate whether deep-sea no-take fishery reserves could be an effective measure for restoring overexploited fishing resources after evaluating their population parameters and the current fishery status, which would benefit both conservation and fishing. Specifically, in this thesis, I focused on the case study of Norway lobster stocks present in the northwestern Mediterranean Sea, where the population has experienced significant declines in total landings within the regional fisheries of the Spanish Region of Catalunya. In this **Chapter 3**, I summarized all the discussions obtained throughout the different chapters (sections from **2.1** to **2.6**), which are divided into three main axes. First, it discusses the results obtained concerning the evaluation of the overexploited species, the Norway lobster, providing a comprehensive understanding of its current population and fishery status. Secondly, the effectiveness of the pilot no-take fishery reserve is addressed by examining the design of the marine protected area and assessing its impact on the Norway lobster population and associated species and habitat. Finally, based on the findings from the no-take reserve evaluated in this thesis, different scenarios of networks of no-take fishery reserves were simulated and discussed, aiming to further enhance conservation efforts and sustainable fisheries management.

3.1. Norway lobster population status in the northwestern Mediterranean Sea

The Norway lobster is a benthic crustacean that holds significant commercial value within European fishing stocks, being specifically targeted by the bottom trawl fishery from the northern GSA06 region of the northwestern Mediterranean Sea (Catalan Sea). However, in the past decade, the total landings of this stock have experienced significant declines. **Chapter 2.1** of this thesis aimed to update key biological parameters of the Norway lobster population to better understand its current fishery status and emphasize the importance of implementing appropriate management measures for its sustainable management.

The results showed that Norway lobsters are distributed in a similar bathymetric range from years 2008 to 2021, being primarily found at depths ranging from 300 to 675 m deep in the Catalan Sea (Maynou and Sardà, 1997). While fishing effort diminished in the area (ICATMAR, 2022), the Landing Per Unit Effort (LPUE) of Norway lobsters continued to decline over time. Notwithstanding, landings displayed seasonal patterns, with landings peaking in the summer, particularly in July and August. This was slightly later than the evaluation by Aguzzi et al., (2004), where the highest landings occurred in June. This is probably related to the behavior of the species, as Norway lobsters build burrows that offer a natural protection to bottom trawling activities (Aguzzi et al., 2004; 2023). Thereafter, the number of individuals caught in landings can be considered proportional to the number of individuals emerging from their burrows. Emergence from burrows and movement activity may exhibit seasonal patterns due to light intensity dependance, as we also observed in diel activity patterns in **Chapter 2.3** (Aguzzi et al., 2021; 2023), with spring and summer being the seasons with longer photoperiods. Therefore, Norway lobsters not only display diurnal burrowing behavior but also exhibit seasonal patterns that align with their annual reproductive cycle, which may be the main reason for the seasonal landing variations.

Mating in Norway lobsters occurs outside the burrows and takes place in the spring and summer (Aguzzi et al., 2004). Between autumn and winter there were the lowest landings, which correspond to the brooding period, in which berried females hide inside their burrows throughout autumn until the release of the eggs in early winter (Farmer, 1974; 1975; Company et al., 2003; Rotllant et al., 2005). During the brooding period, the presence of total females decreased, resulting in a change in the sex ratio of landings throughout the year. The size at 50% maturity for females also showed a reduction compared to previous studies in the same area, potentially influenced by fishing pressure. The size estimated was 25.3 mm CL, approximately 5 mm less than proposed by Orsi Relini et al. (1998) with the same population. Changes in population abundance, size, and age at maturity have been observed in response to overfishing in other regions (Galimany et al., 2015; Marković et al., 2016; Molinet et al., 2020).

Crustacean growth is influenced by the molting frequency of the old exoskeleton, which is a discontinuous process (Green et al., 2014). Growth responds differently to environmental conditions, such as water temperature, and factors like high population density and competition for resources (Aiken and Waddy, 1986; Briggs, 2002; Johnson et al., 2013). Indeed, Norway lobster populations can exhibit diverse demographic patterns influenced by area-specific fishing pressure and variable environmental factors, including habitat characteristics (Abelló et al., 2002). Norway lobsters are long-lived species with slow growth rates, typically ranging from 4 to 5 mm per year (Sardà, 1985; Bianchini et al., 1998). **Chapter 2.1** revealed that the Length-Weight Relationship (LWR) exhibited positive allometry for both males and females, although the largest individuals in terms of landings were consistently males. This suggests that volumetric growth (body mass) outpaces length growth (body length), with both sexes growing at similar rates. Other studies conducted in the GSA06 region reported similar LWR (Sardà et al., 1998), while in the GSA17 region, corresponding to the northern and central Adriatic Sea, the population exhibited a negatively biometric relationship (Angelini et al., 2020).

To minimize the impact on the Norway lobster stock, new management measures are needed (Ridgway et al., 2006; Lolas and Vafidis, 2021). Fishing pressure appears to be reducing the size at 50% maturity, and fisheries are targeting individuals below the Minimum Conservation Reference Size (MCRS), which is currently 20 mm CL in the Mediterranean Sea (Regulation (UE) 1380/2013, 11/12/2013; Regulation (EU) 2019/1241, 20/06/2019). The establishment of no-take reserves is suggested as an effective measure for sustainable fisheries management (Sala and Giakoumi, 2018; Melaku Canu et al., 2020; Vigo et al., 2020; 2023). Overall, this section highlights the need for appropriate management strategies and the potential benefits of implementing no-take reserves to protect the Norway lobster population and ensure its long-term sustainability.

3.2. Evaluation of the pilot no-take fishery reserve

3.2.1. Identifying the predators of Norway lobster

To effectively recover an overexploited population within a spatial closure, such as a no-take fishery reserve, it is crucial to assess predator densities in the area, as they can impact restoration efforts and lead to habitat regime shifts (Daskalov et al., 2007; Clement and Hay, 2017). While the Atlantic cod (*Gadus morhua*) is the primary predator of Norway lobsters in Atlantic waters, potential predators in the Mediterranean Sea, where Atlantic cod is not present, remain unknown (Chapman, 1980; Dombaxe, 2002). In **Chapter 2.2**, the main predators of Norway lobsters were identified by using intrinsic markers (DNA and SIA) in the northwestern Mediterranean Sea, where the pilot no-take fishery reserve was established. In particular, DNA analyses of stomach contents revealed species that recently preyed on Norway lobsters, while isotope analyses from muscle tissues showed assimilation of all consumed preys in recent months (Boecklen et al., 2011).

Regarding the results obtained, the teleost *Lophius budegassa* occasionally preyed on Norway lobsters, while *Galeus melastomus* and *Sepietta oweniana* showed higher indices of past predation. The most significant predators, indicating higher values of recent and past predation, were primarily cephalopods, specifically *Sepietta* sp., followed by *Toradopsis eblanae* and *Abralia veranyi*. Previous studies suggested that some of these predators feed primarily on demersal crustaceans such as *Alpheus glaber* (Bergström, 1985; Fanelli et al., 2009; Quetglas et al., 2009). Other predator species identified in this Chapter were the teleost *Conger conger, Merluccius merluccius*, and the cephalopods *Pteroctopus tetracirrhus*, *Ilex coindetii*, and *Todarodes sagittatus*, which presented intermediate values, indicating Norway lobsters may be part of their diet composition. However, this study did not differentiate the life cycle stage of preyed Norway lobsters. Next steps could be assessing and testing the predation on different sizes (including larvae) and evaluating the presence of predator avoidance among larger sizes of Norway lobsters across all the predator species analyzed. Some of these predators may opportunistically prey on Norway lobsters, as they are not easy to catch due to their burrowing behavior and are difficult to digest due to their exoskeleton and low fat content (Björnsson and Dombaxe, 2004).

Besides identifying potential predators using DNA analyses and stable isotopes in **Chapter 2.2**, a Predation Index was also estimated. This index integrated both DNA and stable isotopic results while taking into account the abundance of each predator within the study area. Following this comprehensive evaluation, the cephalopods *S. oweniana*, *Sepietta* sp., and *A. veranyi* remained the most likely predators of Norway lobsters. The abundance data used in this chapter were obtained from experimental trawling surveys conducted in the Norway lobster grounds at depths between 300 and 450 meters, and the species that were considered predators also came from these surveys. It is crucial to acknowledge that the Predation Index may vary based on different factors such as the type of habitat, species composition, and the number of predator species included in the analysis. These variations are significant because the Predation Index assigns a value by comparing all predator species considered in the study, taking into account factors such as DNA, isotope niche overlap, and predator densities. The inclusion of multiple factors allows for a comprehensive assessment of predation dynamics and helps rank the predator species based on their respective values. Therefore, when interpreting the Predation Index, it is important to consider the specific characteristics of the habitats, the species present, and the data used in the analysis to ensure accurate and meaningful conclusions about predator-prey relationships. For instance, in depths between 100 and 200 meters, *M. merluccius* is more abundant compared to the Norway lobster grounds, where its predatory impact is diminished due to its low density in the area (Recasens et al., 1998). An intriguing finding when considering predator densities was the finding that species such as the demersal shark *Scyliorhinus canicula*, which exhibited low values in both Norway lobster DNA and isotopic niche overlap, gained significant importance as a potential predator due to its high abundance in the study area (Navarro et al., 2016).

The information presented in this study holds valuable implications for adapting and establishing effective fisheries management strategies to restore the population of Norway lobster in the Mediterranean Sea while mitigating potential negative outcomes. In addition to assessing the impact of the no-take reserve on Norway lobsters, **Chapters 2.4** and **2.5** also evaluated the species composition within the habitat, including the potential predators identified in **Chapter 2.2.** The subsequent section, **Chapter 3.2.3**, will provide a detailed analysis of the impacts of the no-take fishery reserve on predators, specifically focusing on assessing its effectiveness.

3.2.2. Importance of the size of the reserve

The effectiveness of no-take reserves relies on the optimal size design to ensure the long-term persistence of populations (Blowes and Connolly, 2012). To achieve this, spatial data on species movement, home ranges, and territorial interactions are crucial in determining an adequate size and location for the targeted species (Katajisto and Moilanen, 2006; Lees et al., 2020). In **Chapter 2.3,** the spatial ecology of Norway lobster was investigated for the first time using acoustic tracking and capture-recapture information.

Tag-recapture experiments are commonly used in the field of ecology to estimate the size and dynamics of animal populations, providing valuable information for conservation efforts, ecological research, and population management (Otis et al., 1978; Chao, 1989). The tag-recapture experiments conducted in this thesis revealed a low recapture rate of only 2.32%. The recaptures were conducted by bottom trawling vessels that usually operate in the surroundings of the no-take reserve. The low recapture rate suggested that most of the 216 tagged individuals remained inside the no-take fishery reserve, as was also observed in a similar study conducted in the north Atlantic Ocean (Haynes et al., 2016). This finding was further supported by the results obtained from acoustic telemetry data.

Acoustic-tracking data of Norway lobsters indicated that this species exhibited a mean travel speed of 0.1–0.2 $m \cdot s^{-1}$, consistent with other studies (Newland et al., 1988), and most of the tagged individuals traveled more than 100 m from the release point before exiting the range of detection. However, some individuals suddenly disappeared, which could be attributed to predation or transmitter failures. The transient disappearance of animals over consecutive days can be explained by periods of burrow occupancy, which may shield the transmission of acoustic signals (Aguzzi et al., 2023). Daily signal observations of some tagged individuals indicated maximum movement activity during daylight, consistent with field and laboratory experiments describing the behavioral rhythm of Norway lobsters (Aguzzi et al., 2003; Sbragaglia et al., 2015). The temporal movement patterns observed are closely related to locomotion and detectability, including those of animals engaged in door-keeping behavior (i.e., animals waiting at their tunnel entrance).

Regarding home ranges, two distinct patterns were observed among individuals. Home ranges were evaluated using the 90% Utilization Density (UD90), which showed a wider and irregular area, while the UD50 indicated smaller and more uniform areas, representing the area in which Norway lobsters settled and built their burrow systems. Indeed, Norway lobsters are territorial crustaceans that typically settle in their own burrows (UD50 or core area) and explore and forage in the surrounding area (UD90), as reported in previous studies (Tuck, 1997; Sbragaglia et al., 2017). The differences in home range and space use among individuals may be attributed to intraspecific variability, including social behavior and environmental factors, which have been well documented in other decapods (Afonso et al., 2008; Giacolone et al., 2019). Individuals of the same population may present different biological rhythms influenced by different environmental factors, which determine their burrow emergence and activity (Aguzzi et al., 2023). Home ranges that exhibited changes and were larger could be associated with habitat selectivity in Norway lobsters still searching for suitable burrow locations (Welsh and Bellwood, 2012). Some of these larger home ranges became smaller over time, indicating the establishment of individuals. The average home range size, considering UD90 and settled individuals, was approximately 30 m^2, which corresponds to the typical area where the species conducts most of its burrow-centered activities. It should be noted that the examined home ranges could be larger due to bathymetric features, such as depth gradients, resulting in less uniform displacement patterns (Wiig et al., 2013).

Among the various factors to consider, the size of no-take marine areas plays a crucial role in ensuring that target species have sufficient space to fulfill their vital requirements (Edgar et al., 2014). The pilot no-take reserve in this study encompasses approximately 10 km^2. In **Chapter 2.3**, it was discovered that the home ranges of Norway lobsters, where most of their day-to-day activities occur, were relatively small, around 30 m^2. Although most individuals reached the detectable distance from the release point, the low rate of recaptures suggests that the majority of individuals remained within the protected area. These findings indicate that the size of the no-take fishery reserve is adequate for covering and protecting a high density of Norway lobsters. However, continuous monitoring of the reserve and its inhabitants is crucial to observe any potential changes resulting from density-dependent behaviors, the absence of fishing pressure, or the influence of the behavioral patterns of potential predators like *C. conger* and *S. canicula*, which are still unknown. Future perspectives include studying the spatial ecology of these identified potential predators from **Chapter 2.2** and maintaining the monitoring of Norway lobster behavior within the protected area.

3.2.3. Assessing the effectiveness

No-take fishery reserves can serve as valuable measures for the recovery of overexploited species, benefiting both conservation efforts and fisheries. However, it is crucial to assess the effects of spatial closures in order to examine their effectiveness. In **Chapters 2.4** and **2.5**, the pilot no-take fishery reserve was evaluated using two distinct methodologies. In **Chapter 2.4**, an evaluation was conducted using a BACI (Before - After - Control - Impact) approach. This involved carrying out experimental trawling surveys before and after four years of implementing the deep-sea no-take reserve. By comparing the data from these surveys, the impact of the reserve could be assessed. In **Chapter 2.5**, the pilot no-take reserve was evaluated after only 2.5 years of implementation using video ROV (Remotely Operated Vehicles) surveys. These non-invasive and alternative methodologies provided an opportunity to assess the reserve without the need for trawling surveys. In both methodologies the no-take reserve was evaluated and compared with a control area with similar characteristics to the reserve, except that it was an actively fished area.

In **Chapter 2.4**, the Norway lobster population within the no-take reserve showed clear signs of recovery compared to the control area and the initial state of the reserve four years ago. Abundance and biomass values were higher in the no-take reserve, indicating population growth. The population increased by 60% compared to the baseline state before the closure, while in the control area, it decreased by 80% compared to the baseline. The size structure of the population also improved within the reserve, with both males and females reaching larger sizes compared to the control area and the baseline. This recovery in size structure is often observed in overexploited species responding to shifts in size-selective mortality within protected areas (Baskett and Barnett, 2015; Moland et al., 2021). The sampling period for the study was consistent, focusing on the brooding period, when females carry their eggs and seek shelter in their burrows. The no-take reserve exhibited a higher abundance of berried females compared to the other two areas, indicating increased potential recruitment with more individuals contributing to the local population and a higher likelihood of spillover of eggs and larvae (Agnalt et al., 2007; Di Salvatore et al., 2021). The combination of higher abundance and larger females can result in a higher reproductive output, producing more offspring in better condition (Hixon et al., 2014; Dick et al., 2017). In **Chapter 2.5**, a non-invasive methodology was employed to evaluate the Norway lobster population using video surveys. Two methodologies, "burrow-system counting" and "animal counting," were utilized to estimate stock abundance and biomass. Both approaches were effective in describing the population of Norway lobsters, with the animal counting method being more reliable and allowing for the examination of the lobsters' activity patterns. The presence of Norway lobsters was more limited at night, with most individuals exhibiting door-keeping behaviors. This supports the understanding that locomotor activity in Norway lobsters inhabiting deep ecosystems below 300 m in depth is predominantly observed during daylight hours (Aguzzi et al., 2003; **Chapter 2.2**). Overall, all evaluated variables, including abundance, mean body size, and biomass, reflected the positive effects of passive restoration in the no-take reserve. The species within the reserve demonstrated a rapid response to protection from fishing, showcasing the potential benefits of such conservation measures. Moreover, the no-take reserve may have also affected the diet composition and trophic biology of Norway lobsters, as described in **Chapter 2.4** Norway lobster's diet consists basically of other decapods, other crustaceans (euphausiids and peracarids), and fish, but in many cases, particularly among medium and small individuals, suspended particulate organic matter constitutes a significant part (Cristo, 1998; Cristo and Cartes, 1998; Santana et al., 2020). Greater food availability and the presence of larger individuals in the no-take reserve may have generated this trophic shift inside the no-take reserve. Spatial closures not only involve positive shifts in single targeted species but also in habitat and ecosystem status (Bourlat et al., 2021).

In both **Chapters 2.4** and **2.5**, the biodiversity and megafaunal assemblages were found to be similar between the no-take reserve and the control area, as well as compared to the baseline monitored using trawling surveys. The species composition showed similarities, but when evaluating at the species level, some organisms exhibited signs of recovery within the no-take reserve. Specifically, using ROV video surveys described in **Chapter 2.5**, after only 2.5 years, two teleost species, *Helicolenus dactylpterus* and *Trigla lyra*, which are also targeted by Norway lobster fishers, were found in higher abundances inside the no-take fishery reserve compared to the control area. The anemones from the family Cerianthidae were found in higher abundance in both areas, but their abundance was even higher in the no-take reserve, indicating that they may also be sensitive to trawling, despite their ability to retract and offer some resistance (Hall-Spencer, 1999; Kenchington et al., 2006). After four years of protection, as detailed in **Chapter 2.4**, H. dactylopterus continued to exhibit signs of recovery in terms of abundance and biomass. T. lyra did not show significant differences compared to the control area and baseline, but two other teleost species, *Coelorhynchus caelorhincus* and *Phycis blennoides*, did exhibit differences. *H. dactylopterus* may be resilient to fishing pressure due to the dispersal of young individuals to northern areas and its effective reproductive strategy, which includes viviparity that confers high fecundity and enhanced survival for embryos and larvae (Muñoz and Casadevall, 2002; Ribas et al., 2006). These teleost species, along with *C. caelorhincus* and *P. blennoides*, have a wide bathymetric distribution in the northwestern Mediterranean Sea, but higher densities are typically found in areas with greater food availability, which may be the case within the no-take reserve (Massutí et al., 1996; García-Ruiz et al., 2020). The increased abundance of Norway lobster and other protected species may have an impact on the population structure of other species that rely on their density and availability, such as their potential predators.

The potential predators identified in **Chapter 2.2** were specifically evaluated in **Chapters 2.4** and **2.5** to observe possible fluctuations due to the recovery of prey species within the no-take reserve (Coll et al., 2006; Daskaloc et al., 2007). This approach is crucial even in small marine protected areas, as a change in predator densities could hinder or undermine the recovery of overexploited species (Clements and Hay, 2017). None of the evaluated potential predators showed signs of higher abundance, biomass, or larger sizes within the no-take reserve. However, in **Chapter 2.4**, during the experimental trawl surveys, the demersal shark *S. canicula* did show higher biomass, likely due to the cessation of the extraction of larger individuals within the protected area. This demersal shark has a wide distribution and high abundances in the Mediterranean but is negatively affected by fishing pressure, leading to reduced population densities (Navarro et al., 2016). *S. canicula* was described as a potential predator of Norway lobsters to consider in the no-take reserve evaluation due to its high densities in their habitats that may influence prey densities (Šantić et al., 2012; Barría et al., 2018). Indeed, it is worthwhile to monitor the population fluctuations of the demersal shark *S. canicula*, even though it is not critically endangered or commercially valuable. As an opportunistic predator of Norway lobsters, its presence could have an impact on the dynamics of the Norway lobster population within the protected area. Additionally, monitoring the population fluctuations of *S. canicula* can provide valuable insights into the overall health and resilience of the ecosystem. Changes in predator populations can indicate shifts in the structure and functioning of the marine community. Therefore, continued monitoring of this predator species can help assess the long-term effectiveness and ecological benefits of the no-take reserve in promoting the recovery of overexploited species and maintaining a balanced ecosystem.

As a non-invasive methodology, the surveys conducted in **Chapter 2.5** were useful for evaluating the seafloor integrity of the no-take reserve. The marine litter and terrestrial vegetation present in all marine habitats, including remote areas, were also quantified and classified (Pham et al., 2014). Both the control area and the no-take reserve showed similar densities of marine litter and terrestrial vegetation, indicating that the cessation of trawling fisheries did not lead to an increased accumulation of marine litter or terrestrial vegetation. These debris are continuously distributed and transported by strong currents and other hydrographic and geomorphological factors in the ocean (Galgani et al., 2000; Barnes et al., 2009). Plastic was the most abundant form of marine litter found, which is globally increasing and known to have documented impacts on marine ecosystems (Sheavly and Register, 2007; Mecho et al., 2021).

Regarding seafloor integrity, after only 2.5 years of closure, the reserve had almost completely recovered from trawl marks. Bottom trawl fisheries are one of the most intensive fishing practices that cause morphological changes to the seafloor, resuspend sediment, alter nutrient cycles, and increase bottom-water turbidity (Puig et al., 2012; Pusceddu et al., 2014). The control area showed more than 60% presence of various trawl mark alterations, while in the no-take reserve, only 5% still showed impacts, but with soft trawl marks already in the process of recovery. The fast recovery could possibly be attributed to hydrodynamic parameters such as tidal currents and natural sedimentation (Linnane et al., 2000). The seafloor integrity status served as a good indicator for measuring the passive recovery of the habitat from trawl fishing pressure.

To conclude this section on the effectiveness of no-take fishery reserves, it is essential to discuss the potential benefits for nearby fisheries. To do this, the spillover effect was evaluated to observe potential benefits to fisheries despite the loss of the spatially closed area (Di Lorenzo et al., 2016; Lenihan et al., 2021). While **Chapter 2.3** defined the behavior of the Norway lobster as territorial with small home ranges, indicating that most tagged individuals should have remained within the protected area, **Chapter 2.4** evaluated the potential spillover of Norway lobster biomass from the no-take reserve into the surrounding fishing area. By evaluating the biomass landed (LPUE data) from 2016 to 2021 in the buffer areas of both the no-take reserve and the control area, a decreasing trend over time was observed, as also noted in the entire Catalan Sea in **Chapter 2.1**. Despite the population decline, the ratio of loss within the buffer of the no-take reserve was lower than that of the control area, possibly due to a mitigation effect resulting from the export of individuals from the no-take reserve. It is important to continue monitoring the effects within and around the no-take reserve to further understand its impact on nearby fisheries.

3.3. Networks of no-take fishery reserves

A network of marine protected areas (MPAs) refers to a system of multiple MPAs that work together to protect a broader range of habitats, species, and ecological processes, thereby enhancing conservation outcomes and promoting the sustainable use of marine resources on a larger scale with an ecosystem-based perspective (Gaines et al., 2010; Mangubhai et al., 2015). The interconnected nature of these networks enables the movement of marine species, including adult individuals, larvae, and eggs dispersal. This facilitates gene flow, population resilience, and the maintenance of healthy ecosystems (Christie et al., 2010).

However, designing effective networks of MPAs presents various challenges and issues (Rees et al., 2018; Kininmonth et al., 2019). Some of these challenges include inadequate MPA coverage or size to adequately protect and conserve marine ecosystems, the difficulty of minimizing negative impacts on fisheries, and determining the most effective locations for conservation while considering nearby fisheries (Claudet et al., 2010; Gleason et al., 2013). Systematic conservation planning approaches and decision-support tools for optimization can help address some of these problems (Possingham et al., 2006; Giakoumi et al., 2011).

There are four key principles that are required when designing a conservation network of marine reserves. These principles, called CARE, are fundamental to conserving biodiversity in the long term and consist of ensuring Connectivity, Adequacy, Representativeness, and Efficiency (Linke et al., 2011; Kukkala et al., 2013). Connectivity refers to the exchange of individuals, populations, communities, or ecosystems (Daigle et al., 2020) among habitats through migration, larvae, currents, or even non-spatial processes such as disease. When a minimum conservation target is set for habitat types or species, the goal is to achieve the Adequacy of the network by representing and containing enough of every conservation feature. Representativeness is also a crucial principle that aims to ensure that the network selected conserves and protects all the biodiversity present in the region. Then, Efficiency aims to find balance between conservation and the many other activities, such as commercial interests, that are occurring in the area (Possingham et al., 2006; Sarkar et al., 2006).

3.3.1. Incorporating a dynamic ocean management

Chapter 2.6 examined and compared different approaches to designing a network of spatial closures that incorporate dynamic management. These approaches considered seasonal variations in species biomass and aimed to achieve both conservation and a sustainable multi-specific deep-water fishery. The results indicated that dynamic management scenarios required regulation of larger areas, primarily through temporal closures. However, these options resulted in lower opportunity costs for fisheries while demonstrating a greater capacity for biomass conservation. Thus, they proved to be more effective measures for conservation.

Dynamic management has been applied in marine, freshwater, and terrestrial ecosystems to manage rapidly shifting features across different spatial scales (Hermoso et al., 2011; Adams et al., 2014; Dunn et al., 2016). Most existing dynamic management strategies focus on a single target species (Howell et al., 2008) or rely on bycatch events to initiate management actions (Dunn et al., 2016). Other studies solely focus on changing environmental variables, such as temperature or currents, driven by ecological, oceanographic, and atmospheric processes (Hazen et al., 2017; Ortuño Crespo et al., 2020). In this study, we tested four dynamic management scenarios that accounted for seasonal variations in targeted species, fisheries landings, and total fishery income. The goal was to ensure effective conservation and a sustainable fishery while minimizing opportunity costs.

Dynamic management strategies are valuable for highly mobile species as well as demersal species like the Norway lobster (Dunn et al., 2016; Hazen et al., 2017). In this case, dynamic scenarios presented a theoretical methodology using the popular systematic conservation tool, Marxan software, to adapt permanent and spatial closures to the variability in Norway lobster landings, which can be attributed to the biology of the species (Aguzzi et al., 2007; 2023). These strategies can be implemented not only for the conservation and sustainable fishery of the Norway lobster and its coexisting vulnerable species but also for other species, regions, and temporal scales.

No-take fishery reserves, which are permanent spatial closures, have proven to be effective and useful tools for conservation (Sala and Giakoumi, 2011). There are other spatial measures called Other Effective Area-based Conservation Measures (OECMs) defined by the Convention on Biological Diversity (CBD) that can complement protected areas and achieve positive conservation outcomes, even if they are managed for other reasons (CBD, 2018). In the context of fisheries management and marine conservation, Fishery Restricted Areas (FRAs) are the most relevant OECMs (Petza et al., 2019). They involve permanently or temporarily restricting specific fishing activities to recover exploited fishing stocks, habitats, and deep-sea ecosystems (Borrini-Feyerabend & Hill, 2015). However, identifying and selecting suitable areas for conservation is a challenging task (MacKinnon et al., 2015; Alves-Pinto et al., 2021). This problem was addressed by identifying and prioritizing the most suitable areas using a systematic conservation tool (Burns et al., 2023). The proposed permanent closures can be characterized as no-take marine reserves focused on conservation, while the temporary closures can be considered a type of FRAs that promotes sustainable fisheries (GFCM, 2021; Chiarini et al., 2022).

In conclusion, we compared the effectiveness of a static approach with different dynamic scenarios, which demonstrated better outcomes at a lower opportunity cost. However, it is crucial to integrate specific socioeconomic objectives into conservation practices to ensure equity among various stakeholder groups and fishery associations in the planning region. This integration can significantly impact conservation outcomes and management efficiency and effectiveness (Halpern et al., 2013; Gurney et al., 2015; Klein et al., 2015).

3.3.2. Socioeconomic factors and the importance of equity

Global conservation policy recognizes the need to integrate ecological, social, and economic goals for successful marine conservation and management (Scholz et al., 2011; Markantonatou et al., 2021). Despite the increasing spatial coverage of Marine Protected Areas (MPAs) and other spatial measures, their effectiveness and equity have often fallen short (De Santo, 2013; Spalding et al., 2016). Many designed protected areas have experienced biological failures due to a lack of consideration for social factors, leading to issues such as food insecurity and loss of livelihood and income (Ban and Frid, 2018; Sowman and Sunde, 2018). Local support for conservation is strongly influenced by perceptions of management impacts and governance, which are often negative, highlighting the need to improve socio-economic and conservation outcomes (Jones, 2009; Bennett and Dearden, 2014).

In conservation efforts, there are three primary dimensions of social equity that must be considered and monitored in protected areas (McDermott et al., 2013; Pascual et al., 2014; Schreckenberg et al., 2016). These dimensions serve as indicators for evaluating the inclusiveness and fairness of conservation planning and management. The first dimension is recognitional equity, which involves ensuring the representation of the rights, cultures, and identities of local groups' livelihoods in conservation planning and management. The second dimension is procedural equity, which emphasizes the effective participation of all groups in decision-making and rule-setting processes. The third dimension is distributional equity, which focuses on the fair distribution of benefits and burdens among various groups. Although some recent studies have developed indicators for assessing equity across these dimensions, they may not be applicable to local groups, such as small-scale fishers (Zafra-Calvo et al., 2017; Bennet et al., 2020).

The area of study of this thesis comprises the Catalan fishery, which is divided among multiple fishery associations operating in different fishing grounds (Fig. 3.1). Therefore, ensuring an equitable distribution of fishing limitations is desirable. The West Med MAP (Regulation EU 2019/1022 of the European Parliament and Council of June 20; European Commission, 2019) aims to conserve demersal stocks and endure sustainable operations in the Western Mediterranean Sea by reducing fishing effort (i.e., reducing fishing time by vessel or number of fishing vessels). However, it has already been suggested that this measure is insufficient for recovering stocks (Sola et al., 2020). To manage fishery activity and achieve sustainable fisheries, the bottom trawlers associated with each of the different ports are forced to cease all fishing activity for around 2.5 months at different periods without following any biological advice (see Fig. 3.1; BOE No. 26, 31/01/2023). Just recently, a fishery monitoring process was initiated to gather high-quality data and establish a foundation for providing biological advice to fisheries (ICATMAR, 2021). Moreover, some research projects have been developed to address the needs of fishers and stakeholders (BITER; PID2020-114732RB-C31). One of these projects is associated with this Ph.D. thesis and originated from an agreement between scientists and two fisheries associations (RESNEP; CTM2017-82991-C2-1-R).

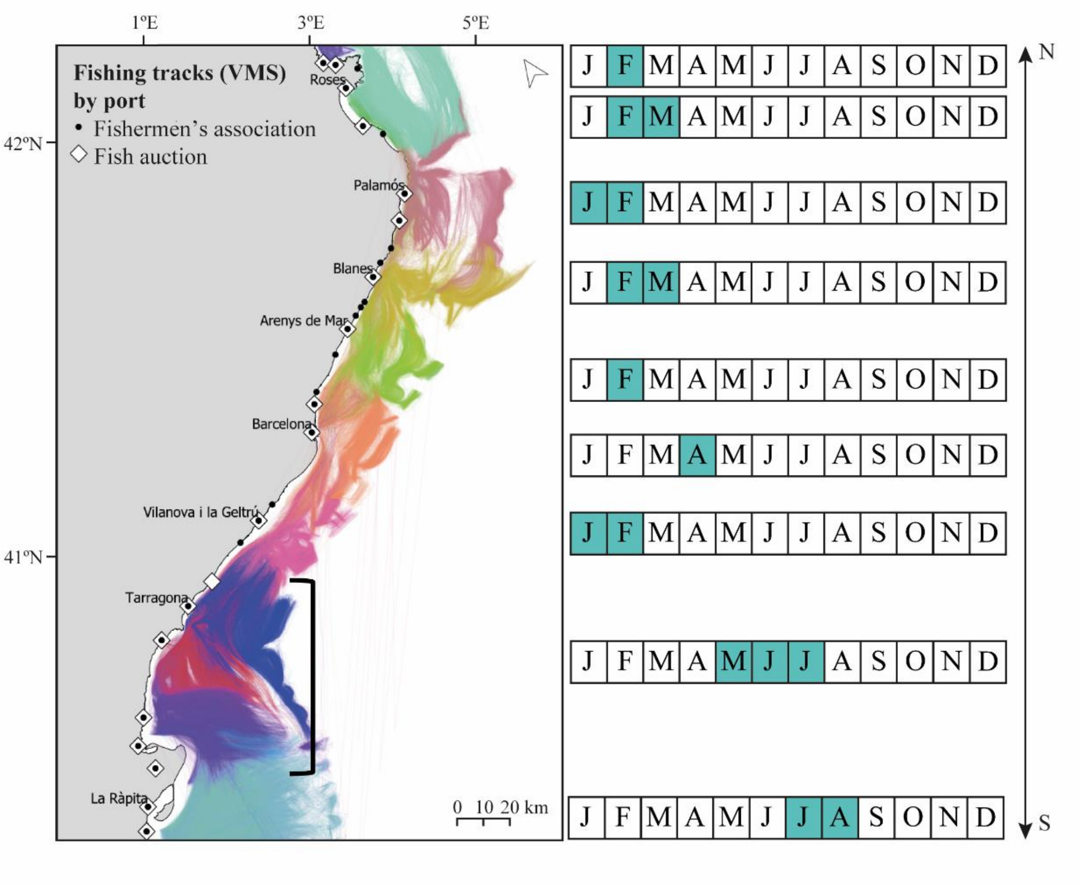

Figure 3.1. The socioeconomic context of the Catalan bottom trawl fisheries. Fishing activity primarily occurs locally, as represented by the Vessel Monitoring System (VMS) tracks. The temporal fishing closures from the trawling fleet in 2022 (in green on the calendar) differ in each fishermen's association, and they do not follow any biological advice. Figure adapted from ICATMAR, 2022.

Future perspectives should prevent any single fishing association or fishing ground from shouldering the unfair burden of the restrictions or experiencing disproportionate impacts. Incorporating socioeconomic and equity objectives, as well as a dynamic management approach, into the design of MPAs or other spatial closures is essential to guaranteeing the long-term success of both biodiversity conservation and fisheries goals and promoting an equitable distribution of fishing limitations. The next step, which is already in progress, involves using a systematic conservation tool (such as Marxan, Marxan with Zones, or Prioritization) to select and prioritize the most suitable areas in different subareas associated with each fishing association in the Catalan coast. Multiple objectives will be set for each subarea, tailored to the specific needs of each fishery association. To do this, we plan to set multiple objectives for each subarea that will be adapted to the necessities of each fishery association. Large-scale marine protected areas (LMPAs) can offer many advantages over smaller and multiple marine MPAs as they meet a variety of objectives (Gaines et al., 2010; Wilhelm et al., 2014), are politically and administratively easier to manage, and are less expensive to establish (Balmford et al., 2004; McCrea-Strub et al., 2011). However, LMPAs exhibit unique characteristics in terms of form, function, and conceptualization, and they still need to incorporate and scope the human dimensions of governance, politics, and social and economic outcomes (Gruby et al., 2016). To achieve a successful and effective MPA, it is essential to set multiple biological and social objectives, as they are strongly correlated and should be equally considered (Christie, 2004; Ban et al., 2017) We suggest, as also observed in many other areas (O'Leary et al., 2018), that in areas such as the Catalan coast divided by multiple groups, the establishment of multiple small spatial closures may be more adequate than establishing a unique, larger area to better represent the equity and necessities of the local fisheries.

Chapter 4. Summary of Conclusions

The main conclusions derived from the present Ph.D. thesis are:

1. Annual landings of Norway lobster of trawling fisheries in the northwestern Mediterranean Sea have experienced a significant decline during the last two decades.

2. The population of Norway lobsters in the northwestern Mediterranean Sea has shown an evident reduction in size at 50% maturity, suggesting high fishing pressure and insufficient management measures.

3. Norway lobsters may be experiencing a subtle shift in their reproductive cycle, with spawning and brooding occurring approximately 1 to 2 months earlier.

4. The main predators of Norway lobsters in deep-sea Mediterranean waters, identified using genetic and isotopic markers, were the cephalopods *Sepietta oweniana* and *Abralia veranyi*.

5. The inclusion of predator density data was a good indicator for identifying key predator species that may have the highest influence on prey populations, providing pivotal information to develop accurate predictions and assessments of predator-prey dynamics.

6. The identification of the main predators of Norway lobster contributes to understanding prey-predator interactions and the ecological role of predators in Norway lobster fishing grounds, providing valuable information for ecosystem-based fisheries management, evaluating the effectiveness of marine protected areas, and restoring Norway lobster populations in the Mediterranean Sea.

7. Combining acoustic tracking and capture-recapture data provided description of the spatial ecology of Norway lobsters in the deep-water Mediterranean Sea. The findings serve as a baseline for designing no-take reserves by providing insights into their movement patterns, habitat use, and population dynamics.

8. Norway lobster individuals acoustically tagged dispersed a few hundred meters once deployed over a delimited area with acoustic arrays, displaying a territorial and solitary behavior, indicating individual establishment in burrows.

9. The low recapture rate of tagged individuals indicates the majority of Norway lobsters remained within the no-take marine reserve, suggesting it is possible to protect Norway lobster populations using medium-small no-take marine reserves.

10. The no-take reserve in deep Mediterranean waters has improved the abundance, biomass, and body size of Norway lobsters, as well as the population parameters of other species and the integrity of the seabed.

11. The no-take reserve influenced the diet composition and trophic biology of the Norway lobsters, with individuals inside the reserve consuming resources placed at higher positions in the food web.

12. The no-take reserve also had a positive spillover effect, with higher biomass observed around its borders compared to the surroundings of the control area. The high presence of berried females in the no-take reserve suggests an increase in the potential for recruitment, resulting in more individuals added to the local population and a potential spillover of eggs and larvae.

13. At the community level, while diversity and species richness remained similar between the no-take reserve and a control area, there was an increase in the population descriptors of four teleost species (*Coelorinchus caelorhincus, Helicolenus dactylopterus, Trigla lyra, and Phycis blennoides*), one elasmobranch (*Scyliorhinus canicula*), and different sessile species of the family Cerianthidae in the no-take reserve.

14. The recovery of the no-take reserve helped to restore seafloor morphology and reduce the impacts associated with otter bottom trawling, such as nutrient cycle alterations, sediment resuspension, and increased bottom-water turbidity.

15. While experimental trawling surveys provide more species community information, video surveys offer a non-invasive methodology that allows for a comprehensive assessment of the population of Norway lobsters in the no-take reserve as well as habitat recovery indicators. These surveys also provided other valuable information as the behavior patterns of some species and the visual characteristics of the seabed.

16. The recovery rate of the Norway lobster population in the studied area suggests that marine protected areas (MPAs) can provide quick benefits in locations near fishing grounds with elevated fishing mortality and stocks below sustainable fishing levels.

17. Dynamic management demonstrated greater effectiveness in achieving conservation and fisheries targets. While permanent closures are effective in conserving biomass and preserving habitats, their combination with temporal closures can achieve conservation targets at a lower opportunity cost for fisheries.

18. The benefits of spatial closures extend beyond retaining existing biomass, as they can increase species density and biomass and reduce unintended catches of non-target species.

19. Identifying suitable areas for conservation is challenging. Planning decision-support tools are a useful measure to prioritize areas that meet all conservation targets while minimizing impacts on socio-economic activities.

20. Incorporating socioeconomic and equity objectives, along with a dynamic management approach, into the design of MPAs and spatial closures is essential for long-term success in achieving both biodiversity conservation and fisheries goals.

21. More effective conservation and management efforts are needed to address challenges posed by changing conditions, such as climate change. Monitoring of dynamic management networks, including biomass and species abundance, predator densities, and ecological impacts, is necessary to assess the effectiveness of reserves and make necessary adjustments.

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Annex I – Supplementary materials

Supplementary materials – Chapter 2.1

Table S2.1.1. Data on Norway lobsters of annual landings (in kg) and total incomes (in €), and fishing effort (total number of days of the entire fleet) off the coast of Catalonia from 2000 to 2021. Data obtained from the Fisheries Department Service of the *Generalitat de Catalunya*.

Year	Landings (kg)	Incomes (€)	Fishing effort
2000	322,853	5,522,027	19,576
2001	358,019	7,402,786	25,587
2002	29,243	6,421,732	25,063
2003	265,209	6,285,006	23,911
2004	286,306	6,982,301	24,447
2005	281,437	7,239,611	23,559
2006	337,333	8,526,531	23,773
2007	355,058	8,336,023	22,667
2008	310,827	6,800,817	23,266
2009	396,893	7,118,555	22,542
2010	371,308	6,653,685	22,071
2011	331,951	6,317,725	22,294
2012	335,879	5,749,883	20,280
2013	347,513	5,633,631	19,681
2014	332,274	6,108,770	20,366
2015	209,324	4,626,820	18,465
2016	173,321	3,845,414	16,379
2017	176,823	4,093,695	15,967
2018	191,605	4,249,397	14,701
2019	183,704	4,174,236	14,506
2020	130,892	3,471,217	13,076
2021	112,206	3,331,655	12,174

Table S2.1.2. Spatial similarity matrix comparing the presence of *N. norvegicus* from 2008 to 2021 (see Figure 3 for annual spatial distribution of catches). Values represent Cohen's kappa coefficient ranges from − 1 to + 1, where − 1 represents complete disagreement, 0 indicates agreement no better than that expected by chance and + 1 indicates complete agreement.

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
2008													
2009	**0.45**												
2010	0.47	**0.54**											
2011	0.56	0.48	**0.52**										
2012	0.51	0.47	0.46	**0.53**									
2013	0.47	0.40	0.47	0.53	**0.53**								
2014	0.42	0.32	0.39	0.44	0.49	**0.56**							
2015	0.41	0.35	0.42	0.45	0.50	0.49	**0.48**						
2016	0.39	0.3	0.43	0.50	0.42	0.47	0.41	**0.48**					
2017	0.32	0.32	0.33	0.38	0.40	0.38	0.34	0.41	**0.52**				
2018	0.33	0.30	0.33	0.39	0.36	0.38	0.36	0.43	0.48	**0.47**			
2019	0.38	0.33	0.35	0.43	0.42	0.42	0.42	0.45	0.49	0.52	**0.50**		
2020	0.29	0.28	0.31	0.37	0.37	0.37	0.36	0.43	0.51	0.51	0.49	**0.54**	
2021	0.28	0.25	0.27	0.34	0.35	0.34	0.35	0.35	0.46	0.49	0.46	0.50	**0.55**

Table S2.1.3. Bathymetry range similarity matrix comparing the LPUE of *N. norvegicus* from 2008 to 2021. Values represent Spearman's correlation coefficients that range from − 1 to + 1, indicating the direction and the strength of the relationship between 2 variables, being stronger closer to -1 or 1 and independent variables closer to 0.

	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
2008													
2009	**0.99**												
2010	0.98	**0.99**											
2011	0.98	0.99	**0.99**										
2012	0.95	0.96	0.98	**0.97**									
2013	0.98	0.98	0.99	0.99	**0.98**								
2014	0.99	0.98	0.99	0.99	0.98	**0.99**							
2015	0.97	0.95	0.96	0.97	0.96	0.97	**0.97**						
2016	0.99	0.97	0.98	0.98	0.97	0.98	0.99	**0.98**					
2017	0.98	0.95	0.94	0.93	0.92	0.93	0.96	0.96	**0.98**				
2018	0.99	0.97	0.96	0.96	0.95	0.96	0.98	0.97	0.99	**0.98**			
2019	0.99	0.98	0.96	0.96	0.95	0.96	0.97	0.96	0.99	0.99	**0.99**		
2020	0.99	0.99	0.98	0.98	0.97	0.98	0.98	0.96	0.99	0.96	0.98	**0.99**	
2021	0.99	0.99	0.97	0.96	0.96	0.97	0.97	0.95	0.99	0.97	0.99	0.99	**0.99**

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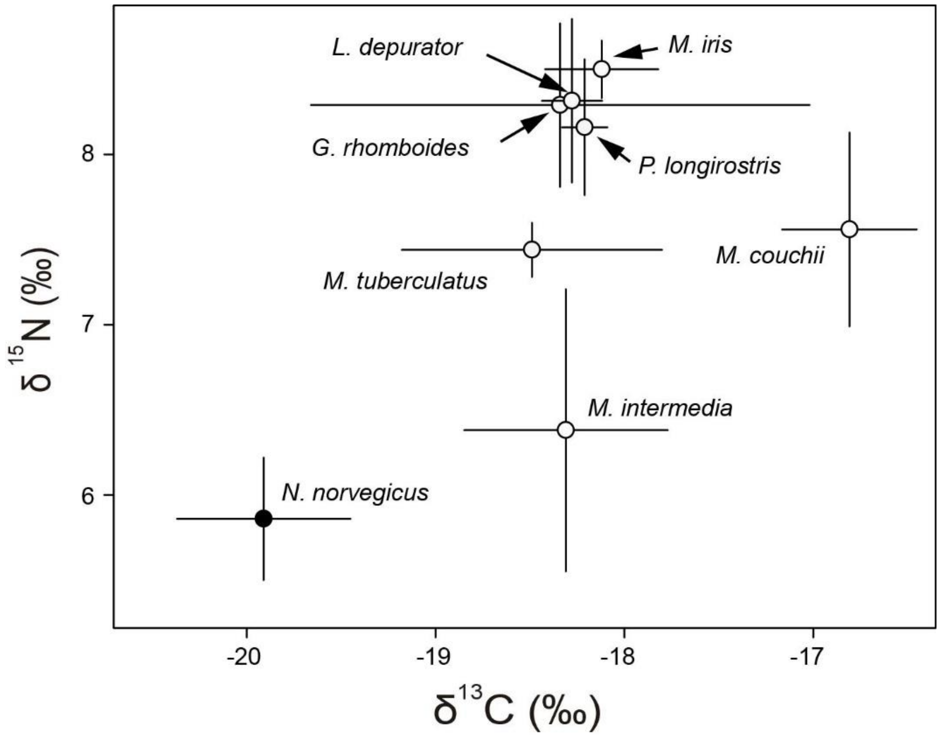
Figure S2.2.1. Mean and standard deviation of $\delta^{15}N$ and $\delta^{13}C$ of *Nephrops norvegicus* and seven cohabiting crustaceans (*Liocarcinus depurator, Munida iris, M. intermedia, Goneplax rhomboides, Parapenaeus longirostris, Macropipus tuberculatus* and *Monadaeus couchii*) from the northwestern Mediterranean Sea. The stable isotope values of cohabiting crustaceans were obtained from published studies developed in the NW Mediterranean Sea (Barría et al. 2015, Polunin et al. 2001).



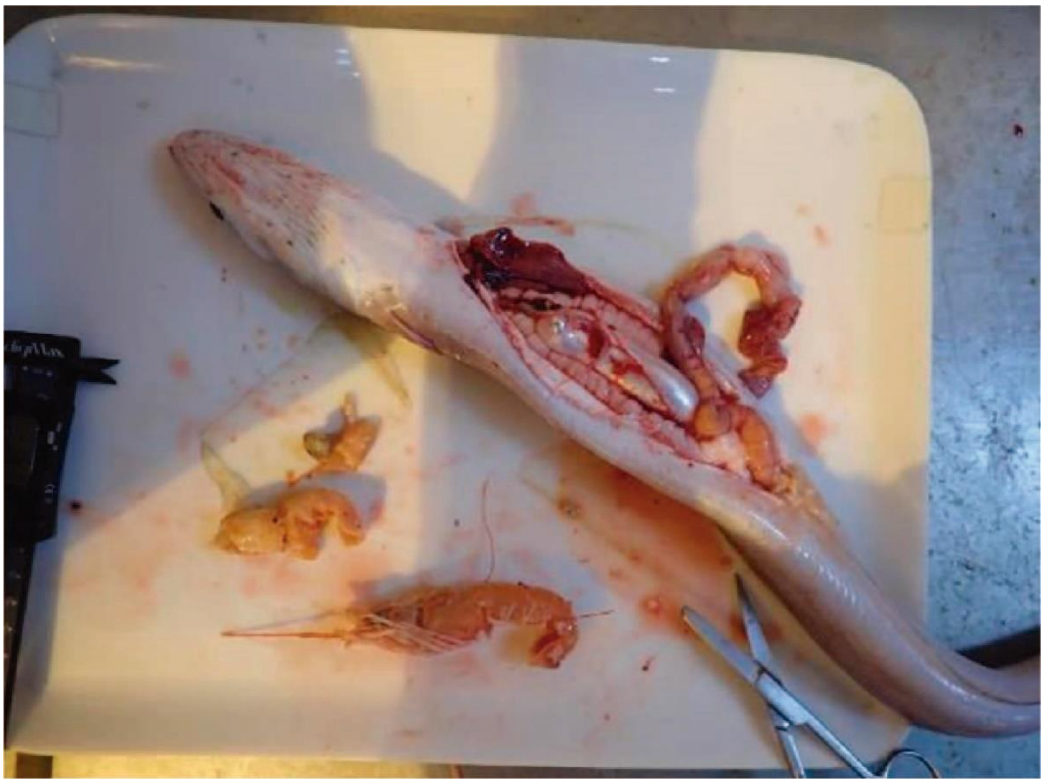
References:

Barría, C., Coll, M., & Navarro, J. (2015). Unravelling the ecological role and trophic relationships of uncommon and threatened elasmobranchs in the western Mediterranean Sea. *Marine Ecology Progress Series*, *539*, 225-240.

Papiol, V., Cartes, J. E., Fanelli, E., & Rumolo, P. (2013). Food web structure and seasonality of slope megafauna in the NW Mediterranean elucidated by stable isotopes: relationship with available food sources. *Journal of Sea Research*, *77*, 53-69.

Polunin, N. V. C., Morales-Nin, B., Pawsey, W. E., Cartes, J. E., Pinnegar, J. K., & Moranta, J. (2001). Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. *Marine Ecology Progress Series*, *220*, 13-23.

Figure S2.2.2. *Conger conger* with two individuals of *Nephrops norvegicus* captured in a creel trap for *N. norvegicus* placed in the study area during a research vessel campaign conducted in 2019.



Supplementary materials – Chapter 2.3

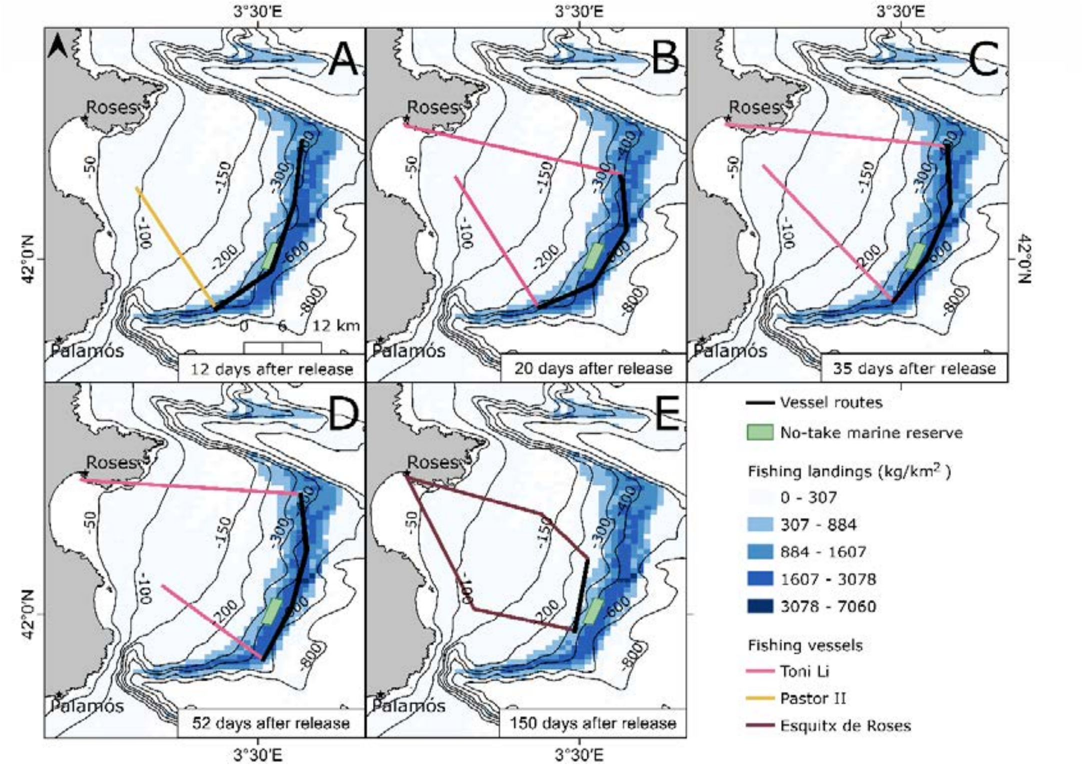


Figure S2.3.1. Trajectories of the trawlers that recaptured the 5 Norway lobsters with coded tags (previously released inside the no-take reserve). The number of days after the release is also indicated. The recaptured Norway lobsters in the panels AD were also instrumented with an acoustic tag.

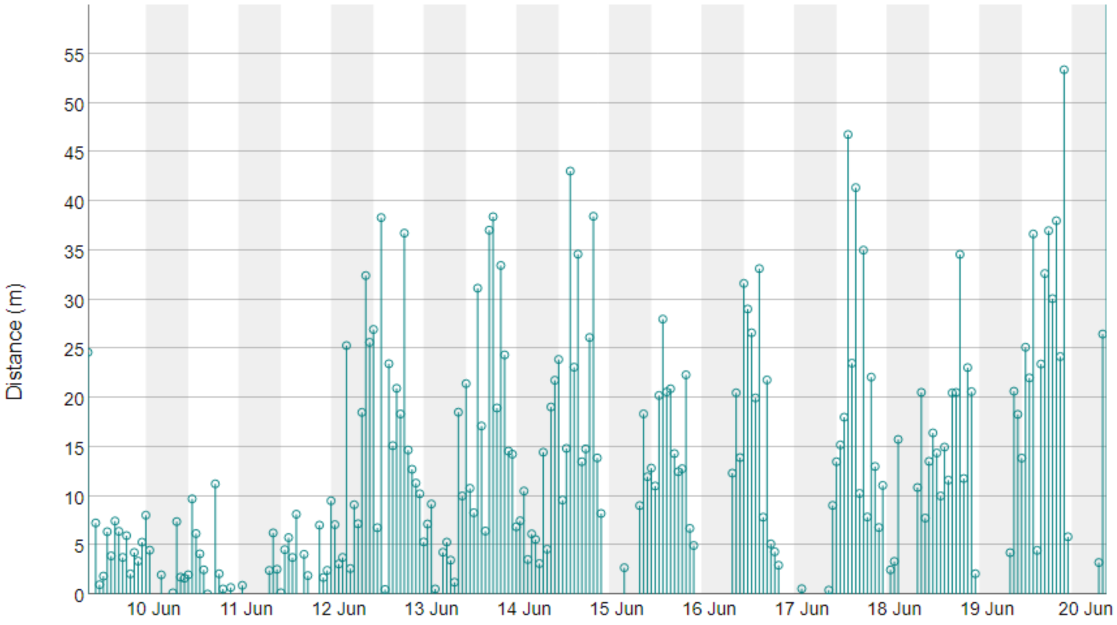


Figure S2.3.2. Distance in metres covered per hour of individual 14459 captured on 20th of June by the fishing vessel Pastor II. Dark shadows represent dark hours.

Table S2.3.1. Kernel UD estimates in 95% and 50% for all individuals in each period. The animal acoustic identified (ID) is also reported.

ID	MONTH	UD90 (m^2)	Mean value (UD90)	SD (UD90)	UD50 (m^2)	Mean value (UD50)	SD (UD50)
14456	June	41,295	41,295	0	7,350	7,350	0
14457	June	12	13.5	2.12	3	3	0
	July	15			3		
14458	June	8,671	8,671	-	2,335	2,335	0
14459	June	243	243	-	43	43	0
14462	June	447	447	-	115	115	0
14463	June	171	77.25	63.16	35	17.25	12.84
	July	36			6		
	August	44			10		
	September	58			18		
14464	June	5,051	5,051	-	1,168	1,168	0
14465	June	47,022	19,912.33	23,478.43	7,355	3,359	3,460.66
	August	6,168			1,372		
	September	6,547			1,350		
14468	June	396	492.5	365.61	50	66.5	55.41
	July	736			73		
	August	820			138		
	September	18			5		
14470	June	21,195	21,195	-	7,435	7,435	0
14471	June	135	135	-	37	37	0
14472	June	1,994	1,994	-	725	725	0
14474	June	20,168	20,168	-	5,767	5,767	0
14475	June	2,786	736.25	1,366.59	719	188.75	353.56
	July	53			8		
	August	33			7		
	September	73			21		
14477	June	5,650	5,650	-	1,503	1,503	0
14483	June	10,391	10,391	-	3,434	3,434	0
14484	June	3,076	3,076	-	605	605	0
15829	June	44,495	44,495	-	13,156	13,156	0
15830	June	47	17.75	19.72	7	3.25	2.63
	July	11			2		
	July	4			1		
	September	9			3		

Table S2.3.2. Values about all the interactions among individuals and overlapping among home ranges. Coefficient of Association (CA) values are reported (in metres, m).

Interactions	UDOI (UD90)	UDOI (UD50)	1 m	5 m	10 m	20 m	50 m
June							
ID 14456 – ID 14457	0	0	0	0	0	0	0.0037
ID 14456 – ID 14458	0.1458	0.0061	0	0	0.0025	0.0025	0.0551
ID 14456 – ID 14459	0	0	0	0	0	0	0
ID 14456 – ID 14462	0.0054	0	0	0	0	0	0
ID 14456 – ID 14463	0.0013	0	0	0	0	0.0009	0.0045
ID 14456 – ID 14464	0.0811	0.0108	0	0	0	0.0018	0.1313
ID 14456 – ID 14465	0.1752	0.0069	0	0.005	0.005	0.0076	0.0076
ID 14456 – ID 14468	0	0	0	0	0	0	0.0009
ID 14456 – ID 14470	0.0464	0.0006	0	0.0027	0.0027	0.0027	0.0107
ID 14456 – ID 14471	0.0009	0	0	0	0.0015	0.0108	0.023
ID 14456 – ID 14472	0.0003	0	0	0	0	0	0.0025
ID 14456 – ID 14474	0.0102	0	0	0.0025	0.0025	0.0025	0.0049
ID 14456 – ID 14475	0.0506	0	0	0	0.0021	0.0154	0.0842
ID 14456 – ID 14477	0.0184	0	0	0	0	0	0.0081
ID 14456 – ID 14483	0.0291	0	0	0	0	0.0027	0.0027
ID 14456 – ID 14484	0.0101	0	0	0	0.0025	0.0025	0.0049
ID 14456 – ID 15829	0.1219	0.00318	0	0	0	0	0.002
ID 14456 – ID 15830	0.0001	0	0	0	0.0012	0.0018	0.0096
ID 14457 – ID 14458	0	0	0	0	0	0	0
ID 14457 – ID 14459	0	0	0	0	0	0.0004	0.0755
ID 14457 – ID 14462	0	0	0	0	0.0014	0.0029	0.0072
ID 14457 – ID 14463	0	0	0	0	0	0	0
ID 14457 – ID 14464	0	0	0	0	0	0	0
ID 14457 – ID 14465	0	0	0	0	0	0	0
ID 14457 – ID 14468	0	0	0	0	0	0.0003	0.2765
ID 14457 – ID 14470	0.0003	0	0	0	0	0	0.0005
ID 14457 – ID 14471	0	0	0	0	0.0005	0.1069	0.1131
ID 14457 – ID 14472	0	0	0	0	0	0	0.0011
ID 14457 – ID 14474	0.0018	0.0004	0	0	0	0.0064	0.0149
ID 14457 – ID 14475	0	0	0	0	0	0	0
ID 14457 – ID 14477	0	0	0	0	0	0	0
ID 14457 – ID 14483	0.0004	0	0	0	0	0	0.0055
ID 14457 – ID 14484	0	0	0	0	0	0.0005	0.0059
ID 14457 – ID 15829	0.0002	0	0	0	0	0	0.002
ID 14457 – ID 15830	0	0	0	0	0	0	0.2875
ID 14458 – ID 14459	0	0	0	0	0	0	0.0091
ID 14458 – ID 14462	0.0917	0.0236	0	0.0009	0.0179	0.258	0.2732
ID 14458 – ID 14463	0	0	0	0	0	0	0.0452
ID 14458 – ID 14464	0.4240	0.0603	0	0	0	0	0.0009
ID 14458 – ID 14465	0.0096	0	0	0	0	0	0.0011
ID 14458 – ID 14468	0	0	0	0	0	0	0.0096
ID 14458 – ID 14470	0.0067	0	0	0	0	0	0.0012
ID 14458 – ID 14471	0	0	0	0	0	0	0
ID 14458 – ID 14472	0.0009	0	0	0	0	0	0.0122
ID 14458 – ID 14474	0.0002	0	0	0	0	0	0.0011
ID 14458 – ID 14475	0.0005	0	0	0	0	0	0.0313
ID 14458 – ID 14477	0.0003	0	0	0	0	0	0.0012
ID 14458 – ID 14483	0.0009	0	0	0	0	0	0.0012
ID 14458 – ID 14484	0.0353	0.0013	0	0	0	0.0011	0.0445
ID 14458 – ID 15829	0.0633	0.0113	0	0	0	0	0
ID 14458 – ID 15830	0	0	0	0	0	0	0.149
ID 14459 – ID 14462	0	0	0	0	0	0.0021	0.2532
ID 14459 – ID 14463	0	0	0	0	0	0	0
ID 14459 – ID 14464	0	0	0	0	0	0	0
ID 14459 – ID 14465	0.0001	0	0	0	0	0	0
ID 14459 – ID 14468	0.5942	0	0.0024	0.0224	0.1165	0.1957	0.2024
ID 14459 – ID 14470	0.0001	0	0	0	0	0	0
ID 14459 – ID 14471	0	0	0	0	0	0	0

ID 14459 – ID 14472	0.0552	0	0	0	0.004	0.0403	0.0819
ID 14459 – ID 14474	0.0080	0	0	0.0013	0.0067	0.0081	0.0174
ID 14459 – ID 14475	0	0	0	0	0	0	0
ID 14459 – ID 14477	0	0	0	0	0	0	0
ID 14459 – ID 14483	0	0	0	0	0	0	0
ID 14459 – ID 14484	0.0052	0	0	0	0	0.0081	0.0741
ID 14459 – ID 15829	0.0011	0	0	0	0	0	0.0096
ID 14459 – ID 15830	0	0	0	0	0	0	0.1661
ID 14462 – ID 14463	0	0	0	0	0	0	0
ID 14462 – ID 14464	0	0	0	0	0	0	0
ID 14462 – ID 14465	0.0032	0	0	0	0	0	0
ID 14462 – ID 14468	0	0	0	0	0.0005	0.0028	0.0755
ID 14462 – ID 14470	0.0085	0	0	0	0	0	0
ID 14462 – ID 14471	0	0	0	0	0.0052	0.0105	0.0192
ID 14462 – ID 14472	0	0	0	0	0	0.003	0.0486
ID 14462 – ID 14474	0	0	0	0	0	0	0.0121
ID 14462 – ID 14475	0	0	0	0	0	0	0
ID 14462 – ID 14477	0	0	0	0	0	0	0
ID 14462 – ID 14483	0	0	0	0	0	0	0
ID 14462 – ID 14484	0.0127	0	0	0	0	0.0122	0.0856
ID 14462 – ID 15829	0.0001	0	0	0	0	0	0
ID 14462 – ID 15830	0	0	0	0	0	0	0.1668
ID 14463 – ID 14464	0	0	0	0	0	0	0.1192
ID 14463 – ID 14465	0	0	0	0	0	0.0012	0.0037
ID 14463 – ID 14468	0	0	0	0	0	0	0
ID 14463 – ID 14470	0	0	0	0	0	0	0.0013
ID 14463 – ID 14471	0	0	0	0	0	0	0
ID 14463 – ID 14472	0	0	0	0	0	0	0
ID 14463 – ID 14474	0	0	0	0	0	0	0.0012
ID 14463 – ID 14475	0.0164	0	0	0	0	0.0352	0.1812
ID 14463 – ID 14477	0	0	0	0	0	0.0013	0.0025
ID 14463 – ID 14483	0	0	0	0	0	0	0.0013
ID 14463 – ID 14484	0	0	0	0	0	0	0.0024
ID 14463 – ID 15829	0.0035	0	0	0	0	0.0033	0.0076
ID 14463 – ID 15830	0	0	0	0	0	0	0.0005
ID 14464 – ID 14465	0	0	0	0	0	0.004	0.004
ID 14464 – ID 14468	0	0	0	0	0	0	0
ID 14464 – ID 14470	0	0	0	0	0	0.0045	0.0045
ID 14464 – ID 14471	0	0	0	0	0	0	0
ID 14464 – ID 14472	0	0	0	0	0	0	0
ID 14464 – ID 14474	0	0	0	0	0	0.0039	0.0077
ID 14464 – ID 14475	0.001	0	0	0	0	0.0012	0.0969
ID 14464 – ID 14477	0	0	0	0	0	0.0045	0.0045
ID 14464 – ID 14483	0	0	0	0.0045	0.0045	0.009	0.009
ID 14464 – ID 14484	0	0	0	0	0	0.0039	0.0039
ID 14464 – ID 15829	0.0639	0.0094	0	0	0	0	0
ID 14464 – ID 15830	0	0	0	0	0.0007	0.0007	0.0013
ID 14465 – ID 14468	0.0002	0	0	0	0	0	0
ID 14465 – ID 14470	0.0011	0	0	0.0152	0.0152	0.0152	0.0152
ID 14465 – ID 14471	0	0	0	0	0	0	0
ID 14465 – ID 14472	0.0024	0	0	0	0	0	0
ID 14465 – ID 14474	0.0005	0	0	0	0.0099	0.0099	0.0099
ID 14465 – ID 14475	0	0	0	0	0.0015	0.0015	0.0015
ID 14465 – ID 14477	0.0002	0	0	0	0	0	0.031
ID 14465 – ID 14483	0.0004	0	0	0	0	0.0159	0.0317
ID 14465 – ID 14484	0.0094	0	0	0	0.0204	0.0204	0.0204
ID 14465 – ID 15829	0.0005	0	0	0	0	0	0
ID 14465 – ID 15830	0.0003	0	0	0	0.0007	0.0015	0.0015
ID 14468 – ID 14470	0.0007	0	0	0	0	0	0
ID 14468 – ID 14471	0	0	0	0	0	0	0.0005
ID 14468 – ID 14472	0.0667	0	0	0	0.001	0.0021	0.0183
ID 14468 – ID 14474	0.0123	0	0	0	0.0005	0.0016	0.0042
ID 14468 – ID 14475	0	0	0	0	0	0	0.0016
ID 14468 – ID 14477	0	0	0	0	0	0	0
ID 14468 – ID 14483	0	0	0	0	0	0	0
ID 14468 – ID 14484	0.0159	0	0	0	0.0005	0.0031	0.0173
ID 14468 – ID 15829	0.0029	0	0	0	0	0	0.0029

ID 14468 – ID 15830	0	0	0	0.0003	0.0009	0.0198	0.2706
ID 14470 – ID 14471	0.0079	0.0009	0	0	0	0.0063	0.0438
ID 14470 – ID 14472	0.0066	0	0	0	0	0	0
ID 14470 – ID 14474	0.1434	0.0233	0	0.0129	0.0129	0.0129	0.0649
ID 14470 – ID 14475	0	0	0	0	0	0.0016	0.0016
ID 14470 – ID 14477	0.2405	0.0359	0	0	0	0.0247	0.1235
ID 14470 – ID 14483	0.4757	0.1018	0	0	0	0.0256	0.0256
ID 14470 – ID 14484	0.0237	0	0	0.0135	0.0135	0.0135	0.0135
ID 14470 – ID 15829	0.1229	0.0166	0	0	0	0	0
ID 14470 – ID 15830	0.0007	0	0	0	0.0008	0.0008	0.0008
ID 14471 – ID 14472	0	0	0	0	0	0	0
ID 14471 – ID 14474	0.0234	0.0055	0	0.0028	0.0564	0.0705	0.0874
ID 14471 – ID 14475	0	0	0	0	0	0	0
ID 14471 – ID 14477	0	0	0	0	0	0	0.0157
ID 14471 – ID 14483	0.0159	0.0011	0	0	0.0063	0.0095	0.0442
ID 14471 – ID 14484	0	0	0	0	0	0	0.0028
ID 14471 – ID 15829	0.0016	0	0	0	0	0	0.0135
ID 14471 – ID 15830	0	0	0	0	0	0	0
ID 14472 – ID 14474	0.0442	0	0	0	0	0.009	0.0631
ID 14472 – ID 14475	0	0	0	0	0	0	0
ID 14472 – ID 14477	0.0016	0	0	0	0	0	0
ID 14472 – ID 14483	0.0036	0	0	0	0	0	0
ID 14472 – ID 14484	0.1664	0.0129	0	0	0	0.02778	0.1296
ID 14472 – ID 15829	0.0051	0	0	0	0	0	0.0099
ID 14472 – ID 15830	0.0141	0	0	0.0015	0.0088	0.0204	0.0401
ID 14474 – ID 14475	0	0	0	0	0.0015	0.0015	0.0015
ID 14474 – ID 14477	0.0049	0	0	0	0	0	0.0265
ID 14474 – ID 14483	0.2886	0.0489	0	0	0	0.027	0.027
ID 14474 – ID 14484	0.0337	0	0	0	0.0092	0.0183	0.0367
ID 14474 – ID 15829	0.0385	0.0014	0	0	0	0	0.0049
ID 14474 – ID 15830	0.0006	0	0	0.0007	0.0007	0.0007	0.0044
ID 14475 – ID 14477	0	0	0	0	0	0.0031	0.0031
ID 14475 – ID 14483	0	0	0	0	0.0016	0.0016	0.0031
ID 14475 – ID 14484	0	0	0	0.0015	0.0029	0.0029	0.0237
ID 14475 – ID 15829	0.0253	0	0	0	0	0	0
ID 14475 – ID 15830	0	0	0	0	0.0005	0.0005	0.0207
ID 14477 – ID 14483	0.0772	0.0018	0	0	0.02667	0.02667	0.02667
ID 14477 – ID 14484	0.0249	0	0	0	0	0.0279	0.0279
ID 14477 – ID 15829	0.1931	0.0428	0	0	0	0	0.0059
ID 14477 – ID 15830	0.0025	0	0	0	0	0	0.0007
ID 14483 – ID 14484	0.0246	0	0	0	0.0141	0.0141	0.0141
ID 14483 – ID 15829	0.0584	0.0017	0	0	0	0	0.006
ID 14483 – ID 15830	0.0016	0	0	0	0	0.0015	0.0023
ID 14484 – ID 15829	0.0219	0	0	0	0	0	0.0049
ID 14484 – ID 15830	0.0212	0	0	0.0058	0.0227	0.0358	0.0446
ID 15829 – ID 15830	0.0009	0	0	0	0	0	0.0123
July							
ID 14457 – ID 14463	0	0	0	0	0	0	0
ID 14457 – ID 14468	0	0	0	0	0	0.0003	0.2352
ID 14457 – ID 14475	0	0	0	0	0	0	0
ID 14457 – ID 15830	0	0	0	0	0	0	0.2811
ID 14463 – ID 14468	0	0	0	0	0	0	0
ID 14463 – ID 14475	0	0	0	0	0	0.0017	0.1442
ID 14463 – ID 15830	0	0	0	0	0	0	0
ID 14468 – ID 14475	0	0	0	0	0	0	0
ID 14468 – ID 15830	0	0	0	0.0005	0.0046	0.0498	0.4173
ID 14475 – ID 15830	0	0	0	0	0	0	0
August							
ID 14463 – ID 14465	0	0	0	0	0	0	0
ID 14463 – ID 14468	0	0	0	0	0	0	0
ID 14463 – ID 14475	0	0	0	0	0.0049	0.0425	0.3252
ID 14463 – ID 15830	0	0	0	0	0	0	0
ID 14465 – ID 14468	0	0	0	0	0	0	0
ID 14465 – ID 14475	0	0	0	0	0	0	0
ID 14465 – ID 15830	0	0	0	0	0	0	0
ID 14468 – ID 14475	0	0	0	0			

ID 14468 – ID 15830	0	0	0	0.0002	0.003	0.0181	0.2491
ID 14475 – ID 15830	0	0	0	0	0	0	0
September							
ID 14463 – ID 14465	0	0	0	0	0	0	0
ID 14463 – ID 14468	0	0	0	0	0	0	0
ID 14463 – ID 14475	0	0	0	0	0.0163	0.1683	0.2853
ID 14463 – ID 15830	0	0	0	0	0	0	0
ID 14465 – ID 14468	0	0	0	0	0	0	0
ID 14465 – ID 14475	0	0	0	0	0	0	0
ID 14465 – ID 15830	0	0	0	0	0	0	0
ID 14468 – ID 14475	0	0	0	0	0	0	0
ID 14468 – ID 15830	0	0	0	0	0	0	0.2417
ID 14475 – ID 15830	0	0	0	0	0	0	0

Electronic Material

Video S2.3.1. Short movie showing a creel with a Norway lobster (*Nephrops norvegicus*) captured in the no-take marine reserve of Palamós-Roses (northwestern Mediterranean Sea), to be instrumented with acoustic tags during 2019. The creel was placed at 340 m depth and the movie was recorded with the ROV Liropus 2000 on-board the RV Sarmiento de Gamboa.

***Available as "Video_S2_3_1.mp4" in folder* PhD_Vigo_Videos:**

https://www.dropbox.com/sh/fhnlzsarne25to2/AADYWcw-2hPM8IR5u9BvaIPia?dl=0

Video S2.3.1. Release-system consisting of 2 cylindrical PVC containers, where acoustic-tagged Norway lobsters (*Nephrops norvegicus*) were placed with a dissolving latch on the door mechanism (designed to dissolve after 5-10 min longer than the estimated time for the release-system to sink to the seabed). The movie was recorded with the ROV Liropus 2000 on-board the RV Sarmiento de Gamboa.

***Available as "Video_S2_3_2.mp4" in* PhD_Vigo_Videos:**

https://www.dropbox.com/sh/fhnlzsarne25to2/AADYWcw-2hPM8IR5u9BvaIPia?dl=0

Supplementary materials – Chapter 2.4

Table S2.4.1. Information of the experimental fishing surveys conducted in 2017 and 2021, inside the control (Con) and in the no-take reserve (NTR).

ID	Year	Area	Date	Initial (Lat, Lon)	Final (Lat, Lon)	Mean depth (m)	Swept area (km^2)
1	2017	NTR	23/08/2017	41.9866, 3.5088	42.0314, 3.5494	329	0.1320
2	2017	NTR	23/08/2017	42.0325, 3.5286	41.9762, 3.5237	329	0.1378
3	2017	Con	24/08/2017	42.1075, 3.5491	42.0470, 3.5622	339.4	0.1498
4	2017	NTR	25/08/2017	41.9854, 3.5079	42.0308, 3.5502	321.8	0.1352
5	2017	Con	25/08/2017	42.0578, 3.5407	42.1077, 3.5718	322.8	0.1344
6	2017	NTR	25/08/2017	42.0313, 3.5280	41.9736, 3.5244	328.6	0.1411
7	2021	Con	24/08/2021	42.0636, 3.5445	42.1112, 3.5759	363.6	0.1360
8	2021	Con	24/08/2021	42.1002, 3.5495	42.0495, 3.5566	352.6	0.1304
9	2021	NTR	25/08/2021	41.9887, 3.5120	42.0325, 3.5345	360.9	0.1665
10	2021	NTR	25/08/2021	42.0227, 3.5273	41.9741, 3.5235	355.5	0.1353
11	2021	NTR	25/08/2021	42.0208, 3.5341	41.9740, 3.5112	352.6	0.1384
12	2021	Con	26/08/2021	42.0640, 3.5529	42.1121, 3.5610	355.9	0.1345
13	2021	Con	26/08/2021	42.0984, 3.5621	42.0484, 3.5559	362.1	0.1398
14	2021	NTR	27/08/2021	41.9883, 3.5154	42.0359, 3.5380	346.2	0.1403
15	2021	NTR	27/08/2021	42.0193, 3.5359	41.9737, 3.5139	360.3	0.1344
16	2021	NTR	27/08/2021	42.0220, 3.5397	41.9743, 3.5166	368.7	0.1409
17	2021	Con	30/08/2021	42.0613, 3.5468	42.1106, 3.5578	347.5	0.1388
18	2021	Con	30/08/2021	42.0977, 3.5652	42.0488, 3.5572	367.9	0.1368

Table S2.4.2. Number of individuals (N), the mean and standard deviation of the body mass, the cephalothorax length (CL, in mm) and stable isotope values of Norway lobsters before the closure (Bef) and after 4 years in the control (Con) and the no-take reserve (NTR).

	N	body mass (g)	CL (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Bef	40	21.74 ± 7.48	33.95 ± 3.91	-19.66 ± 0.45	5.97 ± 0.36
Con	15	16.29 ± 8.31	31.06 ± 4.63	-19.05 ± 0.29	5.99 ± 0.33
NTR	15	30.75 ± 11.29	37.71 ± 4.80	-18.75 ± 0.1 6	6.69 ± 0.29

Table S2.4.3. Overlap of Kernel Utilization Densities between areas before the closure in 2017 and after 4 years in the no-take reserve and the control. We represented the core or K50%, the K75% and the K95% contours. Values range from 0 to 1, indicating overlap at 1 and segregation at 0.

Interaction		**K50%**	**K75%**	**K95%**
Before the closure *vs.*	Control	0.334	0.362	0.394
	No-take Reserve	0	0.046	0.153
Control *vs.*	Before the closure	0.621	0.634	0.686
	No-take Reserve	0	0.184	0.309
No-take Reserve vs.	Before the closure	0	0.159	0.507
	Control	0	0.362	0.589

Table S2.4.4. Annual landings from 2016 to 2021 represented in LPUE (kg·fishing effort), biomass (kg) and total revenues (in Euros) from different areas (NTR Buffer: buffer no-take reserve; Con Buffer: buffer control; Con: Control; and NTR: no-take reserve).

	Area (km^2)	Year	LPUE	KG	Euros
NTR Buffer	22	2016	115.28	3 792.91	70 023.73
		2017	101.29	3 084.05	59 139.72
		2018	152.03	3 422.89	69 949.23
		2019	135.02	3 392.38	68 729.99
		2020	82.18	1 481.91	38 213.44
		2021	74.24	1 762.00	47 323.11
Con Buffer	22	2016	116.49	3 487.19	59 569.62
		2017	100.86	3 058.62	54 912.01
		2018	137.14	3 586.88	69 999.22
		2019	128.15	3 339.87	67 128.65
		2020	76.72	1 295.79	30 730.37
		2021	58.29	1 397.83	35 132.21
Con	10	2016	53.94	1 524.91	25 982.43
		2017	46.44	1 529.92	27 627.68
		2018	61.28	1 312.20	25 839.08
		2019	62.59	1 425.87	27 532.73
		2020	36.63	500.59	115 541.36
		2021	26.47	684.89	17 164.86
NTR	10	2016	54.99	1 970.60	35 743.15
		2017	45.05	1 600.53	30 703.91

Table S2.4.5. Mean and standard deviation of abundance and biomass of the megafauna species observed before the closure (B) and after 4 years in the control area (C) and the no-take reserve (NTR). The potential predators of Norway lobster based on Vigo et al. (2022) are indicated with a (P).

	Abundance (N·km^{-2})			**Biomass (kg·km^{-2})**		
Species	**B**	**C**	**NTR**	**B**	**C**	**NTR**
TELEOSTEI						
Arctozenus risso	9 ±22	1 ±3	2 ±6	36 ±88	3 ±7	12 ±30
Argentina sphyraena	177 ±143	1,411 ±1,360	1,043 ±364	3,954 ±3,284	22,100 ±11,591	21,692 ±6,342
Argyropelecus hemigymnus	63 ±113	105 ±81	36 ±36	22 ±38	46 ±43	67 ±15
Arnoglossus rueppelii	0	0	15 ±37	0	0	17 ±42
Capros aper	5 ±12	14 ±17	3 ±4	86 ±211	203 ±254	32 ±50
Chauliodus sloani	31 ±53	1 ±3	0	144 ±180	8 ±18	0
Chlorophthalmus agassizi	2 ±4	227 ±102	370 ±222	108 ±91	3,340 ±3,483	2,104 ±1,609
Coelorinchus caelorhincus	78 ±62	707 ±463	2,038 ±487	151 ±87	2,686 ±1,753	21,384 ±9,465
Conger conger (P)	22 ±31	83 ±70	27 ±30	2004 ±2471	6,845 ±6,111	3,229 ±3,888
Epigonus denticulatus	30 ±38	50 ±80	77 ±90	80 ±103	130 ±212	186 ±222
Epigonus telescopus	0	1 ±3	0	0	30 ±72	0
Gadella maraldi	0	0	10 ±24	0	0	13 ±31
Gadiculus argenteus	1,169 ±702	17,416 ±5,069	14,836 ±9,197	5,422 ±4,427	112,172 ±51,047	104,278 ±44,112
Gaidropsarus biscayensis	56 ±45	15 ±23	7 ±18	412 ±366	48 ±83	27 ±66
Glossanodon leioglossus	5 ±11	0	0	3 ±7	0	0
Helicolenus dactylopterus	91 ±49	77 ±54	1,321 ±332	6,118 ±3,484	5,594 ±3,940	118,070 ±29,756
Lepidopus caudatus	0	1 ±3	36 ±45	0	37 ±90	1,202 ±1,577
Lepidorhombus bosci	270 ±103	297 ±112	217 ±79	8,368 ±1,942	8,102 ±2,238	5,721 ±2,548
Lepidorhombus whiffiagonis	0	5 ±6	2 ±4	0	16,166 ±20,091	7,038 ±11,153
Lestidiops jayakari	9 ±15	0	0	32 ±50	0	0
Lophius budegassa	40 ±21	48 ±16	33 ±14	12,284 ±22,151	3,117 ±3,380	17,776 ±28,550
Lophius piscatorius	4 ±4	0	1 ±3	14,317 ±33,791	0	7,179 ±17,585
Macroramphosus scolopax	0	1 ±3	8 ±18	0	12 ±28	85 ±208
Maurolicus muelleri	0	1 ±3	10 ±24	0	2 ±5	19 ±46
Merluccius merluccius	133 ±80	167 ±97	202 ±87	34,683 ±18,379	39,784 ±29,383	57,710 ±30,276
Micromesistius poutassou	183 ±81	343 ±220	218 ±90	10,584 ±5,200	14,576 ±8,798	10,582 ±3,867
Molva macrophtalma	59 ±50	380 ±127	216 ±114	1,577 ±1,452	11,998 ±3,667	6,394 ±3,746
Mora moro	0	0	7 ±18	0	0	9 ±23
Myctophidae	1,617 ±2943	925 ±547	1,210 ±618	5,554 ±3,453	2,011 ±1,313	2,476 ±1,307
Phycis blennoides	420 ±216	2,929 ±898	3,846 ±851	16,970 ±6,908	68,411 ±16,944	105,863 ±19,609
Stomias boa	39 ±44	13 ±24	9 ±12	77 ±69	272 ±513	120 ±159
Symphurus nigrescens	25 ±48	49 ±57	42 ±54	184 ±392	521 ±679	356 ±470
Synchiropus phaeton	0	0	2 ±5	0	0	33 ±80
Trigla lyra	491 ±190	607 ±113	403 ±121	4,547 ±1870	5,665 ±2,026	3,575 ±1,418
Trigla spp.	0	4 ±9	6 ±15	0	0	0
Trisopterus capelanus	42 ±47	0	0	233 ±249	0	0
CEPHALOPODS						
Abralia veranyi (P)	542 ±303	125 ±94	430 ±268	2,376 ±1,431	556 ±403	1,924 ±1,241

Ancistrocheirus lesueurii	3 ±6	0	0	36 ±89	0	0
Bathypolypus sponsalis	0	0	1 ±3	0	0	59 ±145
Eledone cirrhosa	21 ±23	12 ±18	15 ±23	2140 ±2167	2,469 ±3,117	1,488 ±2,349
Histioteuthis bonnellii	10 ±25	0	0	202 ±495	0	0
Illex coindetii (P)	8 ±16	105 ±102	62 ±32	794 ±1869	2,721 ±2,278	2,208 ±1,107
Octopus salutii	0	0	1 ±3	0	0	30 ±74
Rossia macrosoma (P)	6 ±9	13 ±11	38 ±14	419 ±571	713 ±480	1,876 ±1,097
Scaergus unicirrhus	6 ±12	8 ±17	10 ±17	947 ±1546	432 ±785	548 ±881
Sepia orbignyana	0	9 ±11	1 ±3	0	375 ±587	41 ±100
Sepietta spp. (P)	2,473 ±2,211	4,389 ±2,048	3,646 ±732	16449 ±9215	28,450 ±8,155	24,105 ±6,830
Sepiolidae (P)	0	12 ±23	7 ±18	0	34 ±66	9 ±22
Todarodes sagittatus (P)	7 ±9	10 ±8	1 ±3	548 ±875	4,768 ±5,188	481 ±1,177
Todaropsis eblanae (P)	5 ±9	42 ±26	19 ±25	389 ±673	4,214 ±2,419	1,339 ±1,664
CRUSTACEA						
Aegaeon lacazei	14 ±16	26 ±47	44 ±55	8 ±9	23 ±51	23 ±30
Alpheus glaber	23 ±37	7 ±18	0	14 ±25	2 ±4	0
Chlorotocus crassicornis	57 ±34	258 ±98	609 ±274	19 ±46	384 ±119	804 ±378
Dardanus arrosor	21 ±25	21 ±13	30 ±12	212 ±315	317 ±229	424 ±273
Deosergestes henseni	5 ±12	0	0	4 ±9	0	0
Eusergestes arcticus	45 ±97	0	38 ±62	17 ±38	0	6 ±9
Goneplax rhomboides	3 ±6	23 ±35	28 ±51	11 ±27	23 ±31	21 ±41
Ligur ensiferus	0	0	7 ±18	0	0	2 ±5
Liocarcinus depurator	36 ±46	0	0	256 ±299	0	0
Macropipus tuberculatus	43 ±53	3 ±6	0	224 ±204	14 ±33	0
Macropodia tenuirostris	0	7 ±18	8 ±20	0	7 ±16	5 ±12
Medorippe lanata	0	1 ±3	0	0	8 ±18	0
Meganyctiphanes norvegica	0	10 ±23	0	0	2 ±5	0
Monodaeus couchii	12 ±15	41 ±75	170 ±200	39 ±64	34 ±64	84 ±96
Munida intermedia	41 ±52	33 ±38	25 ±39	119 ±154	70 ±85	40 ±63
Munida iris	63 ±70	0	0	125 ±120	0	0
Nephrops norvegicus	1,610 ±300	315 ±127	3,949 ±473	26,477 ±5,127	7,022 ±2,816	122,228 ±10,618
Pagurus alatus	2 ±6	0	0	4 ±10	0	0
Pagurus excavatus	5 ±7	0	0	49 ±94	0	0
Pagurus prideaux	5 ±7	0	0	35 ±57	0	0
Parapenaeus longirostris	1,029 ±287	4,340 ±912	2,587 ±741	15,827 ±4,188	53,639 ±10,167	31,969 ±9,630
Pasiphaea sivado	1,612 ±1,591	515 ±609	5,975 ±6,925	2,181 ±2,546	2,476 ±5,332	3,819 ±3,505
Plesionika gigliolii	0	0	51 ±63	0	0	69 ± 130
Plesionika heterocarpus	849 ±605	8,508 ±3,842	5,983 ±2,415	3,270 ±1,728	28,050 ±13,576	17,865 ±6,734
Plesionika narval	0	24 ±27	7 ±17	0	10 ±12	4 ±11
Pontophilus spinosus	1 ±3	0	7 ±18	2 ±5	0	13 ±33
Processa canaliculata	0	57 ±74	171 ±198	0	52 ±80	148 ±180
Processa nouveli	0	51 ±97	95 ±117	0	37 ±79	54 ±60
Processa sp.	185 ±147	0	0	132 ±108	0	0
Solenocera membranacea	262 ±141	144 ±166	234 ±219	567 ±326	299 ±364	460 ±470
ECHINODERMATA						
Astropecten arancianus	10 ±24	0	0	15 ±36	0	0
Astropecten irregularis	12 ±16	0	0	27 ±36	0	0
Holothuria forskali	0	1 ±3	5 ±12	0	23 ±56	67 ±165
Parastichopus regalis	0	1 ±3	0	0	161 ±395	0
ELASMOBRANCHS						
Dipturus batis	0	1 ±3	0	0	486 ±1190	0
Raja spp.	5 ±12	0	0	182 ±445	0	0
Scyliorhinus canicula (P)	1,196 ±482	908 ±344	1,209 ±500	85,223 ±22,944	121,399 ±51,631	240,697 ±113,151

Table S2.4.6. Number of individuals (n), mean and standard deviation of the body size of the species that presented significant differences before the closure (Bef) and after 4 years in the control area (CA) and the no-take reserve (NTR). Depending on the species, the body size was measured differently (Measure): TL= total length (in cm); AL= preanal length (in cm), ML=mantel length (in cm), CL= cephalothorax length (in mm).

	Bef		CA		NTR		Method
Species	n	mean+sd	n	mean+sd	n	mean+sd	
TELEOSTEI							
Argentina sphyraena	142	135.53 ±35.66	1,161	125.40 ±41.06	903	150.55 ±34.46	TL
Coelorinchus caelorhincus	64	29.45 ±15.77	578	28.11 ±9.92	1,727	42.45 ±15.16	AL
Conger conger	19	324.95 ±169.98	68	388.66 ±51.93	24	422.79 ±82.78	TL
Gadiculus argenteus	963	74.39 ±21.15	14,240	87.77 ±18.05	12,801	91.98 ±17.49	TL
Helicolenus dactylopterus	76	161.32 ±30.08	62	167.66 ±28.97	1,130	177.58 ±36.47	TL
Micromesistius poutassou	150	195.55 ±41.97	281	184.70 ±15.29	182	238.43 ±22.83	TL
Molva macrophthalma	49	224.94 ±16.63	310	245.45 ±20.53	183	238.43 ±22.83	TL
Phycis blennoides	347	164.56 ±60.21	2,380	139.5 ±47.27	3,277	144.76 ±53.98	TL
Trigla lyra	403	99.18 ±26.61	495	105.83 ±20.09	345	103.20 ±12.95	TL
CEPHALOPODS							
Abralia veranyi	448	32.25 ±5.21	102	35.45 ±6.03	373	34.20 ±4.51	ML
CRUSTACEANS							
Chlorotocus crassicornis	48	16.08 ±3.01	210	14.92 ±2.63	512	13.86 ±2.69	CL
Nephrops norvegicus	1329	28.42 ±3.83	257	31.25 ±4.54	3,387	34.73 ±4.65	CL
Parapenaeus longirostris	885	30.95 ±4.11	3,541	28.53 ±3.36	2,206	28.30 ±4.03	CL
Plesionika heterocarpus	705	16.97 ±1.59	6,972	15.92 ±1.35	5,039	15.62 ±1.54	CL
ELASMOBRANCHS							
Scyliorhinus canicula	993	251.92 ±104.95	741	340.35 ±9.98	1,211	368.97 ±73.86	TL

Supplementary materials – Chapter 2.5

Table S2.5.1. ROV surveys performed in February 2020 in the no-take reserve (NTR) and the control area (C).

Survey	Area	Date DD/MM/YY	Start Time	Time period (h)	Swept Area (km^2)	Initial Latitude	Initial Longitude	Depth Mean ± SD (m)	Depth range min – max (m)
1	C	03/02/20	7:80	5.87	7.95	42º 06.3934' N	003º 33.7934' E	354 ± **20**	327–382
2	C	08/02/20	18:78	3.75	5.42	42º 06.3942' N	003º 33.7925' E	365 ± 13	334–382
3	C	03/02/20	14:42	7.48	8.36	42º 03.4686' N	003º 32.7542' E	362 ± 20	338–396
4	C	09/02/20	3:37	3.37	4.21	42º 04.5767' N	003º 33.3836' E	348 ± 11	338–365
5	C	03/02/20	22:45	4.73	5.98	42º 06.2501' N	003º 34.3033' E	382 ± 17	353–409
6	C	08/02/20	6:22	7.45	8.28	42º 03.3730' N	003º 33.2800' E	385 ± 22	360–424
7	NTR	06/02/20	7:33	5.03	7.19	42º 01.8830' N	003º 31.7013' E	344 ± 3	334–348
8	NTR	07/02/20	23:93	3.10	4.79	41° 58.9408' N	003º 30.6625' E	343 ± 1	341–346
9	NTR	06/05/20	12:95	7.10	8.43	41º 58.8717' N	003º 30.9210' E	359 ± 2	353–362
10	NTR	07/02/20	16:40	6.57	8.15	42º 01.7499' N	003º 32.2155' E	359 ± 2	355–362
11	NTR	07/02/20	8:18	7.42	6.87	41º 59.2293' N	003º 31.3918' E	375 ± 2	370–376
12	NTR	06/02/20	22:47	7.20	8.20	41º 58.8717' N	003º 30.9210' E	374 ± 2	369–376

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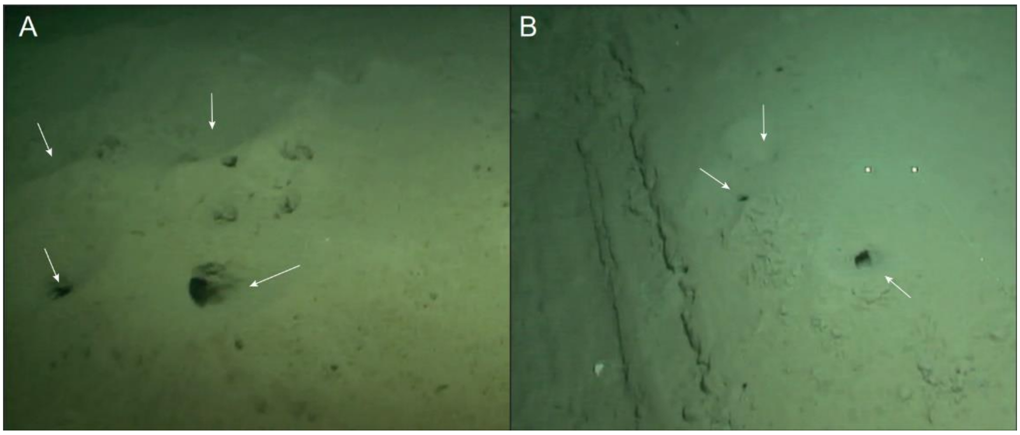

Figure S.2.5.2. Burrow-systems and burrow structures of a Norway lobster. A: 4 tunnel burrow entrances in the no-take reserve; B: a flattened three tunnel burrow entrances in the control area.

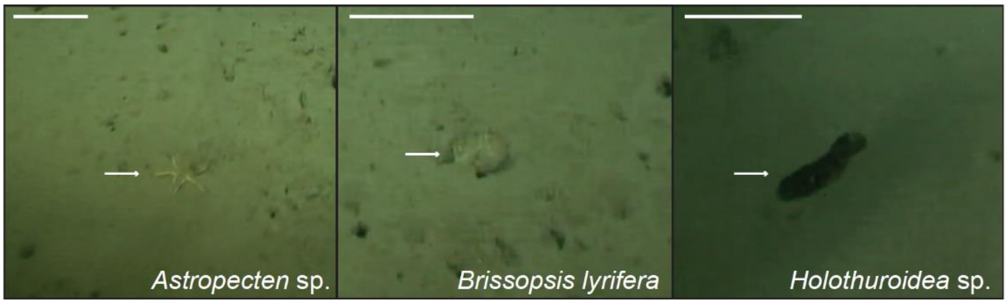

Figure S2.5.3. Pictures of the Echinodermata species and genera identified.

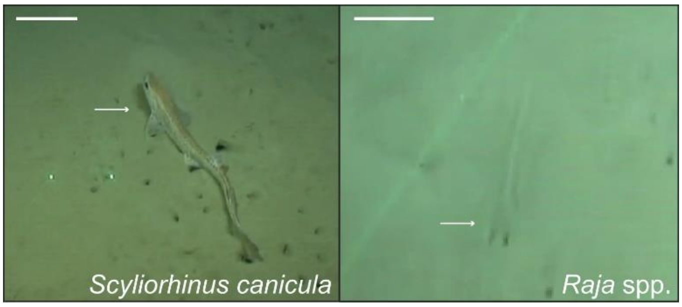

Figure S2.5.4. Pictures of the Elasmobranchii species

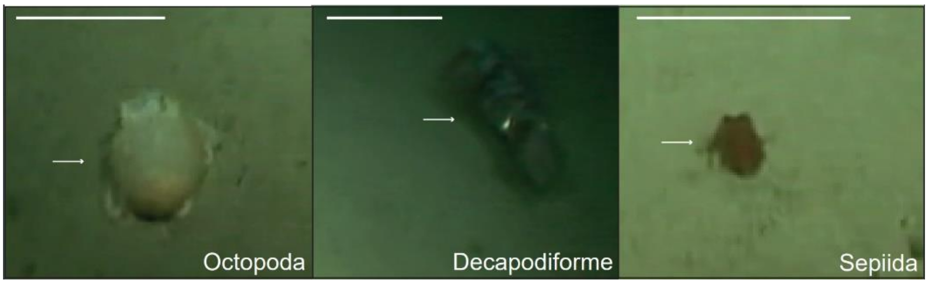

Figure S2.5.5. Pictures of the Cephalopoda groups identified.

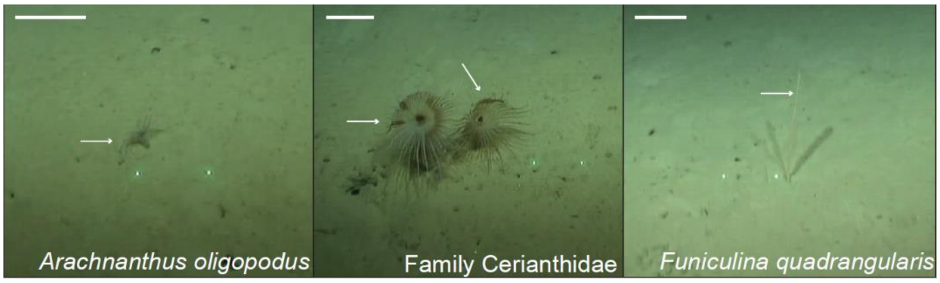

Figure S2.5.6. Pictures of the Cnidaria identified.

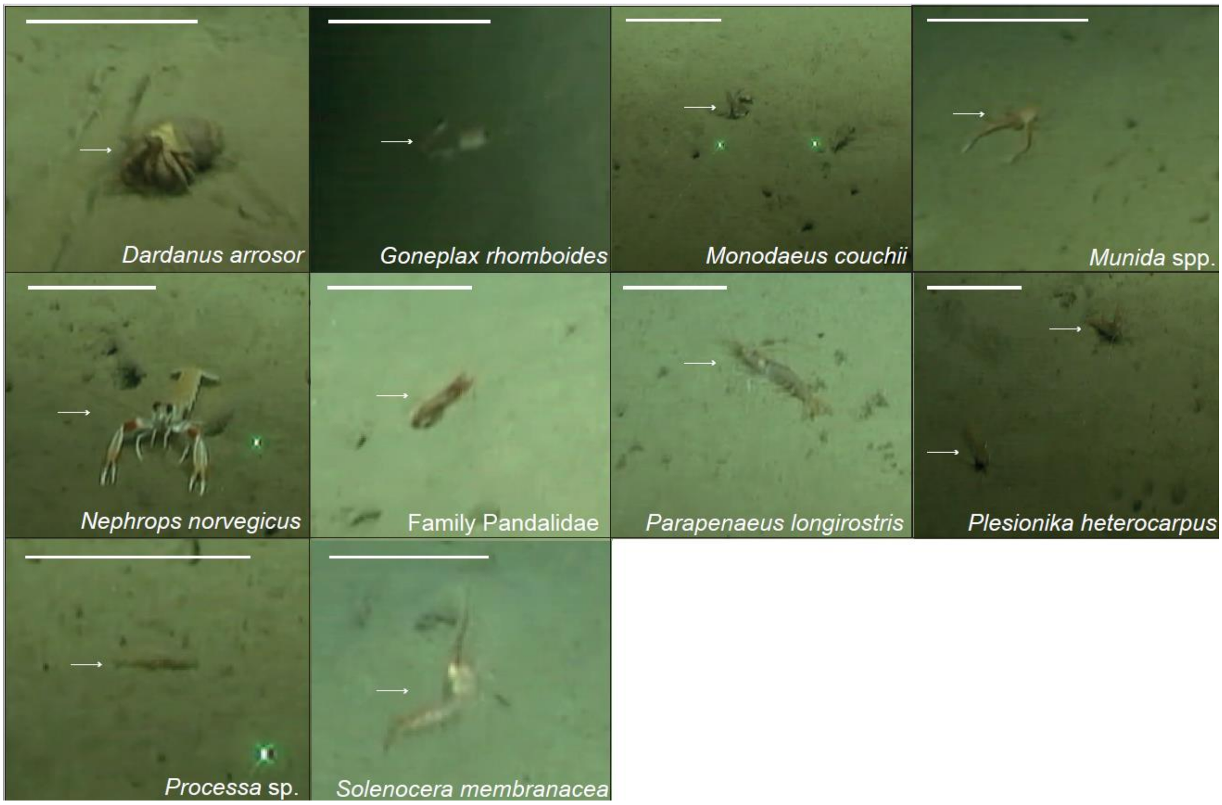

Figure S2.5.7. Groups of the Crustacea species and groups identified.

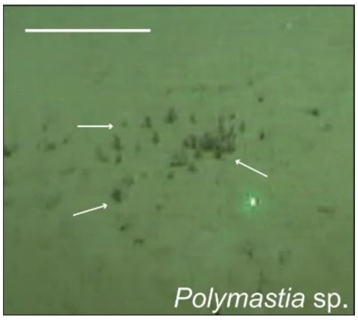

Figure S2.5.8. Picture of the only Porifera genera identified.

Figure S2.5.9. Pictures of the Teleost species and genera identified.

Table S2.5.10. Identification of the cephalopods captured in the ROV visual transects conducted in the control and the no-take reserve.

	Control	**No-take reserve**
Decapodiformes		Enoploreurhoidea *Illex coindetii* Oegopsida
Octopoda	*Eledone cirrhosa* *Incirrata* sp.	*Eledone cirrhosa* *Incirrata* sp. *Octopus salutii* *Opisthoteuthis calypso* *Pteroctopus tetracirrhus*

Supplementary materials – Chapter 2.6

Table S2.6.1. Spatial similarity matrix comparing the presence of Norway lobster from the best solution outputs at each scenario. Values represent Cohen's kappa coefficient ranges from -1 to +1, where -1 represents complete disagreement, 0 indicates agreement no better than that expected by chance and +1 indicates complete agreement.

	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
Scenario 1	NA	NA	NA	NA	NA
Scenario 2	0.49	NA	NA	NA	NA
Scenario 3	0.45	0.75	NA	NA	NA
Scenario 4	0.52	0.87	0.70	NA	NA
Scenario 5	0.50	0.65	0.68	0.70	NA

Table S2.6.2. Spatial similarity matrix comparing the presence of Norway lobster from the selection frequency outputs at each scenario. Values represent Pearson correlation coefficient that range from -1 to +1, indicating the direction and the strength of the relationship between 2 variables, being stronger closer to -1 or +1, and independent variables closer to 0.

	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
Scenario 1	NA	NA	NA	NA	NA
Scenario 2	0.54	NA	NA	NA	NA
Scenario 3	0.55	0.91	NA	NA	NA
Scenario 4	0.61	0.92	0.88	NA	NA
Scenario 5	0.56	0.86	0.95	0.93	NA

Table S2.6.3. Protection equality values of conservation features at each scenario representing the equality with all closures and with only the permanent closures.

	Scenarios				
	1	2	3	4	5
All Closures	0.85	0.81	0.80	0.82	0.83
Permanent Closures	0.85	0.78	0.81	0.78	0.82

Annex II-
Published Papers

Published papers:

- **Chapter 2.2.**
  Using molecular and stable isotope markers to identify the main predators of *Nephrops norvegicus* in the Mediterranean deep- water ecosystems.
  Maria Vigo, Joan Navarro, Joan Giménez, Núria Andón, Andrés Martínez-Lage, Joan B. Company, and Guiomar Rotllant
  Marine Ecology Progress Series, 695, 95–108 (2022).
  https://doi.org/10.3354/meps14110

- **Chapter 2.3.**
  Spatial ecology of Norway lobster (*Nephrops norvegicus*) in Mediterranean deep-water environments: implications for designing no-take marine reserves.
  Maria Vigo, Joan Navarro, Ivan Masmitja, Jacopo Aguzzi, José Antonio García, Guiomar Rotllant, Nixon Bahamón, and Joan B. Company
  Marine Ecology Progress Series, 674, 173–188 (2021).
  https://doi.org/10.3354/meps13799

- **Chapter 2.4.**
  Before-after control-impact (BACI) assessment of the effects of a deep-water no-take reserve on overfished Norway lobster (*Nephrops norvegicus*) population and their coexisting demersal megafauna.
  Maria Vigo, Joan Navarro, Guiomar Rotllant, Nixon Bahamón, Marta Carretón, Juliana Quevedo, Alba Rojas, and Joan B. Company
  ICES Journal of Marine Science, fsad130 (2023)
  https://doi.org/10.1093/icesjms/fsad130

- **Chapter 2.5.**
  ROV-based monitoring of passive ecological recovery in a deep-sea no-take fishery reserve.
  Maria Vigo, Joan Navarro, Jacopo Aguzzi, Nixon Bahamón, José Antonio García, Guiomar Rotllant, Laura Recasens, and Joan B. Company
  Science of The Total Environment,
  883, 163339 (2023).
  https://doi.org/10.1016/j.scitotenv.2023.163339

Vol. 695: 95–108, 2022
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Using molecular and stable isotope markers to identify the main predators of *Nephrops norvegicus* in Mediterranean deep-water ecosystems

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ABSTRACT: To obtain a better understanding of the functioning of ecosystems and how they respond to disturbance, it is necessary to identify the relevant biotic interactions and specific trophic roles. Predation is one of the most important biotic interactions that can also define the spatial patterns of other species. Many predators are considered key species for the functioning and maintenance of ecosystems, as they play an important ecological role that can influence the dynamics at lower trophic levels. The Norway lobster *Nephrops norvegicus* is one of the most valued European fishing stocks. However, its value and capture have declined over the last decade. In the Atlantic Ocean, Atlantic cod *Gadus morhua* is the main predator of *N. norvegicus*. However, this species is not present in the Mediterranean Sea, and little is known about which species might prey on *N. norvegicus* in this area. Here, we combine 2 methodologies — genetic identification of stomach contents and stable isotope analyses — to identify, for the first time, the main predators of *N. norvegicus* in the Mediterranean Sea. Moreover, we have created the Predation Index, which determines the most influential predator affecting *N. norvegicus* population dynamics. Our results reveal that the major predators are the cephalopods *Sepietta* spp. and *Abralia veranyi*, which probably affect the early stages of *N. norvegicus*, followed by the elasmobranch *Scyliorhinus canicula* and the bony fishes *Merluccius merluccius*, *Trigla lyra*, and *Conger conger*. To evaluate possible fluctuations in the *N. norvegicus* population, we consider the assessment of these predator populations crucial.

KEY WORDS: Ecological role · Feeding ecology · Fisheries · Food web · Norway lobster · Predation Index · Prey DNA · Resource management · Trophic ecology

1. INTRODUCTION

Determining the trophic role of a particular organism is pivotal to understanding its ecological function in the ecosystem and to designing effective management actions. This involves identifying the environmental factors and biotic interactions that could influence or play an essential role in population dynamics and species distribution (D'Amen et al. 2018). Recognizing these factors could also be useful for predicting how marine ecosystems will respond to changing environmental conditions (Wisz et al. 2013). Among biotic interactions, predator–prey interactions are key in affecting the spatial patterns of species (Ritchie et al. 2012). Predators play an important role in all ecosystems, influencing the dynamics of species at lower trophic levels (Estes 1996, Ritchie & Johnson 2009).

Ecosystem modelling, which also considers consumer–prey interactions, is being widely used for

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ecosystem-based fishery management (Buchary et al. 2002). This holistic approach includes the type and magnitude of the species interactions involved, analyzing biomass and abundance at several trophic levels from plankton to apex predators (Fogarty 2014). This entails a prior understanding of which prey–predator interactions exist in the environment to be managed. Similarly, in the assessment of the effectiveness of marine protected areas (MPAs), evaluating predator densities is crucial, even in small MPAs, as an increase in predators could prevent the restoration of overexploited species (Clements & Hay 2017) or a lack of them could lead to habitat regime shifts (Daskalov et al. 2007). Nevertheless, the trophic role that individual species play within marine ecosystems is still often unclear, precluding the prediction of the consequences of their removal or recovery. In the case of ecosystem-based fisheries management, a lack of knowledge of biotic interactions could lead to a misinterpretation of the consequences of overfishing, resulting in inconsistent trophic patterns constraining the viability of stocks and their predators (Shackell et al. 2010).

Despite the importance of this ecological information, there is still a huge knowledge gap regarding the main predators of some well-studied marine species. This is the case for Norway lobster *Nephrops norvegicus* in the Mediterranean Sea. This demersal decapod is one of the most important crustacean species for the European fishing industry, being considered an important target species across European waters. It is a common decapod crustacean distributed in the northeast Atlantic Ocean and the Mediterranean Sea, inhabiting the muddy bottoms of the continental shelves and slopes, at depths from 10 to 800 m (Johnson et al. 2013, Ungfors et al. 2013). The management of this stock involves a mixture of EU regulations (Common Fisheries Policy; CFP) and national legislation, though *N. norvegicus* stocks seem to have been fished above scientific advised levels (Sardà 1998, Letschert et al. 2021). Over the last decade the Mediterranean stocks of *N. norvegicus* from the northwestern Mediterranean Sea (Spanish waters) have declined in abundance (from 400 t in 2009 to 200 t in 2019). In the Mediterranean Sea, most management policies are not successfully enforced, as the current state of the stocks is not reviewed (Sardà 1998). To better understand the temporal changes in species abundance, distribution and biology, this approach to fisheries management needs to be changed. Moreover, to prevent possible trade-off consequences due to fluctuations of other species populations that may be associated with *N. norvegicus*, it is essential to understand their ecological role and importance as a trophic resource for predators. Despite the large amount of research conducted on *N. norvegicus*, knowledge about its main predators in the Mediterranean Sea is scarce. In the Atlantic waters, its main predator is the Atlantic cod *Gadus morhua* (Chapman 1980, Brander & Bennet 1986, Dombaxe 2002), which is distributed within a similar depth range (Johnson et al. 2013). In contrast, information about its main predators in the Mediterranean Sea, where *G. morhua* is not present, is limited to only a few studies that suggest that cephalopods, some demersal elasmobranchs, and the bony fish *Conger conger* could be important (Coll et al. 2006, El-Amine Abi-Ayad et al. 2011, Šantić et al. 2012, Navarro et al. 2014). However, describing the diet of cephalopods and elasmobranchs, and identifying specific prey using traditional stomach content analyses, is complicated because they usually have empty stomachs and, in the case of cephalopods, it is difficult to identify stomach contents due to the high efficiency of their beaks in crushing food and their rapid enzymatic stomach activity (Guerra 1978, Ibáñez et al. 2021). For this reason, the actual trophic importance of *N. norvegicus* for these predators may be underestimated.

As an alternative to stomach content analysis, the use of trophic indicators such as molecular or stable isotope analyses (SIA) could help to determine the diet composition of marine predators (Guerreiro et al. 2015, Olmos-Pérez et al. 2017). In the case of molecular techniques, it is possible to determine the presence of a specific prey by detecting its DNA in the stomach contents of a potential predator (Dunshea 2009). Also, stable isotopes of nitrogen (denoted as $\delta^{15}N$) and carbon (denoted as $\delta^{13}C$) have been used extensively to study the trophic ecology of marine predators (Shiffman et al. 2012, Navarro et al. 2013, Giménez et al. 2021). This approach is based on the fact that $\delta^{15}N$ and $\delta^{13}C$ values are transformed from dietary sources to consumers at predictable ratios (Kelly 2000): the incorporation of the carbon isotope ratio ($^{13}C/^{12}C$) of primary producers into consumer tissues and the enrichment of the nitrogen isotope ratio ($^{15}N/^{14}N$) due to the incorporation of the heavy isotope of nitrogen (^{15}N) by the consumer from its diet. Stable isotopes alone cannot completely resolve the consumption of *N. norvegicus* due to the limitation of the technique (i.e. simulated predators based on a predator that only feeds on *N. norvegicus*). Combination with other techniques, such as DNA analysis, is beneficial and enhances the interpretation of the results. A more precise interpretation would be possible if stable isotope information on all putative prey were available to infer diet through stable isotope mixing models. The combination of different methodologies could solve complex ecological questions by providing more accurate information about the structure and functioning of marine food webs and be a useful tool to validate results. Moreover, due to the different integration time of each of these 2 methodologies, their combination could provide information about the trophic importance of a particular prey at the short-term scale (DNA integrates in days due to rapid digestion times; Aguilar et al. 2017) and the long-term scale (SIA in muscle tissues integrates ~2 to 8 mo of the food consumed by a predator, depending on the species; Vander Zanden et al. 2015). For example, in SIA of muscle tissues, the isotopic half-life (ln(2)/λ, days), defined as the time required to reach 50% equilibration with the diet, averages 47 d in the cod *G. morhua* (Ankjaerø et al. 2012), 147 d in the red rock lobster *Jasus edwardii* (Suring & Wing 2009) and 105.3 d in the leopard shark *Triakis semifasciata* (Kim et. al 2012, Malpica-Cruz et al. 2012).

In the present study, our principal objective was to identify the main predators of *N. norvegicus* in the deep-sea ecosystems (315 to 475 m depth) of the western Mediterranean Sea using both molecular and stable isotope techniques. We also considered possible predators of the early stages of *N. norvegicus*, such as the cephalopods *Sepietta* sp. and *Abralia veranyi*, which are smaller than adult *N. norvegicus*. Moreover, we estimated the predation impact on *N. norvegicus* to portray the significance of the predator–prey interactions taking into account the predator density, which could adversely affect prey consumption (Arditi et al. 2001). For this purpose, a Predation Index (PI) combining the results of this study and the density of each predator identified in the study area was calculated to elucidate the real importance of each predator in the *N. norvegicus* fishing grounds.

2. MATERIALS AND METHODS

2.1. Fieldwork procedures

The study was conducted in the northwestern Mediterranean Sea, in a deep-sea *Nephrops norvegicus* fishing ground (300 to 500 m depth; Fig. 1). This area is composed of muddy habitats of the upper slope of the continental shelf margin, which is crossed by several submarine canyons. These submarine canyons are major geomorphological struc-

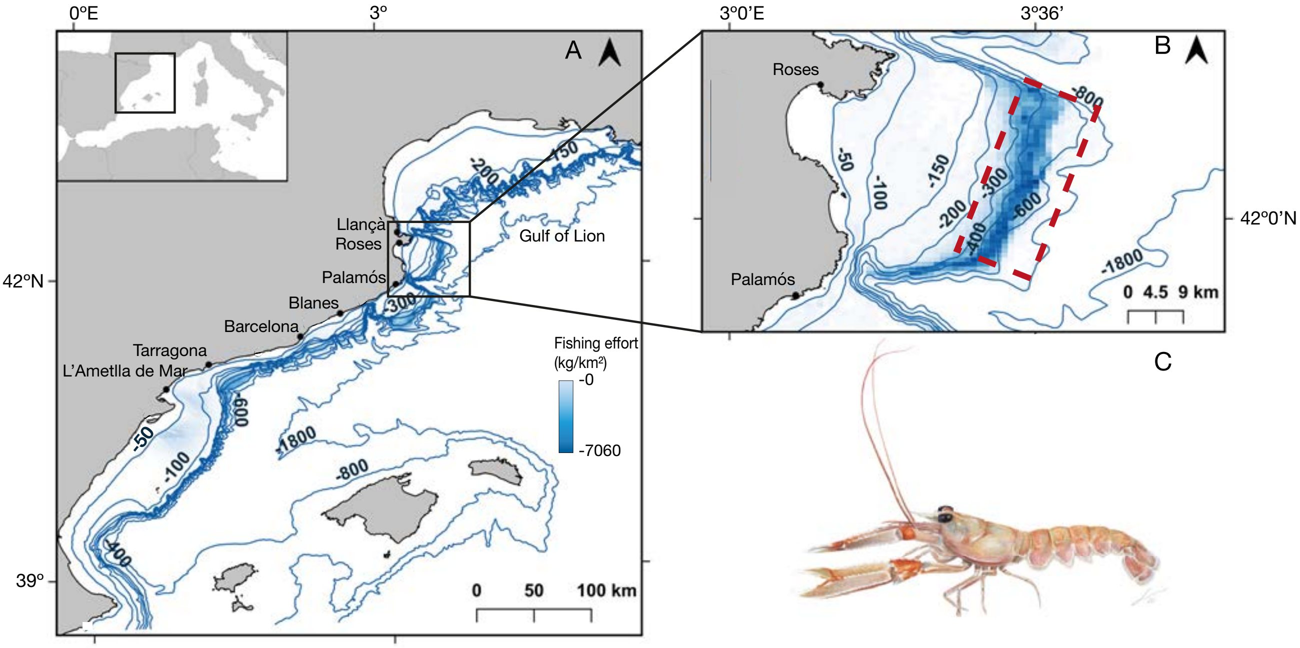

Fig. 1. (A) Study area of Norway lobsters *Nephrops norvegicus* in the northwestern Mediterranean Sea, Spain. (B) Spatial distribution of *N. norvegicus* along the Catalan coast, obtained by combining Vessel Monitoring System (VMS) information and official landing data from the time period 2005–2018 (European Commission 2002–2018, Garcia et al. 2016), and the study area (red rectangle). (C) *N. norvegicus* (illustration by Joan Mir-Arguimbau)

tures of the western Mediterranean Sea, hosting a fishing ground of great economic importance for the local and regional fisheries (Fernández-Arcaya et al. 2017).

To collect potential predators and estimate their abundance, a total of 28 experimental hauls (18 hauls in September 2017 and 10 in September 2019) were performed in this area using commercial trawling gears (square mesh size of 40 mm) covered with a net with a diamond mesh size of 12 mm to collect the maximum number of species and sizes. The headline height of the trawl was around 1.3 m, and the horizontal trawl opening was about 22 m. The total wire of the fishing trawl was between 850 and 950 m. Towing was maintained at a constant speed (2.4 to 2.5 knots) and the duration of each haul ranged between 1 h 31 min and 1 h 44 min. All hauls were conducted in local daylight, coinciding with the diurnal emergence of *N. norvegicus* on the continental slope of these deep-water habitats (Aguzzi et al. 2003, Vigo et al. 2021).

2.2. Abundance of potential predators of *N. norvegicus*

The total catch was classified into *N. norvegicus* and the different species of its potential predators. The abundances of *N. norvegicus* and the different predators were estimated considering the swept area, which is the area that the trawl net has towed, in km^2 following the equation:

$$A = V \times \mathrm{BT} \times H \times 1852 / 10^6 \qquad (1)$$

where A is the total number of individuals per km^2, V is the average speed of the trawls (knots), BT is the towing time (h), H is the horizontal opening of the net (m) and the constant 1852 is the equivalent in nautical miles to make the conversion to km^2 (Sparre & Venema 1998).

2.3. Muscle and stomach content sampling

A total of 20 *N. norvegicus* individuals and potential predators (cephalopods [n = 133], bony fish [n = 78], and elasmobranchs [n = 38]) were collected from the fishing hauls. They were identified at the species level and frozen on board until their dissection at the Institut de Ciències del Mar (ICM - CSIC). In the laboratory, all collected individuals were weighed (in g) and measured (standard body measures in mm: mantel length [ML] for cephalopods, total length [TL], standard length [SL], or anal length [AL] for fish species). We obtained 269 muscle samples, 20 from *N. norvegicus* and 249 from the potential predators of *N. norvegicus,* which were later frozen and preserved for stable isotopic determination. We also extracted the stomach contents of these potential predators of *N. norvegicus* and kept the contents in ethanol-sterilized sample pots.

2.4. Extraction and amplification of DNA from the stomach contents of predators

All collected stomachs were dissected using ethanol-sterilized tools and DNA extraction from the stomach contents was performed using the NZY Tissue gDNA Isolation Kit (NZYTech) following the manufacturer's instructions. DNA quality was analyzed with the NanoDrop ND-1000 spectrophotometer (Thermo Fisher Scientific).

We designed primers with sequences corresponding to a mitochondrial gene from the 16S subunit of the ribosomal ribonucleic acid (following Palero et al. 2009) to identify predation only on Norway lobster. We used the program PRIMER3Plus (Untergasser et al. 2007) to design the primers: R 5′-ACG CTG TTA TCC CTA ARG TAA CTT-3′ and F 5′-GGT GTA GAT TAA GGA ATT CG-3′.

We followed the protocol of the NZYTaq 2x Colourless Master Mix (NZYTech) using a thermocycler with pre-programmed temperatures and times. The optimal PCR conditions consisted of an initial denaturation at 95°C for 5 min, followed by 19 cycles of 95°C for 30 s, 58°C for 30 s, 72°C for 30 s; 20 cycles of 95°C for 30 s, 61°C for 30 s, 72°C for 30 s; and a final step at 72°C for 5 min to make sure that all DNA extracts were amplified. Finally, the sample was stored at 12°C to preserve the reaction for the short term. PCR products were visualized on 2% agarose gels prior to cloning and sequencing to verify amplicon presence and size. We analyzed the results as binary variables: the absence of bands was classified as no detection (value 0) and the presence of a band was considered detection of Norway lobster (value 1).

2.5. Stable isotopic analysis

All muscle samples (*N. norvegicus* and its potential predators) were freeze-dried and powdered, and 0.28 to 0.33 mg of each sample was packed into tin capsules. Stable isotopic analyses were performed at the Laboratory of Stable Isotopes of the Estación Biológica de Doñana CSIC (www.ebd.csic.es/lie/index.html). Samples were combusted at 1020°C using a continuous flow isotope ratio mass spectrometry system (Thermo Electron) by means of a Flash HT Plus elemental analyzer interfaced with a Delta V Advantage mass spectrometer. This applies international standards run every 9 samples: LIE-CV and LIE-PA, previously normalized with the international standards IAEA-CH-3, IAEACH-6, IAEA-N-1, and IAEA-N-2. Stable isotope ratios were expressed in the standard δ-notation (‰) relative to Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric N_2 ($\delta^{15}N$). Based on laboratory standards, the measurement errors (SD) were ±0.1 and ±0.2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. The C:N ratio of all tissues was always lower than 3.5‰, and hence, no correction of the $\delta^{13}C$ values was required to account for the presence of lipids in muscle samples (Logan et al. 2008).

To compare the differences in the $\delta^{13}C$ and $\delta^{15}N$ values between potential predators we used Kruskal-Wallis and Wilcoxon post-hoc tests, using the statistical software R version 4.0.3 (R Core Team 2020).

2.6. Identification of the potential predators of *N. norvegicus* using isotopic values

Based on the stable isotope values, we estimated the qualitative importance of *N. norvegicus* for each sampled predator. This approach consisted of determining whether the isotopic niche of a potential predator overlapped with that of a hypothetical predator (bony fish, elasmobranch, or cephalopod) that only feeds on *N. norvegicus*. If so, then we could assume that this predator includes *N. norvegicus* in its diet (see a similar approach in Popa-Lisseanu et al. 2007). We also checked whether *N. norvegicus* was segregated from the other crustaceans present in the study area. For this, we revised all the published data on the stable isotope values of the cohabiting crustaceans present in the study area, confirming that *N. norvegicus* was segregated in its stable isotope values from the other cohabiting crustaceans (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m695p095_supp.pdf).

As isotopic niche, we calculated 3 different kernel utilization density (KUD) estimators that contained 50%, 75%, and 95% of the isotopic niche of each species. KUD is estimated across a regular network of equally spaced points, with the extent of the grid larger than that of the observations (Venables & Ripley 2002, Eckrich et al. 2020). The contour lines used are defined in relation to the Euclidean distance of each observation to the centroid in bivariate space (Robinson 2021). For these predictions, different diet-to-tissue discrimination factor values based on published studies were used for cephalopods ($\Delta\delta^{13}C$ = −0.20 ± 0.5‰, $\Delta\delta^{15}N$ = 3.37 ± 0.95‰; Golikov et al. 2020), bony fish ($\Delta\delta^{13}C$ = 1.3 ± 0.1‰, $\Delta\delta^{15}N$ = 3.35 ± 0.2‰; Caut et al. 2009), and sharks/rays ($\Delta\delta^{13}C$ = 0.49 ± 0.32‰, $\Delta\delta^{15}N$= 1.95 ± 0.26‰; Hussey et al. 2010). We used the rKIN package (rKIN; https://github.com/salbeke/rKIN) in R version 4.0.3 (R Core Team 2020) to compute the KUDs and calculate their overlap.

2.7. Combining molecular and trophic markers

We combined and plotted the results for the percentage of stomachs containing *N. norvegicus* DNA (% DNA) for each of the different potential predators and the 95% contour of the KUD overlap (K 95%) of the isotopic niches estimated from the isotopic values for each predator. Species with low values for both metrics should not be considered as predators of *N. norvegicus*, while species with high values could be major predators of *N. norvegicus*. Species that appear in the lower-right section of the plot (only high values of % DNA; see Fig. 5) could be casual predators of *N. norvegicus* with short-term predation importance. On the contrary, if species appear in the upper-left section of the plot (high values of K 95%, stable isotopes), they present a long-term marker, indicating that they had preyed on *N. norvegicus* in the past months (~2 to 8 mo).

2.8. Estimating the impact of each predator on the population of *N. norvegicus*

By using % DNA or K 95%, we estimated the relative importance in number (I) of each potential predator of *N. norvegicus* by calculating the percentage of abundance of each predator in relation to the abundance of all predators together. The abundance of predators was obtained from the fishing surveys conducted in the study area. The importance index (I_x) was obtained with the following equation:

$$I_x\ (\%) = [(PA_x/100) \times (E/100)] \times 100 \qquad (2)$$

where PA is the percentage of abundance of a specific predator x in relation to the abundance of all potential predators and E is the % DNA or the K 95%. For each predator, we estimated a Predation Index (PI) based on the average I values obtained with % DNA and K 95%.

3. RESULTS

3.1. DNA results

From the 249 stomachs of 20 potential predator species (see Table 1), *Nephrops norvegicus* DNA was detected mainly in the cephalopods *Todaropsis eblanae* (% DNA = 73.33%), *Abralia veranyi* (72.73%), *Sepietta* sp. (66.67%), *Pteroctopus tetracirrhus* (50 %), *Todarodes sagittatus* (42.86%), and *Illex coindetii* (38.46%). In bony fish, *N. norvegicus* DNA was detected mainly in *Lophius budegassa* (75 %), *Merluccius merluccius* (35.71%) and *Conger conger* (33.33%). In the other 13 potential predators analyzed, less than 25% of individuals had *N. norvegicus* DNA in their stomachs, and it was absent in 7 of the species (Table 2).

3.2. Stable isotope results

When comparing the stable isotopic values of *N. norvegicus* and its potential predators, we found that *N. norvegicus* was completely segregated from them all in δ^{15}N and δ^{13}C values (Fig. 2). Among predator species, we found significant differences (Kruskal Wallis tests, $p < 0.05$) in both δ^{15}N and δ^{13}C values (Table 1, Fig. 2). The species that presented the lowest values of δ^{13}C and were the most significantly different from *N. norvegicus* (−19.91 ± 0.46‰) (based on Wilcoxon post-hoc tests, $p < 0.05$) were the bony fishes *C. conger* (−18.63 ± 0.27‰) and *Trigla lyra* (−18.86 ± 0.24‰), and the elasmobranchs *Scyliorhinus canicula* (−17.80 ± 0.48‰), *Raja* sp. (−17.80 ± 0.48‰), and *Galeus melastomus* (−18.65 ± 0.13‰). For δ^{15}N values, the predators most segregated from *N. norvegicus* (5.86 ± 0.36‰) and with the highest values of δ^{15}N (based on Wilcoxon post-hoc tests, $p < 0.05$) were the cephalopod *A. veranyi* (10.34 ± 0.56‰), the bony fish *L. budegassa* (10.51 ± 0.28‰), and the elasmobranch *S. canicula* (9.13 ± 0.23‰) (see Table 1).

Regarding the 95% contour of KUD overlap between the isotopic area of a potential predator that consumes only *N. norvegicus* and each predator species (Figs. 3 & 4), we found higher K 95% values for the elasmobranch *G. melastomus* (64.3%) and the

Table 1. Results obtained from the stable isotope analyses of each species considered as a potential predator of Norway lobster. n: number of individuals or samples; values are mean ± SD

Species	n	Body mass (g)	δ^{13}C (‰)	δ^{15}N (‰)
Crustacea				
Nephrops norvegicus	20	26.39 ± 7.52	−19.91 ± 0.46	5.86 ± 0.36
Cephalopods				
Abralia veranyi	9	4.89 ± 1.15	−19.76 ± 0.55	10.34 ± 0.56
Eledone cirrhosa	16	223.10 ± 93.71	−18.97 ± 0.28	8.27 ± 0.46
Illex coindetii	12	139.71 ± 58.03	−19.20 ± 0.30	9.74 ± 0.77
Rossia macrosoma	20	76.91 ± 31.94	−18.49 ± 0.41	8.20 ± 0.22
Octopus saluti	2	282.50 ± 307.59	−18.87 ± 0.21	7.31 ± 0.65
Pteroctopus tetracirrhus	4	412.50 ± 251.58	−18.44 ± 0.19	7.09 ± 1.12
Scaeurgus unicirrhus	2	56.36 ± 0.00	−19.15 ± 0.08	8.04 ± 0.41
Sepietta oweniana	20	9.89 ± 14.30	−19.33 ± 0.17	9.55 ± 0.24
Sepietta spp.	18	5.20 ± 2.20	−19.32 ± 0.22	9.57 ± 0.27
Todarodes sagittatus	9	205.40 ± 306.10	−19.24 ± 0.30	9.85 ± 0.85
Todaropsis eblanae	15	121.37 ± 35.19	−19.38 ± 0.23	9.46 ± 0.37
Bony fish				
Conger conger	29	197.29 ± 229.51	−18.63 ± 0.27	9.30 ± 0.44
Lepidopus caudatus	2	46.00 ± 0.00	−20.16 ± 0.00	9.35 ± 0.00
Lophius budegassa	4	435.00 ± 189.47	−18.62 ± 0.32	10.51 ± 0.28
Merluccius merluccius	14	353.14 ± 124.38	−19.01 ± 0.19	9.79 ± 0.33
Molva macrophtalma	10	29.90 ± 7.47	−19.24 ± 0.19	10.12 ± 0.41
Trigla lyra	18	79.61 ± 12.44	−18.86 ± 0.24	9.46 ± 0.37
Elasmobranchs				
Galeus melastomus	10	15.44 ± 4.21	−18.65 ± 0.13	8.43 ± 0.21
Scyliorhinus canicula	30	207.83 ± 102.86	−17.80 ± 0.48	9.13 ± 0.23
Raja clavata	1	260.00	−17.76	9.08
Raja polystigma	3	77.50 ± 10.61	−18.05 ± 0.64	7.85 ± 1.19
Raja spp.	2	46.00 ± 0.00	−17.67 ± 0.29	8.71 ± 0.32

Table 2. Results obtained from the DNA determination and overlap between the isotopic niches of the potential predators and the simulated predator generated from the *Nephrops norvegicus* isotopic values. K 95%: 95% contour of the isotopic area overlap between the simulated predator and the species analyzed in kernel utilization densities; % DNA: percentage of individuals that contained Norway lobster DNA in their stomach; *A*: abundance (ind. km^{-2}) in the study area; PI: Predation Index value based on % DNA and K 95% values of each species (see Section 2.8.)

Species	K 95%	% DNA	*A*	PI (%)
Cephalopods				
Abralia veranyi	30.3	72.7	274	4.94
Eledone cirrhosa	34.5	0	11	0.04
Illex coindetii	23.9	38.4	59	0.76
Rossia macrosoma	8	19.5	35	0.16
Octopus saluti	0	0	2	0
Pteroctopus tetracirrhus	22.8	50	0	0
Scaeurgus unicirrhus	9.9	0	2	0
Sepietta oweniana	55.9	15	848	6.42
Sepietta spp.	58.1	66.7	233	4.45
Todarodes sagittatus	25.9	42.9	5	0.08
Todaropsis eblanae	22.1	73.3	15	0.30
Bony fish				
Conger conger	25	33.3	21	0.19
Lepidopus caudatus	14	0	0	0
Lophius budegassa	0	75	13	0.21
Merluccius merluccius	0	35.7	161	1.21
Molva macrophtalma	0	0	77	0
Trigla lyra	15.8	0	393	0.49
Elasmobranchs				
Galeus melastomus	64.3	10	91	0.75
Scyliorhinus canicula	6.4	9.1	762	1.8
Raja spp.	21.8	0	1	0

cephalopods *Sepietta* spp. (58.1%) and *S. oweniana* (55.9%), representing the species most likely to be specialized predators of *N. norvegicus*. Other predators that presented relevant overlap values were the cephalopod species *Eledone cirrhosa* (34.5%), *A. veranyi* (30.3%), and *Todarodes sagittatus* (25.9%) (Table 2). The K 95% of the other 14 sampled predators, including all bony fishes and the rest of cephalopods and elasmobranchs, was lower than 25% (Table 2, see Figs. 3 & 44).

3.3. Short- and long-term markers of *N. norvegicus* in the diet of its predators

The potential predators *Sepietta* spp. and *A. veranyi* presented high values for both % DNA and K 95% (Fig. 5A). For other predators, such as *G. melastomus*, the trophic marker of *N. norvegicus* was high for K 95% and low for % DNA (Fig. 5A), while some, such as *L. budegassa*, presented high % DNA values and low K 95% values (Fig. 5A).

3.4. Abundance of predators in the study area and their estimated predation impact on *N. norvegicus*

The most abundant predators in the *N. norvegicus* grounds were the cephalopods *Sepietta oweniana* (848 individuals [ind.] km^{-2}), *A. veranyi* (274 ind. km^{-2}), *Sepietta* spp. (233 ind. km^{-2}), the bony fish *Trigla lyra* (393 ind. km^{-2}), and the elasmobranch *Scyliorhinus canicula* (762 ind. km^{-2}) (see Table 2).

The PI, which incorporates the importance of % DNA and K 95% in relation to the relative abundance of each potential predator in the environment, was higher for the cephalopods *Sepietta oweniana* (6.42%), *A. veranyi* (4.94%), and *Sepietta* spp. (4.45%), followed by the shark *Scyliorhinus canicula* (1.81%) and the bony fish *M. merluccius* (1.21%) (see Table 2, Fig. 5B).

4. DISCUSSION

In the present study, we identified the main predators of *Nephrops norvegicus* in the deep-sea Mediterranean waters combining 2 methodologies: genetic determination of stomach contents and stable isotope analysis. Our results demonstrate that the major predators of *N. norvegicus* are the cephalopods *Sepietta* spp., as they presented high values using both methodologies. Considering only the short-term marker (% DNA), which consists of the identification of *N. norvegicus* DNA in the stomach contents (i.e. recent consumption), we also identified the bony fish *Lophius budegassa* as a major predator. Considering only the long-term marker (K 95%), which reflects the assimilation in the muscle tissues of *N. norvegicus* consumed a few months ago, we identified the elasmobranch *Galeus melastomus* and the cephalopod *Sepietta oweniana*. Moreover, according to the estimated PI, which also considers the abundance of the predators in the *N. norvegicus* grounds, the main predators are still *Sepietta* spp. and *S. oweniana*, followed by *Abralia veranyi* (see Fig. 5C). These results are useful for understanding prey–predator interactions and their ecological role in *N. norvegicus* grounds, and could also provide pivotal information for ecosystem-based fisheries management, as well as for evaluating the

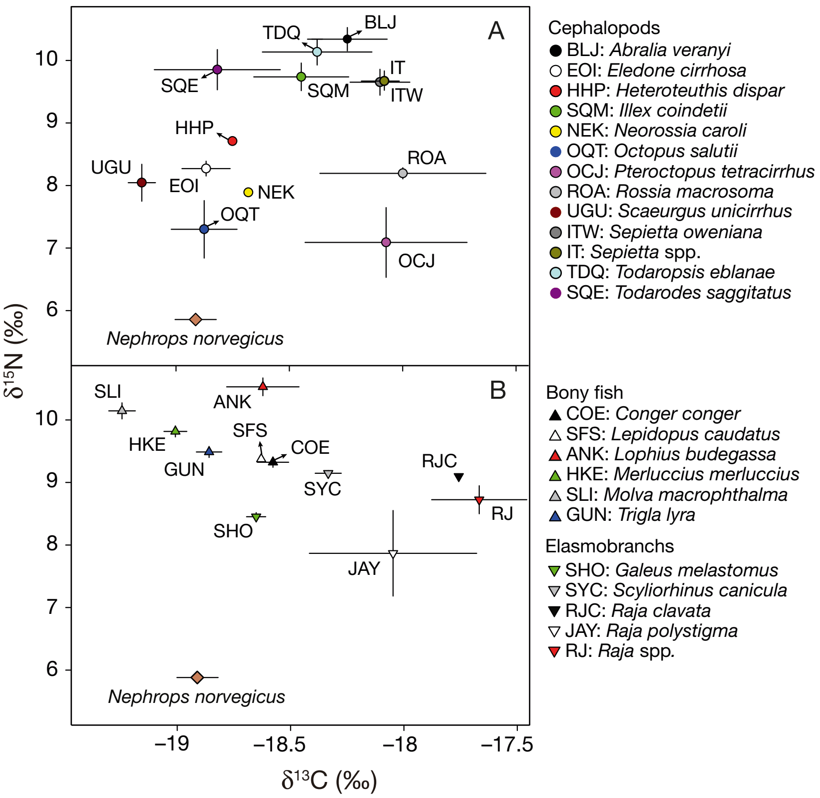

Fig. 2. Mean and standard error of $\delta^{15}N$ and $\delta^{13}C$ values of *Nephrops norvegicus* and potential predators sampled in the northwestern Mediterranean Sea. (A) Cephalopods; (B) bony fish

effectiveness of marine protected areas for the conservation of demersal species.

Using genetic analyses of stomach contents, we identified species that had recently preyed on *N. norvegicus*, while stable isotope analyses from muscle tissue showed the assimilation of all the prey consumed by predators in recent months (Boecklen et al. 2011). As expected, all potential predators showed higher $\delta^{15}N$ values than *N. norvegicus,* reflecting its lower position in the food web. There was isotopic variability among predators, reflecting different trophic habits. For example, within the cephalopods, we found species that occupy higher trophic levels, such as *A. veranyi* that can prey on decapods, larger fish, and other cephalopods (Guerra-Marrero et al. 2020), whereas species such as the cephalopod *Pteroctopus tetracirrhus*, which preys mainly on crustaceans such as *Alpheus glaber* and some fishes (Quetglas et al. 2009), occupy lower trophic positions (Navarro et al. 2013). The range of values found suggests that some predators can exploit resources across entire food webs. *L. budegassa* and *A. veranyi* both showed the highest values, indicating that they may prey on other potential predators, such as *Merluccius merluccius*, and even other cephalopods (Negzaoui-Garali et al. 2008, López et al. 2016, Guerra-Marrero et al. 2020, Lloret-Lloret et al. 2020). The overlap in the different isotopic niches helped us determine if the diet composition of each predator was similar to that of a predator that only consumes *N. norvegicus*. The most similar predators were the demersal shark *G. melastomus*, which has a diet consisting mainly of decapod crustaceans (Fanelli et al. 2009, Barría et al. 2018), and the cephalopods *Sepietta* spp. and *S. oweniana*, which tend to forage from dusk till dawn as adults, preying on demersal and benthic crustaceans (Bergström 1985).

Even though the combined results of the genetics and isotopic niche overlap indicate some specific species as the major predators, it is crucial to keep in mind the density effects of predators, such as predation rate, on *N. norvegicus* (Kunert & Weisser 2003). Predator density could indicate that some species, despite showing less importance based on genetics and isotopic analyses, could have a stronger influence on *N. norvegicus* population dynamics and distribution due to a higher abundance within the habitat (Mchich et al. 2007). Considering the estimated PI along with the % DNA and K 95% results indicates that the major predators were the cephalopods *S. oweniana*, *Sepietta* spp., and *A. veranyi*. Though some bony fishes and elasmobranchs prey occasionally on *N. norvegicus*, the main predators in their grounds are cephalopods, in contrast to the Atlantic Ocean, where the main predator is the bony fish *Gadus morhua* (Björnsson & Dombaxe 2004). The bony fish most closely related to cod in the Mediterranean is *M. merluccius*, which showed a low consumption of *N. norvegicus* based on the % DNA value. In the western Mediterranean, *M. merluccius* is mainly distributed between 100 and 200 m depth (Recasens et al. 1998), segregated from the habitat occupied by *N. norvegicus* (300 to 600 m) (Sardà 1998), which could explain why the crustacean is only occasionally predated by this species. The trophic marker of *N. norvegicus* for *Conger conger*, based on stable isotopes and % DNA values, was

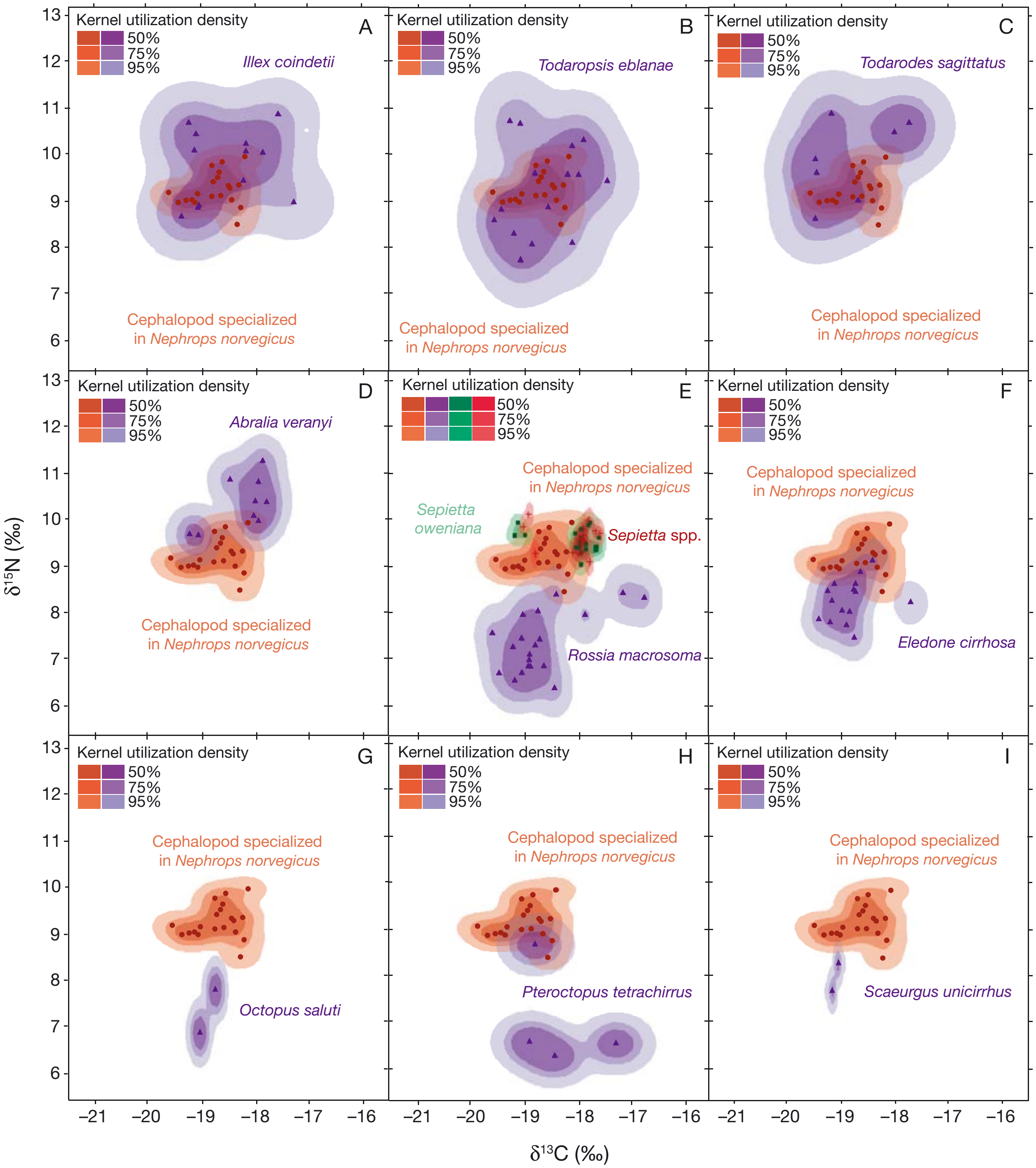

Fig. 3. (A–I) Isotopic niche and overlap of a potential cephalopod that only feeds on *Nephrops norvegicus* and 11 cephalopods inhabiting deep-water ecosystems of the northwestern Mediterranean Sea. Niche size and overlap estimates were generated for the 50%, 75%, and 95% contour levels of the kernel utilization densities. The potential predators that only feed on *N. norvegicus* represent the isotopic niche of the expected stable isotope values of 20 *N. norvegicus* individuals corrected for specific-group isotopic fractionation factors (see Section 2.6.)

similar to that determined for *M. merluccius*, and this species has been directly observed preying on *N. norvegicus* (Fig. S2; O'Sullivan et al. 2004, Matić-Skoko et al. 2012). However, the PI was not high enough for this fish to be defined as a major predator, probably due to its low abundance in the habitat.

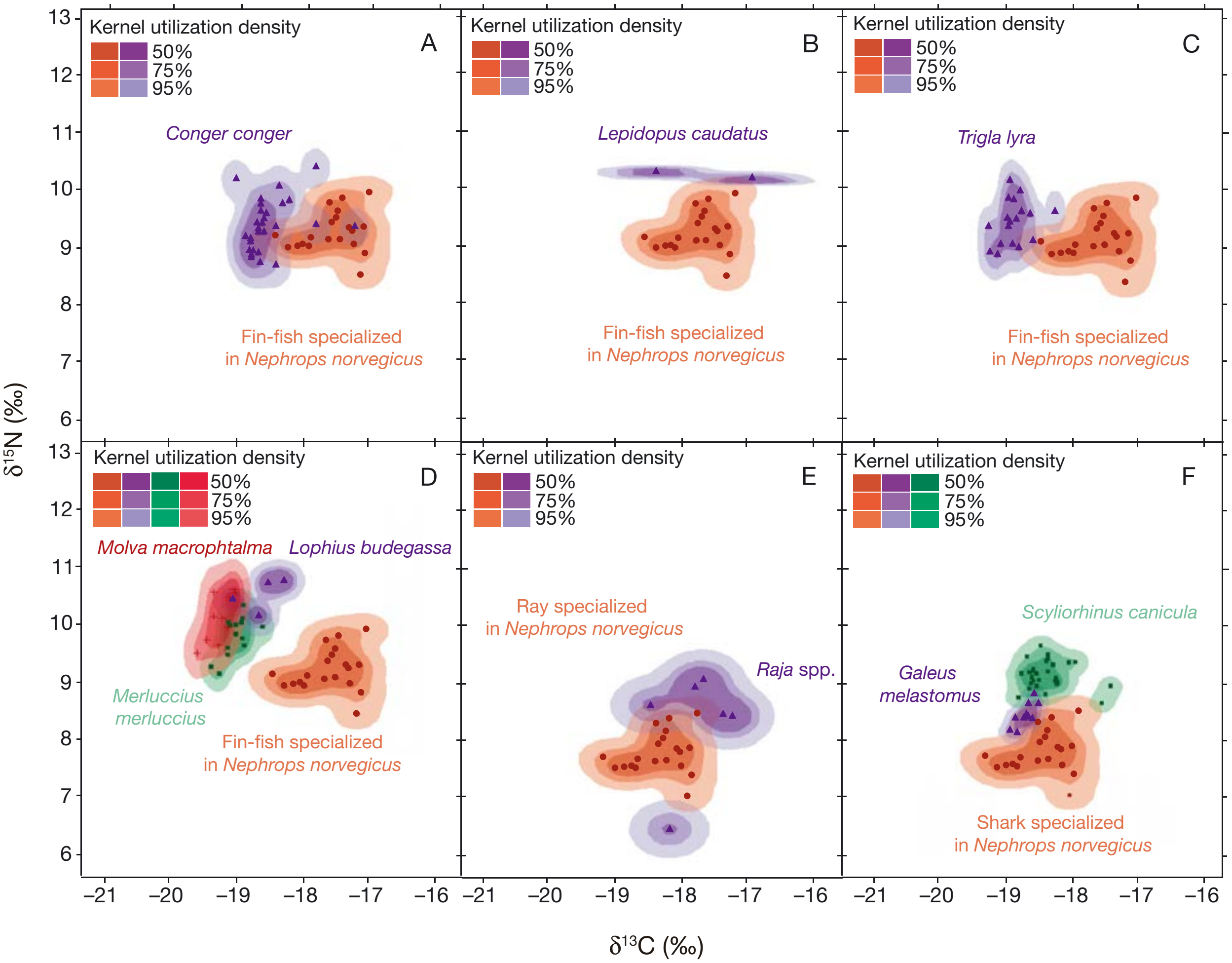

Fig. 4. Isotopic niche and overlap of a potential bony fish, ray and shark that only feed on *Nephrops norvegicus* and (A–D) 6 bony fishes, (E) rays (*Raja* spp.), and (F) 2 shark species inhabiting deep-water ecosystems of the northwestern Mediterranean Sea. See Fig. 3 for an explanation of the niche size and overlap estimates and the potential predators

Some studies have indicated that the combination of unavailability of *N. norvegicus* due to its burrowing behavior and the potential invulnerability of larger individuals could explain the absence of specialized predators (Smith & Herrkind 1992, Wahle 1992, Serrano et al. 2003). In addition, *N. norvegicus* is not an easy prey to catch and digest because of its exoskeleton and its low fat content (Björnsson & Dombaxe 2004); thus, its predation might be more a matter of prey availability than a preference (Chapman 1980).

The identification of predators offers key information for interpreting biological linkages among species and is critical for identifying nature-based solutions for ecosystem-based management used both in fisheries and marine spatial planning. Ecosystem-based modelling can generate predictions of the ecological consequences of activities such as overfishing (Jacobsen et al. 2016). Most predators are considered keystone species in the environments they inhabit (Power et al. 1996), playing an essential ecological role in restoring ecosystems and conferring resilience against future negative impacts, such as biological invasions or climate change (Ritchie et al. 2012). The information provided in the present study could be useful for adapting and creating effective fisheries management and restoring the population of *N. norvegicus* in the Mediterranean Sea while preventing negative future scenarios. An improvement for fisheries management could be the parallel assessment of the major predators identified, to compare the fluctuations between populations. In the management of no-take marine reserves, predators should also be evaluated in terms of abundance and bio-

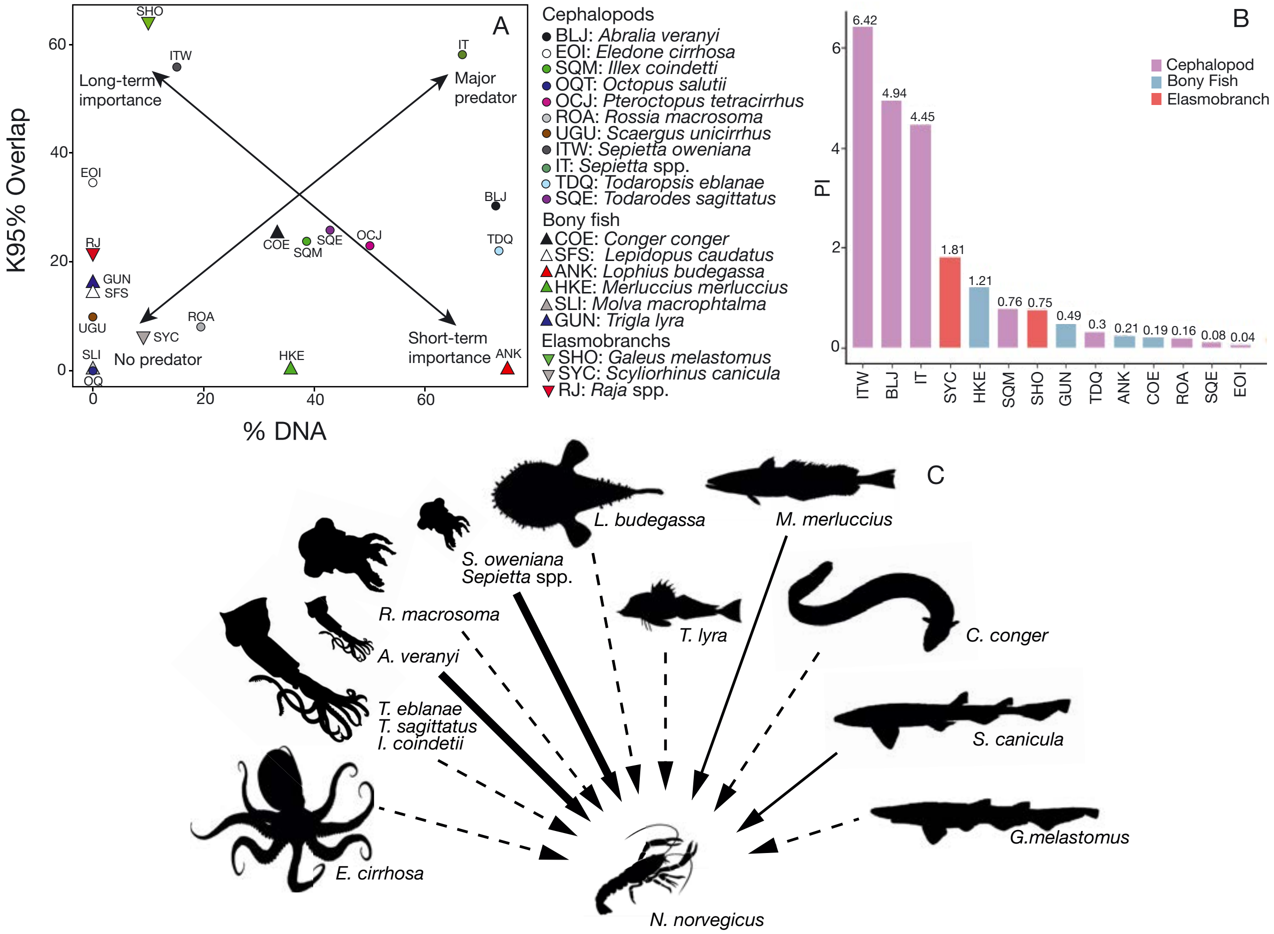

Fig. 5. (A) Classification of the potential predators of Norway lobsters according to their % DNA (percentage of individuals containing *Nephrops norvegicus* DNA in their stomach) and K 95% (95% contour overlap between the isotopic area of the simulated predator and the potential predator) values. Long-term importance: high K 95% value; Short-term importance: high % DNA value; Major predator: % DNA and K 95% values both high; No predator: % DNA and K 95% values both low, meaning that this species does not prey on Norway lobster. (B) Predation Index for each species, from the highest value to the lowest. (C) Trophic network relating the species (silhouettes obtained from https://pngtree.com/ and http://clipart-library.com/) that prey on *N. norvegicus*. Solid and wider arrows: major predators; solid and thin arrows: species of moderate importance; dashed arrows: predators with minor importance

mass, to properly assess the effectiveness of the protected area. Predators such as *Sepietta* spp. and *A. veranyi* might also directly affect the dynamics of *N. norvegicus* populations by reducing recruitment and/or survival.

In this study, we used indirect methods and, therefore, we did not consider whether *Sepietta* spp. and other predators prey only on small-sized *N. norvegicus* individuals or larvae. Consequently, next steps could involve assessing and testing the predation of *Sepietta* spp. and *S. oweniana* on *N. norvegicus* of different sizes (including larvae) and evaluating the presence of predator avoidance of larger *N. norvegicus* across all the predator species analyzed.

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Spatial ecology of Norway lobster *Nephrops norvegicus* in Mediterranean deep-water environments: implications for designing no-take marine reserves

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ABSTRACT: The Norway lobster *Nephrops norvegicus* is one of the most important marine resources for European fisheries. However, overfishing has caused the stocks to decline over the last decades, particularly in the Mediterranean Sea. The implementation of no-take marine reserves could change these current trends, thus achieving a more sustainable fishery. The effectiveness of no-take reserves depends on optimal size design, and because of this, new behavioural data on the spatial ecology of the species are of pivotal importance. Here, for the first time, we investigated the spatial movements and daily activity patterns of Norway lobster in a deep-water (315–475 m depth) no-take marine reserve of 10 km^2 in the continental slope of the northwestern Mediterranean Sea, by combining acoustic tracking and tagging–recapture procedures. The results revealed the territorial behaviour of Norway lobster, centred in small exclusive individual areas where most displacements took place at midday. We found that once settled in a place, their home ranges reached approximate sizes of 17.75 to 736.25 m^2, suggesting that no-take marine areas focussed on recovering Norway lobster populations do not require large extents to be effective. Tag–recapture data indicated minimal spillover of biomass, implying that Norway lobsters are site settled and do not perform large movements. Future studies on larval spread and recruitment would be necessary to focus on the possible spillover benefit for fisheries. The acoustic telemetry system used in the present experiment effectively revealed the range of movement of individuals, and thus represents a promising monitoring tool to assess no-take marine reserve sizes and reciprocal spacing for deep-water demersal resources.

KEY WORDS: Resources management · Fisheries · No-take marine reserves · Home range · Acoustic telemetry · *Nephrops norvegicus*

1. INTRODUCTION

The percentage of sustainable global fishing stocks have decreased considerably; for example, in the Mediterranean Sea, more than 60% of fishing stocks were estimated to be biologically unsustainable, and this percentage is projected to increase over the next decades (Jackson et al. 2001, FAO 2020). This historically intense fishing activity has had a global impact, not only by reducing biodiversity and marine resources, but also by compromising habitats (e.g. Thrush & Dayton 2002, Puig et al. 2012) and consequently, generating global concern regarding unsustainable practices (Costanza et al. 2017, Froese et al. 2018, Rousseau et al. 2019). The Convention on Biological Diversity Aichi Target 11 aimed to implement

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10% of effectively protected marine areas to improve biodiversity and to also enhance social benefits (CBD 2010). Therefore, developing effective management strategies specially focussed on stock recovery and expanding marine protected area (MPA) networks is essential for the sustainable exploitation of marine resources (cf. Sustainable Development Goals; UN 2015, Lillebø et al. 2017).

Mediterranean fishing activity produces almost half of all fishing landings in the European Union (EEA 2015, European Commission 2018). Beyond the possible effects of climate change (Trindade-Santos et al. 2020), the use of high-impact fishing gears is one of the main drivers of ecosystem change in the Mediterranean Sea (Danovaro et al. 2017). Bottom trawl fishing (trawling) is one of the most widespread anthropogenic activities in ocean continental margin areas down to 1000 m (Palanques et al. 2006, Kroodsma et al. 2018). Trawling causes sediment resuspension and removal, eliminating sessile fauna with negative feedback on natural processes to restore a baseline condition in impacted ecosystems (Cook et al. 2013). These practices have many impacts on benthic biodiversity and constitute the main cause of depleted stocks through fishing, removing high proportions of populations (Sciberras et al. 2018). The structure of benthic communities is profoundly altered, with mobile scavengers or opportunistic predators replacing fragile epifaunal species (Tillin et al. 2006, Ramalho et al. 2020). Despite all of these consequences of trawling, the great majority of the European fleet employs this fishing method (Clarke et al. 2015).

The Norway lobster *Nephrops norvegicus* is of great importance in the European fishing industry (Ungfors et al. 2013); however, in the Mediterranean Sea, some stocks are heavily exploited, as fisheries management policies are non-adaptive and include a high proportion of undersized individuals (Sardà et al. 1998, GFCM 2017, STECF 2019, García de Vinuesa et al. 2020). Their dependency upon fragile soft muddy bottoms, where the animals dig burrows, makes lobsters particularly vulnerable to the effects of trawling (Hiddink et al. 2006); moreover, lobsters can avoid capture when they are inside or at the entrance of their burrows, which makes their dependency stronger (Chapman & Rice 1971). As marine ecosystem engineers, the digging behaviour of Norway lobsters provides habitat features of relevance for several other co-existing benthic species. Lobsters could therefore be a potential umbrella species, representing an effective conservation tool to protect other co-occurring species (Roberge & Angelstam 2004). For this reason, the demographic reduction of Norway lobster stocks could broadly affect the coexisting benthic biota (Tuck et al. 1994, Davidson & Hussey 2019) and overall ecosystem functioning, including blue carbon sequestration (Luisetti et al. 2019).

The implementation of MPAs, such as no-take reserves, could be a useful tool for recovering the demographic status of presently over-exploited Norway lobster populations with the correct assessment and monitoring plan (GFCM 2019, Melaku Canu et al. 2021). Although one of the primary aims of MPAs is benefiting and restoring biological diversity, they can also recover and produce healthy fishing resources (Kerwath et al. 2013, Laffoley et al. 2019, Bourlat et al. 2021), benefiting the habitat and all other inhabiting benthic species, including fragile sessile fauna (Ardron et al. 2014, Langton et al. 2020). The implementation of no-take reserves directly improves population densities and individual body sizes not only inside the no-take area, but also in surrounding zones, via biomass spillover, thus benefiting the nearby fisheries (Sala & Giakoumi 2018, Cabral et al. 2020, Sala-Coromina et al. 2021). Positive management experiments with no-take marine reserves and biomass export have already been carried out on crustacean decapod species, such as the European lobster *Homarus gammarus* and the spiny lobster *Palinurus elephas* (Goñi et al. 2010, Follesa et al. 2011, Moland et al. 2013). Presently, in the Mediterranean Sea there are no assessments of the use of no-take reserves closed year-round for the recovery of Norway lobster populations, except for the Pomo Pit area in the Adriatic (Melaku Canu et al. 2021). In the deep-water northwestern Mediterranean Sea, assessments should be carried out in habitats between 300 and 500 m depth, where intensive trawling has been taking place over the past 70 yr (Maynou 1998, Sbrana et al. 2020).

No-take marine reserve size and reciprocal spacing ensure the persistence of populations inside the reserves (Moffitt et al. 2011). The reserves must be designed based on spatial ecological knowledge of the targeted species (Blowes & Connolly 2012). Spatial ecology applied to conservation and management in protected areas is essential to determine the closure design of the protected area and its efficacy in defining animal movement as representative of large-movement species or site-attached species (Lea et al. 2016). To design protected areas considering the biology and behaviour of the species is crucial, as, in some cases, closed areas could lead to instabilities over long periods resulting in negative effects (Smith & Jensen 2008). Although several aspects of the burrowing behaviour and distribution of Norway lobsters have been widely studied (e.g. Sardà 1998, Haynes et al. 2016), information about their spatial ecology is still limited to territoriality and site fidelity or diel activity patterns (e.g. Aguzzi et al. 2003, Power et al. 2019).

Spatial data on movement, home ranges (i.e. where most animals live and perform their day-to-day activities) (Katajisto & Moilanen 2006) and territorial interactions are required to determine the adequate size and location of marine reserves (Lees et al. 2020). Acoustic telemetry could provide these data for deep marine organisms, although the operational challenges it presents for deep-water and deep-sea applications are much greater than those for terrestrial or shallow habitats (e.g. Aspillaga et al. 2016, Crossin et al. 2017).

In the present study, we investigated, for the first time, the spatial ecology of Norway lobsters inhabiting a deep-water no-take marine reserve in the Mediterranean Sea. Specifically, using acoustic tracking and capture–recapture data, we examined: (1) their spatial movement patterns and home range, (2) their diel pattern of movement activity and (3) their spatial territorial interactions. All of this spatial ecological information was necessary to evaluate whether the size of this no-take marine reserve, established in 2017 to recover the depleted stocks of Norway lobsters, is adequate as a conservation measure for this target fishery.

2. MATERIALS AND METHODS

2.1. Study area

This study was conducted in a no-take marine reserve of 10 km^2 located between 315 and 475 m depth in muddy habitats of the continental slope margin of the northwestern Mediterranean Sea (Fig. 1). During the last 20 yr, the total catch of Norway lobsters has declined along with other resources such as European hake *Merluccius merluccius* and the deep-sea red

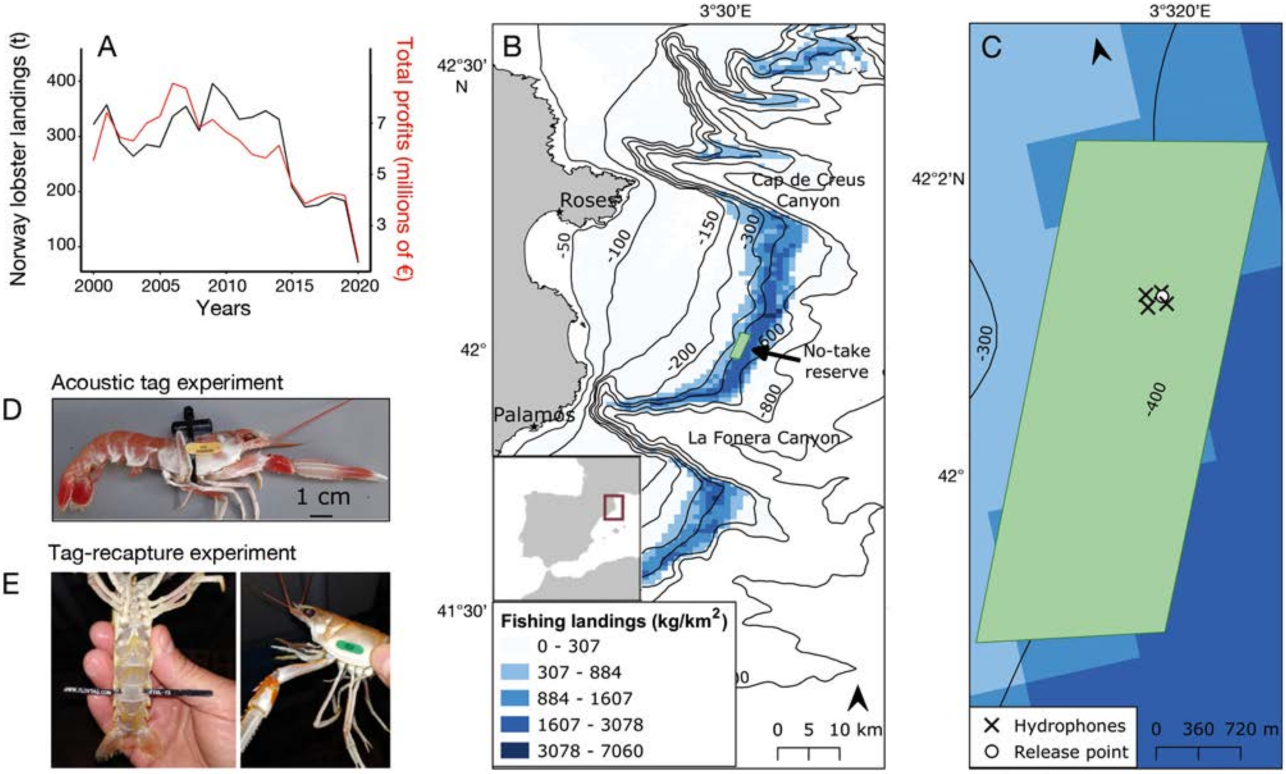

Fig. 1. (A) Evolution of the total biomass and total economic gains of Norway lobster *Nephrops norvegicus* in Catalonia (northwestern Spain) between 2000 and 2020 (DGPAM 2021). (B) Spatial distribution of the accumulated catches of Norway lobster along the Catalan coast (northwestern Mediterranean Sea, Spain), obtained by combining vessel monitoring system information and official landing data in the time period 2005–2018 (Garcia et al. 2016, European Commsion 2020). (C) Locations of the network of hydrophones (black crosses) and the release point (white dot). Black lines in (B) and (C) show bathymetry (m). (D) A Norway lobster equipped with a coded tag and the acoustic transmitter. (E) A Norway lobster equipped with serial numeric coded tags glued to the carapace, and numeric Floy Streamer Tags injected in the 4th abdominal segment. Tags also provide a phone number to contact in case of re-capture by fisherman

shrimp *Aristeus antennatus*. To reverse this situation, the Spanish Government enforced a network of no-take reserves along its Mediterranean continental margin (Order APA/753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753). Our study area corresponded to one of those reserves, closed to all extractive activities in September 2017 and covering 10 km^2 (Fig. 1).

2.2. Passive tag–recapture experiment

A total of 216 Norway lobsters were captured inside the no-take marine reserve using prawn creels (UK-Model, Carapax Company; creel size: 58 cm length × 42 cm width × 32 cm height; see Video S1, www.int-res.com/articles/suppl/m674p173_supp/) during 3 surveys (May–June, September and November 2019) on-board the RVs 'Sarmiento de Gamboa' and 'García del Cid'. Creel bait consisted of salted herring and fresh chicken (following the recommendations of local creel-specialized fishermen). Creels were recovered after 10 h at night conducting all deck operations in dim red light, to avoid retinal damage to captured individuals (Loew 1976, Shelton et al. 1985). All individuals were then transferred in complete darkness, within an individual cell of a compartmented aquarium with continuous marine water flow at 13°C. Carapace lengths (±0.05 mm) were measured and sex determined (thickness of the first pair of pleopods) for all the individuals caught. All captured specimens were labelled with 2 tags: serial numeric coded tags glued to the carapace, and numeric coded Floy Streamer Tags attached with a needle (FTSL-73 and Floy Custom UV Protected Vinyl Laminated Ovals). For tagging the individuals, the needle was sterilized with 95% alcohol and injected through the muscular tissue of the fourth abdominal segment. The first tag was used to ensure that fishermen would not miss the tagged animal and the second tag ensured that the animal would still be tagged after moulting, as was used in other studies of growth in this species (Ulmestrand & Eggert 2001). We performed 3 different surveys conducted onboard research vessels during 2019, releasing a total of 216 tagged Norway lobsters with serial numeric coded tags (85 individuals in May–June, 105 in September and 26 in November). Tagged animals were released in the middle of the no-take marine reserve at 10 m above the seabed during the night following the capture with an auto-release device. All crews of fishing vessels operating in the study area (46 vessels) were requested to report the presence of tagged specimens in their captures.

2.3. Acoustic tracking experiment

A total of 33 Norway lobsters (11 females and 22 males), ranging from 31 to 50.5 mm carapace length (Table 1), were caught by creels, sized, acclimated (as described in Section 2.2) and tagged with serial numeric coded tags and acoustic emitters (VEMCO V7-L1-69k, Innovasea) equipped with a 255 d battery life (length = 18 mm, weight = 0.7 g) glued onto the carapace (Fig. 1). Each acoustic tag sent an acoustic signal (ping) at a frequency of 69 kHz, approximately every 120 s. Each ping emitted by the individual tags included information on the identification number (ID).

The monitoring area of the hydrophone array (2 VR2W-69k and 2 VR2AR-69k hydrophones, VEMCO) covered a radius of ~350 m from the mooring location. The 4 hydrophones were attached to the mooring at 20 m above the bottom and 150 m apart (Fig. 1). The presence of each tagged Norway lobster was reported when the acoustic ID signal was detected by at least 1 of the hydrophones (animals inside burrows were sound-shielded by the sediment), while triangulated postions were obtained when at least 3 hydrophones detected the same acoustic ID signal, time-synchronised (i.e. displacements of animals within the monitoring area) (Fig. 2).

We released all individuals at night, in the middle of the array of the 4 hydrophones moored in advance (labelled A, B, C and D, see Fig. 6) with a release system consisting of a PVC receptacle with a dissolving latch closure on the door (designed to dissolve after 5–10 min more than the estimated time for the release system to sink to the seabed) (adapted from Tuck et al. 2015; see Video S2).

To account for the effect of clock drift of each hydrophone affecting the evaluation of tracking (i.e. the same ping can be received at different hydrophones at slightly different timings so that signals can be erroneously interpreted as a change in position), synchronizing acoustic tags (VEMCO model V7-L1-69k) were attached to each of the 4 moorings (1 m above each hydrophone) and to the release system (Masmitja et al. 2020). After the deployment, the exact position of each hydrophone was registered from the GPS and the ultra short base-line positioning methods by a remotely operated vehicle ('Liropus 2000'). After 4 mo of deployment (September 2019), the 4 hydrophones were recovered on board the RV 'Sarmiento de Gamboa' using an acoustic transponding release device, and all recorded data were downloaded.

Table 1. Details of 33 acoustically tagged Norway lobsters in a no-take reserve in the northwestern Mediterranean Sea during 2019. ID: identification number of each individual; CL: carapace length; tracking time: total days with detections; total detections: total number of pings; detections filtered: total number of detections after filtering procedures; net distance: vector sum of individual displacements; total distance travelled: sum of the length of all trajectories of an individual; total distance/track time: mean total distance travelled each day. Dashes indicate the absence of information from the individuals that were removed after data filtering and processing

ID	CL (mm)	Sex	Tracking time (d)	Total detections	Detections filtered	Net distance (m)	Total distance travelled (m)	Total distance/track time (m d^{-1})
14456	37.1	F	18	732	705	145.44	4007.58	265.13
14457	32.7	F	44	6070	6070	2.44	11 746.71	266.97
14458	34.7	M	12	1692	1692	215.07	3067.66	255.64
14459	32.7	F	11	1379	1379	80.56	3319.23	301.75
14460	44.9	M	1	33	–	–	–	–
14461	40.1	M	106	40 067	–	–	–	–
14462	36	M	5	549	548	173.99	1052.96	1.92
14463	34.05	F	106	11 509	11 509	131.31	22 733.87	1.98
14464	34.1	M	4	407	407	187.85	975.64	2.39
14465	43.4	M	106	3092	2975	150.88	49 352.72	16.59
14466	35.4	M	2	153	–	–	–	–
14467	40.4	M	106	15 415	–	–	–	–
14468	44	M	106	12 676	12 536	36.39	39 228.73	3.13
14469	50.5	M	2	5	–	–	–	–
14470	42	M	3	45	42	169.78	1553.347	36.95
14471	41.2	M	6	597	597	14.14	1942.93	3.25
14472	34.13	M	4	150	110	70.93	517.99	4.71
14473	34.3	F	83	21 043	–	–	–	–
14474	46.6	M	17	113	112	183.63	1383.41	12.35
14475	50.4	M	106	9919	8815	145.14	19 626.18	2.23
14476	34.6	M	106	40 099	–	–	–	–
14477	41.44	M	2	39	39	101.11	874.06	22.41
14478	41.2	M	1	2	–	–	–	–
14479	37	F	106	28 071	–	–	–	–
14480	36.2	F	5	209	–	–	–	–
14481	34.3	F	1	8	–	–	–	–
14482	45.8	M	106	38 241	–	–	–	–
14483	37.5	F	5	36	36	151.69	543.94	22.41
14484	39.7	M	4	107	106	110.02	564.99	15.11
14485	37.5	M	16	712	–	–	–	–
15829	31.7	F	24	381	295	238.92	2267.03	5.33
15830	37.6	M	106	22 103	22 103	20.66	23 240.88	7.68
15831	31	F	106	35 816	–	–	–	1.05

2.4. Estimation of spatial movement of Norway lobsters based on acoustic tracking

Spatial movement of acoustically tagged individuals was estimated by using a triangulation method, detecting signals simultaneously by a minimum of 3 hydrophones. The acoustic tag signal detected by each hydrophone had a different timestamp due to its position and the time of flight of acoustic signals. Therefore, using the time difference of arrival among different hydrophones, and applying regression methods such as least squares (Jin et al. 2018), the position of the sound-emitting source was computed (see Masmitja et al. 2020 for more details).

Before analysing the spatial data, it is essential first to check the data by visualization and then by filtering detections. The aim of this procedure is to eliminate possible individuals that have lost their acoustic tag or unusual detections provoked by a failure of the acoustic tag, which, if they were included in the results, would lead to misinterpretation of the behaviour. Data treatment to compile time series of spatial data was as follows. Firstly, we discarded all triangulated acoustic positions with velocities above a maximum threshold of 0.5 m s^{-1}. This threshold was estimated from the movement analyses of 4 acoustically tagged Norway lobsters caught by 3 fishing vessels at the border of the no-take reserve (Fig. S1 in the

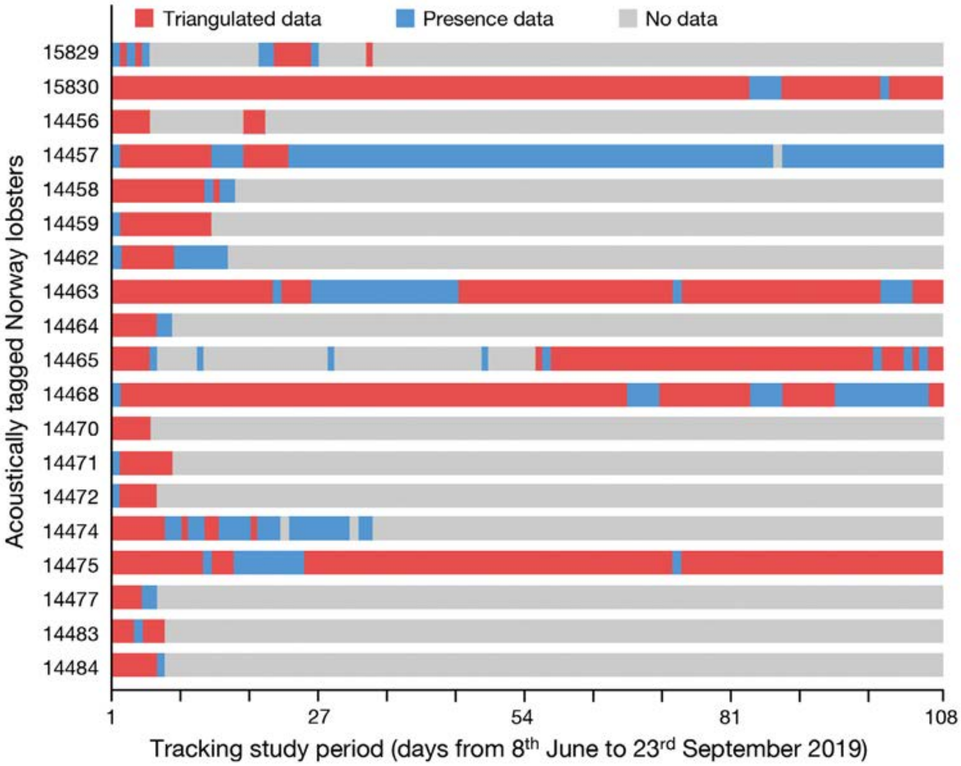

Fig. 2. Overview of the data obtained from each acoustically tagged Norway lobster throughout the study period. 'Triangulation data' include triangulated detections that resulted in precise positions inside the detection area; 'presence data' refers to the number of detections obtained by any of the 4 hydrophones, with no triangulation procedures; and 'no data' indicates a lack of both triangulation and presence data

Supplement, www.int-res.com/articles/suppl/m674p173_supp/). These individuals caught were analysed in terms of velocity (m s^{-1}), total distance travelled (m), trajectories (m) and patterns of detection to be used as a control for the rest of the acoustically tagged Norway lobsters (Table 1, Fig. 3). After processing the acoustic data and performing the filtering procedures, only 19 out of 33 acoustically tagged lobsters were included in the successive spatial and waveform analyses described below.

Spatial movement descriptors in terms of total distance travelled, net distance (m) or tracked time (d), mean velocities (Table 1; Fig. S2) and main trajectories were analysed using the statistical software R version 4.0.3 (R Core Team 2020), using the packages 'trajr', 'moveVis', 'adehabitatLR', and 'adehabitatHR' (Calenge 2006, 2019, McLean & Skowton Volponi 2018, Schwalb-Willmann 2020). Afterwards, we estimated 2 home range descriptors as proxies for analysing different types of area occupation (i.e. home range size) per individual: the 50% probability utilization distribution (UD) as a proxy of the core area (UD50) and the 90% probability UD as proxy for total home range extent (UD90), based on kernel UDs (Katajisto & Moilanen 2006), a non-parametric density estimation of the UD. Both UD50 and UD90 were estimated with the R software package 'adehabitatHR', using the smoothing parameter selection ad hoc, and considering only the speed threshold-filtered positions for each month after release (i.e. June, July, August and September). To test differences over time in both UD50 and UD90, 1-way ANOVAs were conducted using the package 'stats' in R (Bates et al. 2020). Normality and homogeneity of variances were tested with the Shapiro-Wilk normality test using the package 'stats' in R and the Levene test using the package 'car' in R (Bates et al. 2020, Fox et al. 2020). Mean values of UD50 and UD90 were log-transformed before testing the differences over time. Home range overlap among tagged Norway lobsters was also quantified and measured in each month through the UD overlap index (UDOI) for both UD50 and UD90 (Hurlbert 1978), which ranges from 0 to 1 (i.e. respectively for complete spatial segregation and uniform distribution with 100% overlap for a pair of animals).

The interaction among individuals was innovatively investigated with the coefficient of association (CA) that measures the interaction between pairs of

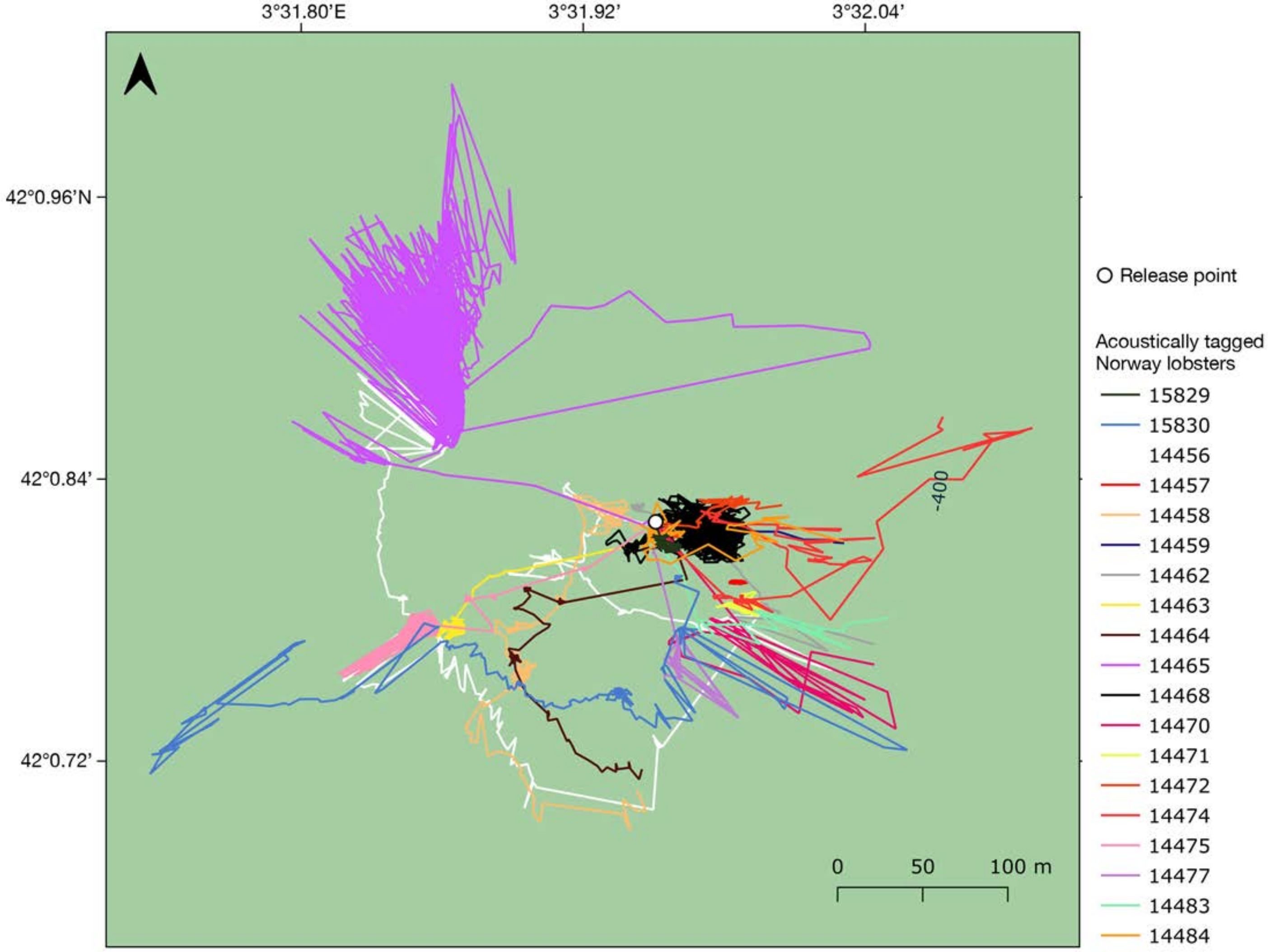

Fig. 3. Individual spatial movements of 19 acoustically tagged Norway lobsters in deep waters of the northwestern Mediterranean. The location of the release point is indicated (white dot); also shown is the approximate depth (400 m)

individuals in terms of spatial attraction or avoidance (i.e. values above or below a threshold of 0.5, respectively; Bauman 1998). The CA was calculated over different inter-individual distances of 1, 5, 15 and 50 m, using the R software package 'wildlifeID' (Long 2019).

The locomotor activity rhythms were characterized for all acoustically tagged individuals (N = 19) in terms of the total distance covered per hour (Fig. S2). Waveform analyses on time series of distance data were conducted to assess the phase (i.e. activity peak) over the 24 h, as follows. Each time series (i.e. 1 per individual) was subdivided into 24 h segments. Values from all individuals were then pooled together at corresponding time intervals, resulting in a single averaged waveform (i.e. as a global activity pattern profile). That averaged curve was plotted over the 24 h made by values plus their standard deviation. On those plots, the phase of the rhythm was identified by superimposing a threshold computed by re-averaging all waveform values together (i.e. the midline estimating statistic of rhythm [MESOR]; Aguzzi et al. 2003). In the resulting waveform, all mean values above MESOR represent a significant activity increment in travelled distance.

2.5. Presence data of Norway lobster from acoustic detections

Parallel to the tracking estimation, we also computed the occupancy area of the 19 acoustically tagged individuals, by using time series detections from each of the 4 hydrophones (A–D) during 4 mo.

The potential area of detection was calculated with the software QGIS 3.10 (www.qgis.org/) creating polygons with a radius of 350 m for each hydrophone and then creating a unique polygon which encompassed the 4 polygons created for each hydrophone. The total area was estimated with the same QGIS software. By analysing each hydrophone individually (without the need to triangulate), we amplified the detection range, consequently increasing the capacity to detect more Norway lobsters. As for triangulation, the furthest position estimated was at approximately 300 m from the hydrophones. Considering the range of detection as a unique area, we split it into 13 subareas according to the hydrophone ranges that overlapped. We then assigned each acoustically tagged individual to the subarea in which we found the most detections. This methodology did not provide the exact location of the individual as with the triangulation method, but it efficiently allowed us to identify the subarea in which an individual spent most of its time.

3. RESULTS

3.1. Capture and recapture of individuals

During the whole period of the coded-tagging experiment, in which 216 individuals were labelled with serial numeric coded tags, we obtained a low recapture rate (i.e. only 5 individuals, equivalent to 2.32% of the total batch). These individuals were recaptured by a fleet of 46 trawlers fishing in the neighbouring areas and operating on a daily basis (i.e. from 07:00 to 16:00 h), 5 d wk^{-1} outside (but very close to) the borders of the no-take reserve (Fig. S1).

3.2. Acoustic tracking of individuals by triangulation

A total of 33 Norway lobsters (11 females and 22 males) ranging from 31 to 50.5 mm carapace length were instrumented with acoustic tags (Table 1). After processing all acoustic data, only 19 of these tagged lobsters (6 females and 13 males) were included in the spatial and waveform analysis. The total distance travelled per day for these individuals ranged from 1.05 to 266.97 m d^{-1} (Table 1). The potential area of detection for triangulated acoustic data covered around 0.28 km^2 (Fig. 3). The acoustic data revealed that in June, most Norway lobsters moved randomly, reaching the edges of the area of detection. In September, only 5 of the 19 tracked individuals established themselves in the monitored area as evidenced by the continuous detection of their presence during the entire monitoring period (Fig. 4).

Home ranges of Norway lobsters obtained by UD50 and UD90 estimations were significantly different over the 4 mo of tracking (UD90: ANOVA, $F_{3,30} = 5.06$, $p < 0.05$; UD50: $F_{3,30} = 5.51$, $p < 0.05$). Home ranges in June were larger (UD50: mean ± SD = 2476.32 ± 3338.67 m^2; UD90: 11223.42 ± 16022.64 m^2; n = 19) than in the following months of July (UD50: 18.4 ± 30.62 m^2; UD90: 170.2 ± 316.74 m^2; n = 5), August (UD50: 305.6 ± 598.88 m^2; UD90: 1413.8 ± 2679.81 m^2; n = 5) and September (UD50: 278.4 ± 599.09 m^2; UD90: 1341 ± 2910.37 m^2; n = 5) (Table 2). The home range defined for all Norway lobsters was estimated by the average home ranges (UD90) obtained from individuals who stayed inside the detection area for the entire experimental period (IDs = 14463, 14468, 14475 and 15830; see Table S1) and ranged from 17.75 to 736.25 m^2.

The UDOI metrics among the home ranges (Table 3) showed no overlap between the areas estimated with UD90, nor with UD50 or core areas. In June, when all acoustically tagged individuals were released together, home ranges presented a higher index of overlap (UDOI UD90: mean ± SD = 0.03 ± 0.08; UDOI UD50: 0.01 ± 0.01).

Mean values of the spatial interactions among individuals estimated with the CA indicated no spatial attraction between acoustically tagged Norway lobsters, as values were always <0.5. CAs were higher for some individuals only in the first month (June) than in the other months (i.e. >0.5, Table 3; the CA values for all individual interactions are indicated in Table S2).

Waveform analyses, pooling together the movement data of all acoustically tagged individuals (n = 19), showed a significant increase in the travelled distance in phase with light intensity. Based on MESOR analysis (mean ± SD =15.42 ± 11.13 m^2), a major peak was identified during light hours, between 08:00 and 17:00 h GMT (Fig. 5).

3.3. Norway lobster detection based on acoustic presence data

Analysing detections for each hydrophone individually, we increased the range of detection to double the triangulation area, around 0.6 km^2 (Fig. 6). The total number of acoustic detections differed among the 13 subareas classified and among the 4 months

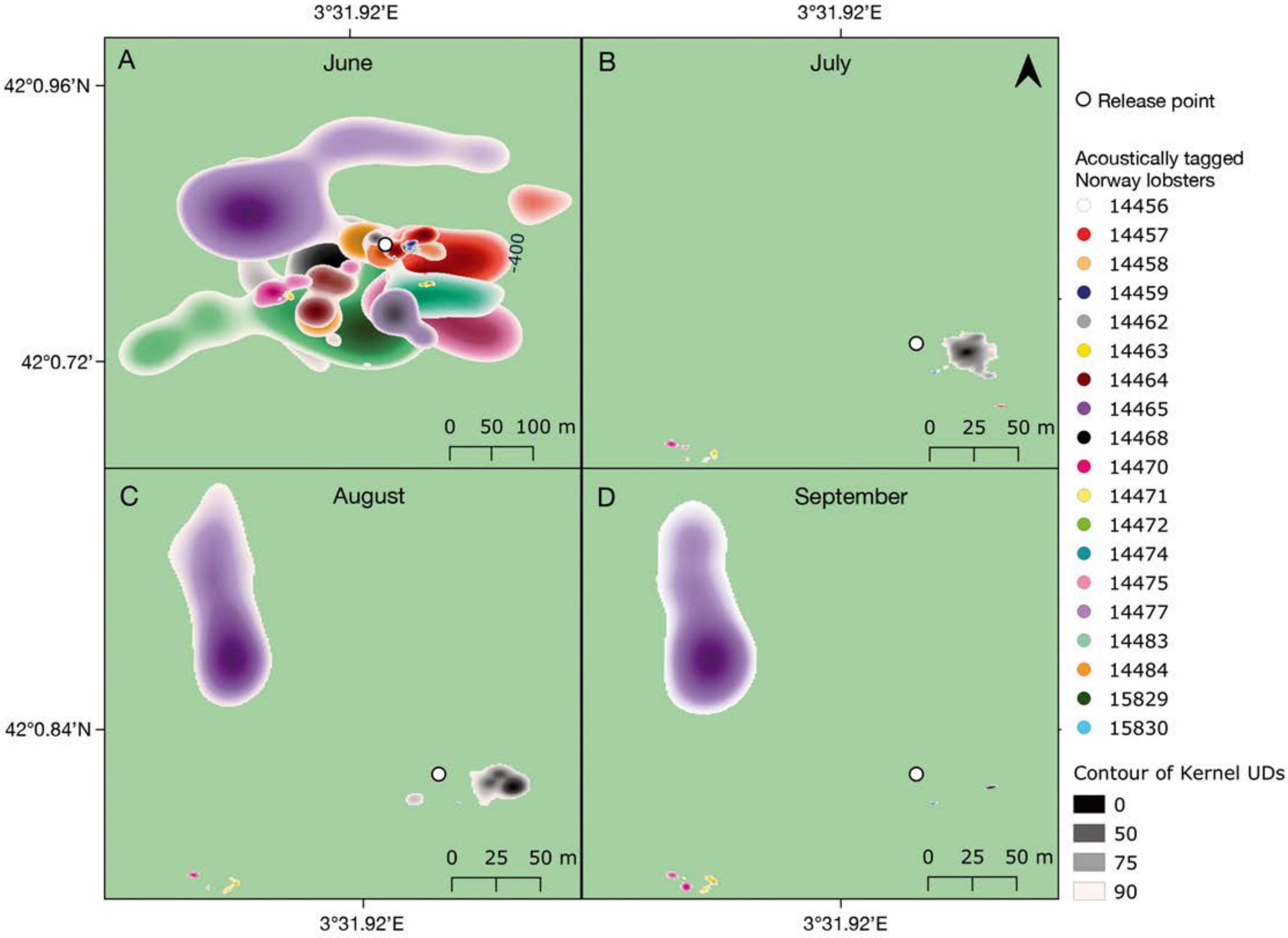

Fig. 4. Home ranges of 19 acoustically tagged Norway lobsters released in 2019 represented by the gradient of kernel utilization during 4 mo of 2019 in the deep waters of the northwestern Mediterranean: (A) June, (B) July, (C) August, (D) September. Also shown in panel A is the approximate depth (400 m)

(Table 4). In June and July, acoustic detections mainly appeared in the central area, in the centre among the 4 hydrophones and in the eastern area, where only 2 hydrophones could make these detections. During August and September, the number of detections increased in the north-eastern areas.

4. DISCUSSION

By combining acoustic tracking and capture–recapture information, we provide the first detailed description of the spatial ecology of Norway lobsters inhabiting the deep-water Mediterranean Sea. Our results revealed that once deployed over a very small area, most individuals dispersed a few hundred metres and showed the same territorial and solitary behaviour already well described in the literature (Sbragaglia et al. 2017). Moreover, those animals displayed a clear temporal pattern of activity, which peaked during light hours at this depth (Aguzzi et al. 2003). Beyond the ecological interest, these spatial data may be valuable for designing other no-take reserves focussed on recovering deep-water populations of Norway lobsters.

Tag–recapture experiments traditionally yield low recapture rates of labelled individuals (Haynes et al. 2016). The 2.32% recapture rate in our study might suggest that most Norway lobsters remained inside the no-take reserve, in agreement with results obtained in similar studies (Haynes et al. 2016) and from the acoustic telemetry data that comprised the spatial movements obtained by triangulation of acoustic positions.

Table 2. Spatial movement metrics of 19 acoustically tagged Norway lobsters tracked in a no-take reserve in the northwestern Mediterranean Sea during 2019. UD90 (UD50): 90% (50%) probability utilization distribution as proxy of the core area (total home range) (m^2); N: sample size; min (max): lowest (highest) number of detections

	N	Mean	SD	Min	Max
June					
UD90	19	11 223.42	16 022.64	12	47022
UD50	19	2476.32	3338.67	3	11140
Total distance (m)	19	2768.92	2953.66	517.99	12 958.48
Velocity (m s^{-1})	19	0.01	0.02	0	0.51
July					
UD90	5	170.20	316.74	11	736
UD50	5	18.40	30.62	2	73
Total distance (m)	5	8637.19	5985.15	3152.56	18 502.08
Velocity (m s^{-1})	5	0.01	0.02	0	0.38
August					
UD90	5	1413.80	2679.81	4	6168
UD50	5	305.6	598.88	1	1372
Total distance (m)	5	13 283.09	13 147.74	4413.24	35 808.19
Velocity (m s^{-1})	5	0.02	0.04	0	0.5
September					
UD90	5	1341	2910.37	9	6547
UD50	5	278.40	599.09	2	1350
Total distance (m)	5	6013.72	4287.69	2872.51	13 447.19
Velocity (m s^{-1})	5	0.01	0.03	0	0.5

Spatial movements estimated by triangulation data showed that most Norway lobsters repeatedly travelled more than 100 m away from the release point, covering more than 10 000 m in 4 mo with a mean speed between 0.1 and 0.2 m s^{-1}. This locomotor displacement speed corresponds to previous reports for Norway lobsters (Newland et al. 1988). Of the 33 acoustically tracked Norway lobsters, we could only analyse 19 individuals after the filtering procedure to make sure our spatial results were accurate for this species. Some of these 19 lobsters disappeared from the detection area within the first week. Some individuals even suddenly disappeared without exiting the range of detection. Disappearance from the monitoring area can be explained by predation at different times after the release by, for example, small-spotted catshark *Scyliorhinus canicula* (Mnasri et al. 2012) or European conger eel *Conger conger* (Matić-Skoko et al. 2012), both of which are abundant in the study area (RESNEP Project unpubl. data). On the other hand, the transient disappearance of animals over multiple consecutive days can be explained by periods of burrow occupancy, shielding the transmission of acoustic signals to hydrophones. Burrow emergence suppression has been observed in berried female Norway lobsters, which reduce their presence on the seabed during late summer in the Mediterranean Sea (Orsi Relini et al. 1998, Aguzzi et al. 2004).

In the present study, we observed 2 home range shape patterns, one wider and irregular and the

Table 3. Norway lobsters tracked (N = 19) in a no-take reserve in the northwestern Mediterranean Sea during 2019. N: number of interactions; min (max) minimum (maximum) values of the utilization distribution overlap index (UDOI) and the mean coefficient of association (CA) index obtained between each pair of individuals reported in each month. UD90 and UD50 are defined in Table 2

	N	Mean	SD	Min	Max
June					
UDOI (UD90)	171	0.03	0.08	0	0.59
UDOI (UD50)		0.01	0.01	0	0.11
CA (1 m)		0.01	0.01	0	0.01
CA (5 m)		0.01	0.01	0	0.02
CA (10 m)		0.01	0.01	0	0.12
CA (20 m)		0.01	0.04	0	0.26
CA (50 m)		0.03	0.06	0	0.29
July					
UDOI (UD90)	10	0	0	0	0
UDOI (UD50)		0	0	0	0
CA (1 m)		0	0	0	0
CA (5 m)		0.01	0.01	0	0.01
CA (10 m)		0.01	0.01	0	0.01
CA (20 m)		0.01	0.02	0	0.05
CA (50 m)		0.11	0.16	0	0.42
August					
UDOI (UD90)	10	0	0	0	0
UDOI (UD50)		0	0	0	0
CA (1 m)		0	0	0	0
CA (5 m)		0.01	0.01	0	0.01
CA (10 m)		0.01	0.01	0	0.01
CA (20 m)		0.01	0.02	0	0.04
CA (50 m)		0.07	0.13	0	0.33
September					
UDOI (UD90)	10	0	0	0	0
UDOI (UD50)		0	0	0	0
CA (1 m)		0	0	0	0
CA (5 m)		0	0	0	0
CA (10 m)		0.01	0.01	0	0.02
CA (20 m)		0.02	0.05	0	0.17
CA (50 m)		0.06	0.12	0	0.29

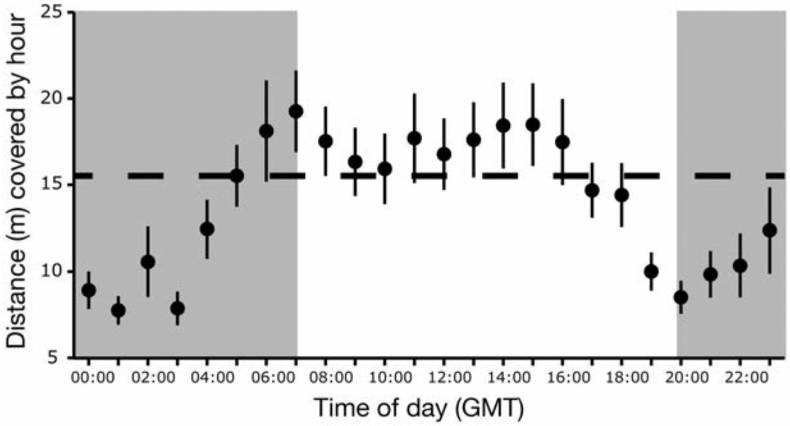

Fig. 5. Overall activity patterns of 19 acoustically tagged Norway lobsters based on the mean ± SD number of metres covered per hour in relation to the time of day. The dashed horizontal line represents the midline estimating statistic of rhythm (MESOR; mean = 15.42); grey-shaded portion of the figure represents the night (before dawn and after dusk)

other smaller and more uniform. Differences in home range sizes and space use due to intraspecific variability that includes social behaviour and environmental factors are well documented in some crustacean decapods such as the European spiny lobster (Afonso et al. 2008, Giacalone et al. 2019). Here, all individuals were about the same size, but sex differences could not be analysed due to the low number of samples. Considering the previous facts, our results indicate that wider home ranges made by linear trajectories could be ascribed to habitat selectivity in animals that may keep looking for a suitable place to establish (Welsh & Bellwood 2012), and in the case of Norway lobsters, to dig their burrows. Smaller home ranges may in fact be effectively larger due to the presence of bathymetric features, such as depth gradient in the no-take marine area, resulting in less uniform lines of displacement (Wiig et al. 2013).

From the beginning of the monitoring survey, some Norway lobsters appeared to settle in small areas around the release point. This fact could be explained as dominant Norway lobsters tend to show burrow-oriented behaviour, remaining close to the entrance most of the time and evicting other animals from their burrows to obtain more spatial resources (i.e. sheltering) (Aguzzi et al. 2008, Sbragaglia et al. 2017). The home range area became significantly smaller within 1 mo, as an indication of the establishment of the individuals in their burrows and the dispersal of most individuals from the detection area. We obtained an average home range size (UD90) ranging from 17.75 to 736.25 m^2, which could correspond to the usual area where the species carries out its behavioural, burrow-centred, activities. This mean home range has a high standard error because it includes the trajecto-

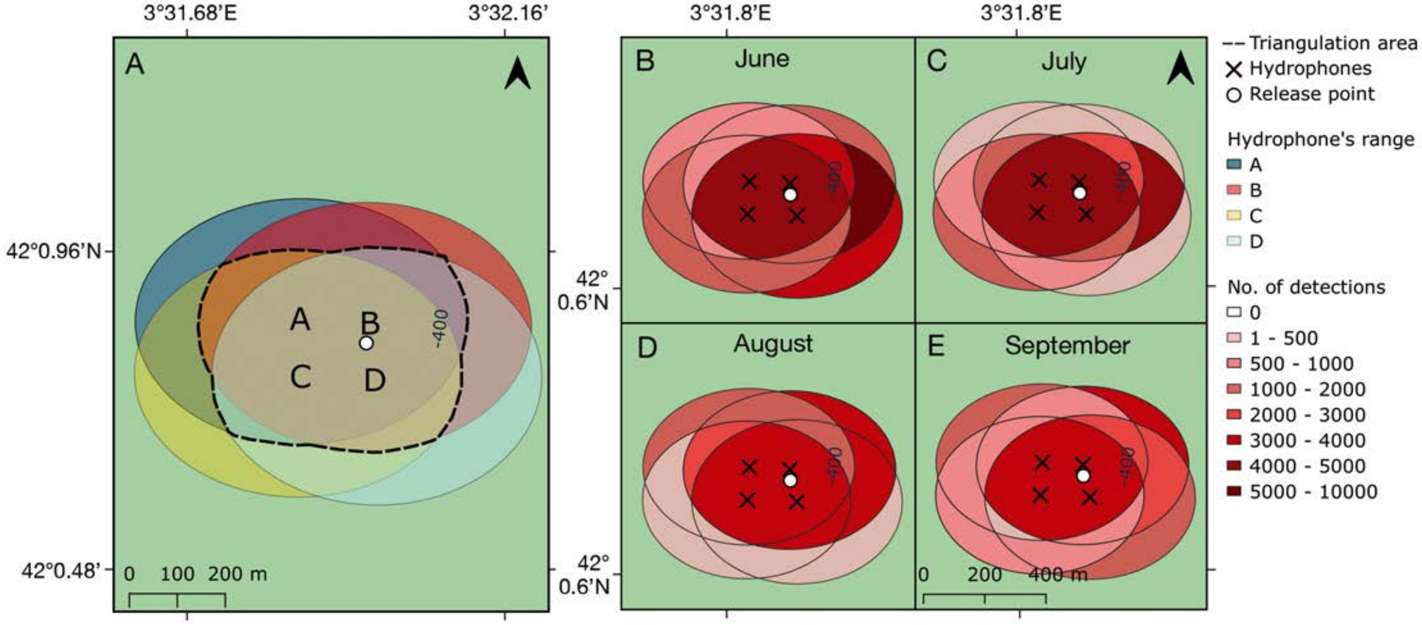

Fig. 6. Detections of acoustically tagged Norway lobsters in the different sets of detection areas within the 4 moored hydrophones. (A) The range of detection of each hydrophone was ~350 m. (B–E) The number of total detections in each area is represented in 4 periods of 27 d. Also shown in each panel is the approximate depth (400 m)

Table 4. Number of total acoustic detections of the 19 acoustically tagged Norway lobsters tracked in a no-take reserve in the northwestern Mediterranean Sea during 2019 in the detection in each hydrophone group

Detection area	June	July	August	September	Total
A	757	167	1760	1740	4424
AB	642	230	1508	970	3350
ABC	818	1907	2635	997	6357
ABCD	4228	3883	1936	480	10527
ABD	3951	2185	1519	2361	10016
AC	1776	644	358	840	3618
ACD	929	667	205	316	2117
AD	282	164	78	1243	1767
B	1843	407	3401	3747	9398
BC	773	379	1044	1539	3735
BCD	1997	1389	3186	591	7163
BD	5425	4007	3219	2066	14717
C	1534	1559	442	826	4361
CD	1708	570	143	524	2945
D	3107	302	192	1493	5094
Total	29 770	18 460	21 626	19 733	89 589

ries made during the first month, where all individuals were looking for a place to settle. One individual, 14465, was not included in the resulting home range calculations as it was defined by a moving behaviour, disappearing and reappearing again in the detection area. Given that Norway lobsters are territorial (Johnson et al. 2008, Sbragaglia et al. 2017), we assumed that inside the UD50 areas (core areas) each acoustically tracked individual settled in its own burrow, then explored and foraged in the area represented by the UD90, moving away from the burrow as reported in previous studies (Tuck et al. 1997).

The estimated home areas were dispersed and segregated inside the detection area over the entire study period, even in June when all individuals were released together. In addition, interactions between individuals were also scarce as a result of their territorial behaviour (Sbragaglia et al. 2017). Acoustically tagged individuals, released together at the same point, likely had a higher level of interaction at the beginning, which promoted their dispersal inside the no-take area until they experienced a sufficient intraspecific pressure release and ultimately settled in burrows. However, more long-term tracking studies with variable numbers (i.e. demographic densities) of reintroduced animals are required to evaluate the effects of agonistic interactions on dynamic settling of individuals, focussing at the same time on population density-associated demographic features such as the body size as a proxy for growth (Merder et al. 2020). By complementing presence data, we doubled the detection range making possible the identification of more acoustically tagged individuals. With this methodology, we observed that many individuals that disappeared in triangulated data results remained inside the no-take marine reserve in the north-eastern detection area, near the point of release of acoustically tagged individuals.

Behavioural rhythms are present at all levels of ecological organization, i.e. from individuals to populations, species and communities, with relevant effects on levels of perceived biodiversity with temporally scattered sampling procedures (Aguzzi et al. 2015). In the present study, for the first time, we monitored the movement behaviour of several individuals concurrently, at a high frequency, in deep-water areas. We observed maximum movement activity in daylight, confirming field and laboratory experiments (Aguzzi et al. 2003, Sbragaglia et al. 2015). The temporal tracked pattern we obtained is fully related to locomotion and detectability, which includes animals engaged in 'door-keeping' behaviour (i.e. animals waiting at their burrow entrance) (Aguzzi et al. 2003). Norway lobsters from deep-water habitats present diurnal burrow emergence during light hours, in contrast to equivalent individuals from northern regions, which inhabit shallower depths with an emergence peak of activity at night (Aguzzi et al. 2003, Chiesa et al. 2010).

A potential management measure to recover overfished marine populations is the implementation of no-take reserves on fisheries grounds (Goñi et al. 2010, Di Lorenzo et al. 2016), which could be applied to highly exploited Norway lobsters. Among the different aspects to be considered, the size of the no-take marine areas is fundamental to ensure that the target species have enough area to meet their vital requirements (Edgar et al. 2014). Based on the spatial movements of the Norway lobsters, we found that the approximate home range area used by settled individuals ranged from 17.75 to 736.25 m^2. Considering the 10 km^2 no-take reserve, we suggest that this area can cover and protect a large number of Norway lobsters.

Our analyses have provided the first insights into the spatial ecology of Norway lobsters after only 2 yr of the establishment of the no-take marine reserve. This species may present fluctuations in density or biomass on spatiotemporal scales, thereby changing their activity patterns and behaviour (Merder et al. 2020). It is therefore important to encourage and promote long-term monitoring projects and programmes to assess whether the observed patterns described in this study are maintained over time. Aside from increasing the number of acoustically tracked individuals inside the no-take marine reserve, another challenging future step in this research should be to include the connectivity factor including more no-take marine reserves generating a network, taking in account the larval dispersal and recruitment (Smith & Jensen 2008).

5. CONCLUSIONS

The present study provides useful information on the spatial ecology of Norway lobsters. We found acoustic telemetry suitable for acquiring *in situ* high-frequency data on the spatial ecology of Norway lobsters, as baseline ecological knowledge for the design of no-take reserves. The study confirms that a no-take area of 10 km^2 should be sufficient to protect Norway lobster populations. It is possible to recover the stock of Norway lobsters by designing small MPAs, as most individuals would remain inside the protected area, thereby avoiding fisheries. To specify the minimum adequate MPA size, we propose performing this experiment in shallower habitats. If the interest is to incorporate other species, we suggest conducting a similar spatial ecology study to understand their spatial behaviour to protect these target species and then determine the adequate MPA size. Long-term monitoring programmes are encouraged to assess changes over time of the spatial patterns of Norway lobsters identified in the present study. Further studies will benefit from increasing the number of acoustically tracked individuals inside the no-take marine reserve and assessing larval connectivity indicators among a no-take marine reserve network.

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Original Article

Before–after control–impact (BACI) assessment of the effects of a deep-water no-take fishery reserve to recover Norway lobster (*Nephrops norvegicus*) overfished populations and coexisting megafauna

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One of the main drivers of marine ecosystem change is fishing activity, bottom trawling being the most intensive fishing practice affecting benthic ecosystems worldwide. In the western Mediterranean Sea, Norway lobster stocks present signs of overexploitation due to trawling pressure, as their biomass and abundance have decreased abruptly during the last few years. No-take fishery reserves, a type of marine protected area where fishing is prohibited, could be efficient management measures to recover Norway lobster overexploited populations and coexisting demersal megafauna. Adopting a BACI (before–after control–impact) approach, we performed experimental fishing surveys before and after 4 years of the implementation of a deep-sea no-take reserve in the northwestern Mediterranean. After 4 years of closure, the Norway lobster population increased in abundance, biomass, body size, and trophic level in the no-take reserve. Our approach also revealed an increase in Norway lobster biomass beyond its boundaries, suggesting a spillover effect. Other demersal fish species also increased in biomass and abundance in the no-take reserve. Based on the results of this study, we suggest that no-take reserves might be an effective measure for recovering the Norway lobster stock and some species present in the same habitat.

Keywords: BACI, closed areas, experimental surveys, fisheries, marine protected areas, Norway lobster, no-take MPA.

Introduction

One of the main drivers of marine ecosystem change, beyond the potential effects of climate change, is fishing activity (Costanza *et al.*, 2017; Rousseau *et al.*, 2019). Since the 1960s, fisheries have spread followed by major declines in catch rates of several marine species (Pauly *et al.*, 2002; Froese *et al.*, 2018), impoverishing marine biodiversity and habitats (Puig *et al.*, 2012; Díaz *et al.*, 2019). Among the different types of fishing gear, bottom trawling is considered the most intensive and extended worldwide fishing practice, being a source of direct physical disturbance to the seabed and having great impact on demersal and benthic deep-water ecosystems (Tillin *et al.*, 2006; Halpern *et al.*, 2008; Olsgard *et al.*, 2008). These impacts can lead to a decrease in diversity, productivity, and biomass of the species found in the impacted habitat (Costanza *et al.*, 2017; Díaz *et al.*, 2019).

In the Mediterranean Sea, most stocks (close to 62.5%) are fished at their maximum sustainable levels or even above (Tsikliras *et al.*, 2015; FAO, 2022). This sea is highly exploited by bottom trawlers that operate at depths between 50 and 800 m (Gorelli *et al.*, 2011; Lucchetti *et al.*, 2021). One of the main targets of bottom trawling is the Norway lobster (*Nephrops norvegicus*), which is distributed on muddy bottoms along the Mediterranean Sea and the northeast Atlantic Ocean (Bell *et al.*, 2006; Aguzzi and Sardà, 2008; Ungfors *et al.*, 2013). This benthic crustacean has been the focus of many studies due to its ecological and economical value as one of the most important target species of commercial European fisheries (Issifu *et al.*, 2022; Aguzzi *et al.*, 2023). The Norway lobster stocks in the western Mediterranean Sea are experiencing signs of overexploitation due to high trawling pressure (Figure 1; Sardà, 1998a; Rotllant *et al.*, 2005). This crustacean is a burrowing species whose galleries provide habitat structures for other demersal species (Roberge and Angelstam, 2004; Aguzzi and Sardà, 2008). Although these galleries may offer some protection from trawling, the severe impacts trawling generates on the seabed make Norway lobsters highly vulnerable to this fishing activity (Campbell *et al.*, 2009).

By restricting fisheries and other extractive activities, marine protected areas (MPAs) have been useful tools in restoring populations of overexploited species, including the Norway lobster, benefiting both fisheries management and marine conservation (Halpern, 2003; Ban *et al.*, 2017; Vigo *et al.*, 2023). MPAs have been used not only for conservation, but also for fishing management (Follesa *et al.*, 2011; Moland *et al.*, 2013; Vigo *et al.*, 2023). No-take fishery reserves are one category of MPAs where all fisheries and extractions are strictly prohibited (Category 1a by the International Union for Conservation of Nature). NTRs have shown direct increases in the population density, biomass, and individual size of the most overexploited populations (Lenihan *et al.*, 2021; Vigo *et al.*, 2023). Moreover, these benefits are observed not only inside the NTR

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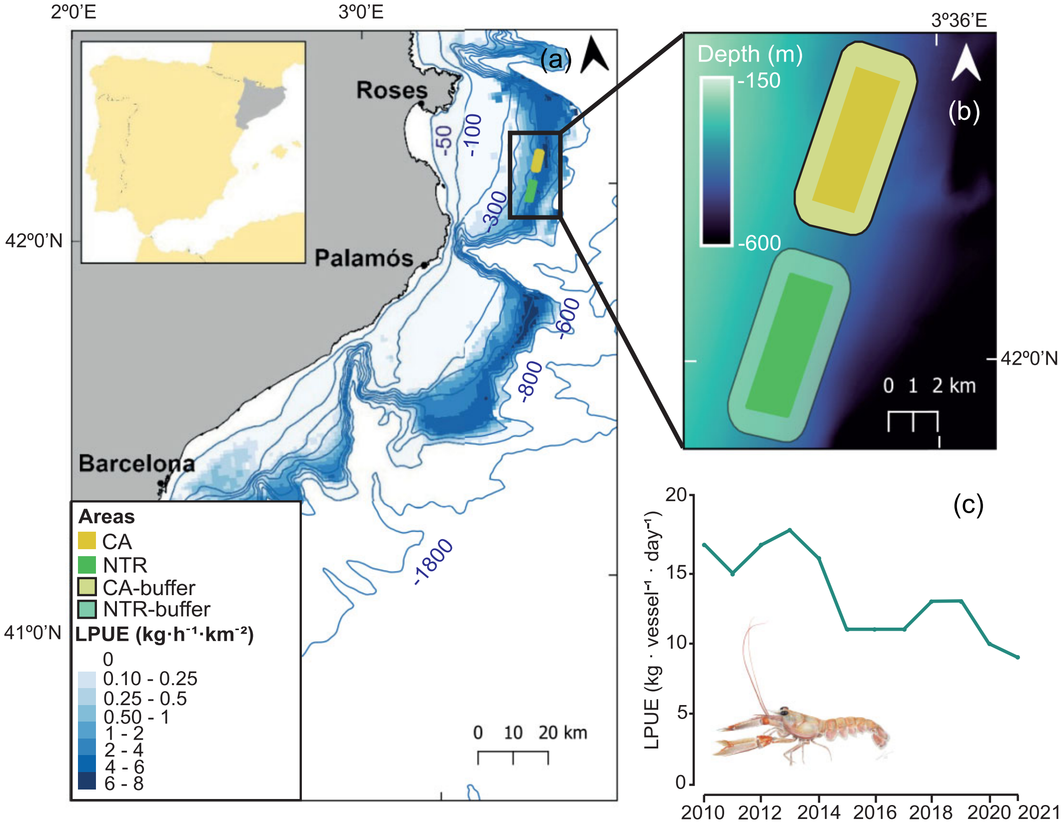

Figure 1. The study area showing the (a) spatial distribution of the annual averaged LPUE (landings per unit effort) of Norway lobster from 2016 to 2021 (European Commission, 2022), and locations of the no-take reserve (NTR) and the control area (CA). (b) Fine bathymetry of the no-take reserve, the control area, and their respective buffer areas, NTR-buffer and CA-buffer. (c) Annual LPUE of *N. norvegicus* represented as biomass in kg landed per day and per vessel in LPUE from Catalan trawler vessels. Norway lobster illustration by Joan Mir-Arguimbau.

but also in the surrounding area (Sala and Giakoumi, 2018), due to a spillover of individuals that benefits nearby fisheries (Goñi *et al.*, 2010; Kerwath *et al.*, 2013).

However, different studies have revealed that not all MPAs are truly effective in achieving their conservation targets (Bennett and Dearden, 2014; Chaigneau and Brown, 2016), due to many factors such as the inadequate size of the protected area or poor management and enforcement (Halpern, 2003; Clements and Hay, 2017; Pendleton *et al.*, 2018). It is therefore crucial to evaluate the MPA management continuously to enhance its effectiveness in achieving the goals and objectives set for the protected area (Hockings *et al.*, 2000; Pomeroy *et al.*, 2005, Vigo *et al.*, 2021). Assessment via a BACI (before–after control–impact) design is a powerful tool in environmental impact assessment (Jones *et al.*, 1992) and the most rigorous design for assessing MPA effectiveness (Ojeda-Martínez *et al.*, 2011; Sciberras *et al.*, 2013). By implementing BACI approaches, ecological variables and population metrics can be studied before and after protection measures are implemented. This should contribute to novel insights into the accurate effects of management measures (Pitcher *et al.*, 2009; Sørdalen *et al.*, 2018, 2020). To evaluate the effectiveness of the MPA, population indicators are measured, abundance and biomass being the most representative (Moland *et al.*, 2013; Rife *et al.*, 2013; Smokorowski and Randall, 2017), although other variables such as trophic status can determine indirect effects and changes in the trophic structure and relationships of marine communities (Smith *et al.*, 2011; Pinnegar *et al.*, 2017).

In this study, we adopted a BACI approach to assess the effect of a pilot deep-water no-take fishery reserve (hereafter called NTR) implemented in the northwestern Mediterranean Sea on the Norway lobster population and its coexisting demersal megafauna. We conducted standardized experimental fishing surveys before the establishment of this NTR (in 2017) and 4 years after the closure (in 2021) in the NTR and a control (fished) area to analyse the effects of the fishing cease on three key population parameters (abundance, biomass, and body size) of Norway lobster and the demersal megafauna community present in this habitat. We also examined the effect of the NTR on the trophic niche (stable isotopic markers) of Norway lobsters before and after closure in both the NTR and CA. Moreover, we examined whether the NTR generated Norway lobster spillover to the surrounding fishing grounds. After only 4 years of protection, we expect evidence of recovery in Norway lobsters, such as higher abundances, larger individuals inside the NTR, changes in trophic niche, and biomass exportation towards the boundaries of the reserve.

Additionally, certain coexisting demersal megafauna species may also exhibit signs of recovery depending on their specific characteristics and life traits. Species with limited mobility and small, well-defined home ranges within the NTR are expected to respond more positively to the protection measures compared to migratory or highly mobile species that spend only a brief period within the reserve (Claudet *et al.*, 2008; Game *et al.*, 2009). Furthermore, species with an r-selected strategy, characterized by a high reproductive output and shorter lifespans, are likely to demonstrate a more rapid response to protection, exhibiting higher densities inside the NTR compared to the CA, benefiting from the absence of fishing pressure and the presence of larger individuals with increased fecundity rates (Dayton *et al.*, 2000; Micheli *et al.*, 2004; Claudet *et al.*, 2010). We examined trajectories of change over time and space and relate them to the species life history characteristics to better understand their response to the NTR. Considering potential predators of Norway lobsters, we do not expect particularly high densities to threaten Norway lobster populations. Finally, it is anticipated that the most exploited species will exhibit higher recovery rates, as previous studies have demonstrated that signs of recovery are more rapidly observed in depleted stocks (Micheli *et al.*, 2004; Claudet *et al.*, 2006).

Material and methods

Study area and surveying procedures

This study was conducted in an NTR and in a fished CA, each spanning an area of 10 km^2 at a depth of 351–475 m in the northwestern Mediterranean Sea (Catalan Sea, Spain; Figure 1a and b). Due to the declining situation of Norway lobster stocks in recent years (Figure 1c), fishing activity in the NTR ceased in September 2017 through an agreement between the two local fishery associations (Roses and Palamós), and it was designated MPA in 2020 by the Spanish Government (Order APA/753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753To). The CA was ecologically and geomorphologically equivalent to the NTR, but bottom trawling activity was permitted. The NTR and the CA were established on the northern flank of the Palamós canyon, where bottom trawling targeting Norway lobster stocks has been carried out for around a century (Sardà, 1998b; Puig *et al.*, 2012). The sediment in the study area is compact slit and clay mud, suitable for the burrowing behaviour of Norway lobsters (Maynou and Sardà, 1997; Vigo *et al.*, 2023).

To evaluate the recovery of the Norway lobster population and the coexisting demersal megafauna in terms of changes in abundance, biomass, and body size in the NTR, we established the baseline situation (BASELINE) of the NTR by conducting standardized experimental trawl surveys before the closure (August 2017) and 4 years later (August 2021). Specifically, to establish the BASELINE, we conducted four fishing surveys in the NTR, and two in the CA, and after 4 years (August 2021), we conducted six surveys in the NTR and six in the CA. Experimental trawling surveys were selected randomly within each sampling area, resulting in different trawl stations at different depths (see Supplementary Table S1). Bathymetry differs slightly between trawl stations, although these differences were not found to be significant concerning the community assemblages nor the Norway lobster distribution and abundance. All experimental fishing surveys were performed with the same vessel (*FV Solraig*), using an otter bottom trawl net of a square mesh size of 40 mm with a cover net of 12 mm mesh size. We performed 1-h hauls at an average speed of 2.5 knots. The swept area (km^2) of hauls was estimated based on vessel speed (S, in knots), average horizontal opening of the net (BT, in m), and haul duration (H, in h) between the initial and final positions of the gear on the bottom (Sparre and Venema, 1998). The value 1852 was used as the conversion factor for nautical miles to metres (1 nm = 1852 m), and the value 10^6 was used to convert m^2 to km^2.

$$\text{Swept area} = \text{BT} \times S \times H \times 1852/10^6.$$

All individuals caught by the hauls were identified at species level, classified taxonomically, counted, weighed, and measured (total length TL for fish, in cm; preanal length AL for filiform shape fish species as macrourids, in cm; cephalothorax length CL for crustaceans, in mm; and mantel length ML for cephalopods, in cm).

Since the number of fishing surveys conducted to establish the BASELINE in the NTR (four) and CA (two) was very low, and because the abundance and biomass of Norway lobster did not differ between both areas (PERMANOVA tests; abundance, Pseudo-F = 2.11, p = 0.07; biomass, Pseudo-F = 0.57, p = 0.73), we decided to group the surveys conducted in the CA and in the NTR (named BASELINE). Thus, we compared the population metrics on Norway lobster and the other megafauna collected during the fishing surveys between the BASELINE situation, the NTR 4 years after the closure (NTR), and the CA 4 years posterior to the closure (CA).

Abundance and biomass of Norway lobster

We estimated the abundance (N km^{-2}; N = number of individuals) and biomass (kg km^{-2}) of all recorded species in each fishing survey, standardized by the swept area (see Supplementary Table S1). We compared the abundance and biomass of each species between BASELINE, NTR, and CA by applying PERMANOVA tests (Anderson, 2001) based on the Bray–Curtis similarity matrix.

Length–frequency distribution and sex-based differences of Norway lobster

The mean size and sex ratio of Norway lobsters at each sampling station (BASELINE, NTR, and CA) were determined based on the average estimated from the mean values obtained from each trawl haul, which served as the sampling units. By calculating the mean values from multiple trawl hauls, we aimed to obtain a representative estimate of the size and sex ratio for each sampling station. We compared the length–frequency of Norway lobsters among BASELINE, NTR, and CA by using non-parametric Kruskal–Wallis tests (as normality and homogeneity of variances were not met) and post-hoc Dunn tests (*dunn.test* package). To test the length–frequency distribution variation among BASELINE, NTR, and CA, we performed Kolmogorov–Smirnov tests using the function *ks.test* from the package *stats*. All calculations were obtained in R software version 4.1.2 (R Core Team, 2021).

We performed two-way ANOVA tests to determine if there was a difference in body size between the sexes and between BASELINE, NTR, and CA. In order to evaluate the sex ratio, we conducted non-parametric Scheirer–Ray–Hare tests to test for differences in abundance between males and females among BASELINE, NTR, and CA. We also calculated the abundance proportions of each sex according to the total population for BASELINE, NTR, and CA separately. Pairwise Kolmogorov–Smirnov tests were conducted to examine for differences in body size distribution between both sexes and among BASELINE, NTR, and CA. The proportion of berried females according to class range size among BASELINE, NTR, and CA was tested using non-parametric Kruskal–Wallis and Dunn tests.

Trophic niche of Norway lobster

To examine the effect of the closure on the trophic niche of Norway lobster, we compared the stable isotope values of δ^{15}N and δ^{13}C in the muscle of 40 individuals collected in the NTR and CA during the BASELINE (20 individuals collected in the CA and 20 individuals collected in the NTR) and of 30 individuals collected after the closure (15 individuals collected in the NTR and 15 individuals collected in the CA) (see Supplementary Table S2). Individuals were randomly selected from each trawl haul at each sampling station (BASELINE, NTR, and CA), sampling individuals with a carapace length (CL) >25 mm. This size threshold was chosen based on previous studies (Sardà, 1991) to ensure that the selected individuals were predominantly sexually mature. By using this size criterion, we aimed to focus on individuals that have reached sexual maturity, which is an important factor when studying population dynamics and assessing the impact of fisheries. The random selection process within the specified size range helped ensure a representative sample of sexually mature individuals from each sampling station. To do this, we extracted white muscle samples from all the individuals after their capture during the experimental surveys. Muscle samples were freeze-dried and powdered, and 0.28–0.33 mg of each sample was packed into capsules and sent to the Laboratory of Stable Isotopes of the Estación Biológica de Doñana CSIC (www.ebd.csic.es/lie/index.html) where stable isotopic analyses were performed (see Vigo *et al.*, 2022 for a detailed description of the stable isotope procedures).

In order to compare the stable isotope values between BASELINE, NTR, and CA, we used Kruskal–Wallis and Wilcoxon post-hoc tests. We also calculated the isotopic niche of Norway lobster during BASELINE and after 4 years in NTR and CA. To do this, we used kernel utilization density (KUD) estimators to characterize the 50% of the isotopic data (core) using the *adehabitatHR* package (Calange, 2014) in R version 4.1.2 (R Core Team, 2021). The KUD method estimates areas of high use across a regular network of equally spaced points, with the grid extent larger than that of the observations (Venables and Ripley, 2002; Eckrich *et al.*, 2020). Interpolation was carried out by fitting contour lines from the Euclidean distances of each observation to the centroid in bivariate space (Robinson, 2022). The overlap among KUDs was calculated using the Utilization Distribution Overlap Index (UDOI; Hurlbert, 1978), in whose values range from 0 (complete spatial segregation of KUDs, no overlap) to 1 (uniform distribution with 100% overlap between pairs of KUDs). We used the *rKIN* package (Albeke, 2017) in R version 4.1.2 (R Core Team, 2021) to calculate the overlap between KUDs.

Spillover of Norway lobsters in the surroundings of the NTR

To investigate the effect of the NTR on the biomass spillover of Norway lobster outside the reserve, we examined the landings per unit effort (LPUE, kg $h^{-1}\cdot km^{-2}$), the biomass landed (kg), the annual revenues (in €), and the fishing effort (time of fishing activity, h) accumulated inside two areas of 22 km^2 with a distance range of about ~1100 m from the border of the NTR and the CA (hereafter called buffer-NTR and buffer-CA, respectively; see Figure 1b). This distance falls within the range where MPA spillover effect is potentially detected (Halpern *et al.*, 2009). The biomass of Norway lobster in these two buffer areas was obtained by crossing the annual VMS (Vessel Monitoring System) data and LPUE from all trawlers fishing in the study area from 2016 to 2021.

Community diversity metrics

We calculated three diversity metrics from the experimental fishing surveys: the species richness (*S*), the Shannon's diversity index (*H'*) (Shannon and Weaver, 1948), and the Chao estimator, which indicates the species richness controlled by the sampling effort (Chao, 2006) between BASELINE, NTR, and CA. These diversity indices were calculated by considering all detected species grouped into four taxonomic categories (teleosts, elasmobranchs, cephalopods, and crustaceans).

Population changes in demersal megafauna

We used multivariate analyses to examine the similarity of species assemblages between BASELINE, NTR, and CA. Abundance and biomass data were square-root transformed to reduce the negative effect of weighting the most abundant species. As for Norway lobsters, we compared the abundance and biomass of the demersal community between BASELINE, NTR, and CA with PERMANOVA tests (Anderson, 2001). When significant differences ($p < 0.05$) between BASELINE, NTR, and CA were detected, we used pairwise multilevel comparisons with Bonferroni-based adjusted *p*-values (Martinez Arvizu, 2020).

For the species that showed significant differences in abundance or biomass between BASELINE, NTR, and CA, we tested for differences in body size using non-parametric Kruskal–Wallis tests (as normality and homogeneity of variances were not met). To perform statistical testing on body size, we utilized the mean size at each sampling station (BASELINE, NTR, and CA), which was derived from the average of the mean sizes estimated at each sampling unit (trawl haul). This approach allowed us to obtain representative mean size measurements for each sampling station by considering the average values derived from multiple trawl hauls. By conducting statistical tests on these mean size measurements, we aimed to assess and compare potential differences in body size among the sampling stations. The species that showed significant differences ($p < 0.05$) were later analysed with the Dunn test. To compare length–frequency distributions between BASELINE, NTR, and CA, we performed two-sample Kolmogorov–Smirnov tests. We categorized the species into three groups based on the fluctuations observed in their abundance, biomass, or size structure across the sampling stations. This categorization helped us better understand these fluctuations: "fluctuations generated by the NTR," species in this group showed consistent values between the BASELINE and CA sampling stations, while their values within the NTR differed significantly; "fluctuations in time," species in this group exhibited similar values between the CA and NTR sampling stations, but these values differed from the BASELINE, suggesting that the observed fluctuations were driven by temporal variations in environmental conditions or fishing pressure; and "fluctuations in time and generated by the NTR", species in this group displayed variations in their values across all sampling stations, including both the CA and NTR, indicating complex dynamics that are influenced by multiple factors, including the closure of the NTR and other environmental or ecological processes. All potential predator species were identified (P) to observe their specific response in time and inside the NTR. All potential predator species were identified to ex-

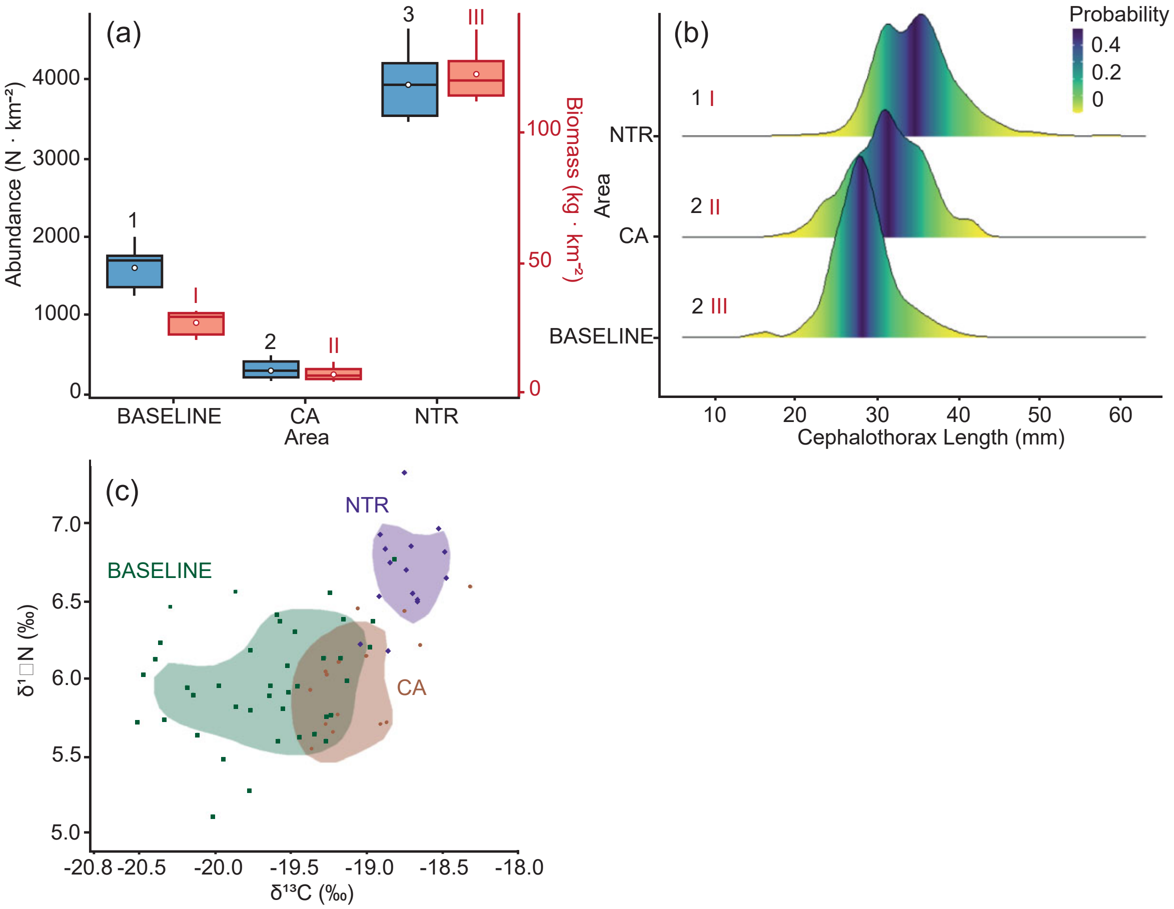

Figure 2. Effects of the no-take reserve on Norway lobsters. (a) Abundance (in blue) and biomass (in red) of Norway lobster in the control area and the no-take reserve at the initial baseline state and 4 years later. Different Arabic numbers for abundance and roman numbers for biomass indicate statistically significant differences. (b) Length–frequency distribution of Norway lobster before the closure (BASELINE) and after 4 years in the control area and no-take reserve, indicating statistically significant differences in mean sizes with Arabic numbers and differences in size distribution with roman numbers. According to colour degradation, the most probable size to coincide with the mean size (CL, mm) is dark blue. (c) Isotopic niche size and overlap estimates of Norway lobsters generated for 50% contour levels kernel utilization density.

amine their specific responses in time and inside the NTR. These predators were identified following Vigo *et al.* (2022), which identified that the predators of Norway lobsters were different cephalopods such as *Sepietta oweniana*, *Abralia veranyi*, *Eledone cirrhosa*, or *Rossia macrosoma*; teleosts such as *Lophius budegassa*, *Merluccius merluccius*, or *Conger conger*; and the demersal shark *Scyliorhinus canicula*.

Results

Norway lobster population changes

Norway lobster abundance and biomass differed significantly between BASELINE, NTR, and CA (abundance, Pseudo-$F = 77.34$, $p = 0.001$; biomass, Pseudo-$F = 93.5$, $p = 0.001$). Specifically, the abundance and biomass of Norway lobster were higher in the NTR compared to the CA (abundance, Pseudo-$F = 101.62$, $p = 0.006$; biomass, Pseudo-$F = 101.62$, $p = 0.006$) and the BASELINE (abundance, Pseudo-$F = 82.55$, $p = 0.009$; biomass, Pseudo-$F = 82.55$, $p = 0.012$). At the CA, Norway lobster abundance and biomass were lower than in the BASELINE (abundance, Pseudo-$F = 101.62$, $p = 0.006$; biomass, Pseudo-$F = 54.61$, $p = 0.006$) (Figure 2a). The abundance and biomass of Norway lobster increased by 60% between the BASELINE and the NTR and decreased by 80% between the BASELINE and the CA.

Body length measurements revealed that most Norway lobsters in the BASELINE and CA ranged between 20 and 40 mm of CL, whereas those in the NTR ranged between 30 and 50 mm of CL (see Table 1, Figure 2b). The sex ratio of Norway lobsters was similar between BASELINE, NTR, and CA ($H_{1,35} = 0.81$, $p = 0.88$). In comparing BASELINE, NTR, and CA, the presence of berried females differed significantly between BASELINE, NTR, and CA ($\chi^2 = 20.19$, $p < 0.0001$). There were more berried females in the NTR (about 28.78% of the total females caught) than in CA (~3.88% of the total females caught; $p < 0.01$) and BASELINE ($p = 0.002$) (see Table 1).

The body size of males and females showed significant differences between BASELINE, NTR, and CA (Table 2; Figure 2b; $\chi^2 = 1598.4$, $p > 0.0001$). In particular, in the BASELINEs, both sexes showed the smallest body sizes (mean and standard deviation; males = 29.10 ± 3.99 mm; females = 27.31 ± 3.25 mm), followed by the CA (males = 31.81 ± 4.85 mm; females = 30.44 ± 3.93 mm), and the NTR (males = 36.02 ± 5.21 mm; females 33.49 ± 3.89 mm) (Table 2).

Table 1. Sex ratio of Norway lobsters by range of size class in CL (mm) before the closure (BASELINE) and after 4 years in the CA and the NTR.

Area	Range	*N*	Sex ratio		
			M (%)	F (%)	Berried-F (%)
BASELINE	0–10	0	0	0	0
	10–20	26 ± 27	9 ± 23 (0.56)	17 ± 23 (1.05)	0
	20–30	1 134 ± 234	624 ± 127 (38.81)	509 ± 137 (31.65)	2 ± 6 (0.39)
	30–40	440 ± 125	346 ± 92 (21.52)	95 ± 44 (5.90)	8 ± 8 (8.42)
	40–50	7 ± 7	7 ± 7 (0.44)	0	0
	50–60	1 ± 3	1 ± 3 (0.07)	0	0
	T	1 608 ± 300	988 ± 191 (61.40)	621 ± 169 (38.60)	10 ± 10 (1.61)
CA	0–10	0	0	0	0
	10–20	1 ± 3	0	1 ± 3 (0.62)	0
	20–30	114 ± 55	62 ± 32 (19.68)	51 ± 26 (16.19)	1 ± 3 (1.96)
	30–40	189 ± 55	113 ± 40 (35.88)	76 ± 50 (24.14)	4 ± 4 (5.26)
	40–50	11 ± 4	11 ± 4 (3.49)	0	0
	50–60	0	0	0	0
	T	315 ± 127	186 ± 61 (59.05)	129 ± 72 (40.95)	5 ± 4 (3.88)
NTR	0–10	0	0	0	0
	10–20	2 ± 6	1 ± 3 (0.03)	1 ± 3 (0.03)	0
	20–30	487 ± 112	209 ± 103 (5.31)	278 ± 49 (7.06)	9 ± 11 (3.24)
	30–40	2 958 ± 464	1 327 ± 166 (33.69)	1 631 ± 361 (41.42)	526 ± 185 (32.25)
	40–50	473 ± 123	443 ± 115 (11.25)	30 ± 29 (0.76)	25 ± 33 (83.33)
	50–60	17 ± 12	16 ± 11 (0.42)	1 ± 2 (0.03)	0
	T	3 938 ± 474	1 997 ± 238 (50.70)	1 942 ± 363 (49.30)	559 ± 195 (28.78)

The number of individuals (N km^{-2}), the number of males M (% of the total), and the number of females F (% of the total). The number of berried females (Berried-F) identified is also indicated (% in the total females identified at each range of size class).

Table 2. Results obtained from the two-way ANOVA test to test for differences in mean size in Norway lobster between sexes (F-F: females; M-M: males; F-M: females and males) before the closure (BASELINE) and after 4 years in the control area (CA) and the no-take reserve (NTR).

	BASELINE		CA		NTR		
Sex	N	CL	N	CL	N	CL	Comparison
F–F	621 ± 169	27.31 ± 3.25	129 ± 72	30.44 ± 3.92	1 942 ± 363	33.49 ± 3.39	BASELINE < CA < NTR
M–M	988 ± 191	29.10 ± 3.99	11 ± 4	31.81 ± 4.85	1 997 ± 238	36.02 ± 5.21	BASELINE < CA < NTR
F–M	1 608 ± 300	28.39 ± 3.81	315 ± 127	31.25 ± 4.54	3 938 ± 474	34.77 ± 4.58	BASELINE: F < M; NTR: F < M CA: F < M

N indicates the number of individuals expresses in mean and standard deviation, CL indicates the Cephalothorax Length expresses in mean and standard deviation (in mm), and Comparison indicates the differences based on the two-way ANOVA tests. The F–M relation indicates the differences in abundance between sex in the same area before the closure (BEF) and after 4 years in the CA and the NTR.

Trophic metric indicators of Norway lobster

The δ^{15}N values in the Norway lobsters collected in the NTR were higher than those in individuals sampled in the BASELINE and CA (Figure 2c; $F_{2,49} = 17.59$, $p < 0.001$; Supplementary Table S2). The KUD estimator showed a clear segregation between the Norway lobsters from the NTR and the individuals sampled in the CA and the BASELINE, which showed a high overlap (Figure 2c).

Spillover effect of Norway lobster

The LPUE of Norway lobster exhibited a similar spatial distribution among years (Figure 3a and b) but decreased between 2016 and 2021 (Figure 3c). The transition over time between accumulated LPUE (kg h^{-1} km^{-2}) inside the buffers around the CA and the NTR showed the same pattern (Figure 3c). The LPUE and annual revenue followed a similar trend, with a maximum in 2018 followed by a negative trend since then to 2021. In 2021, both LPUE and total revenues were higher in the buffer zone around the NTR than in the buffer zone around the CA. Regarding the percentage reduction from 2016 to 2021 (Figure 3c and d; see Supplementary Material, Supplementary Figure S4), we observed that in the buffer of the CA, the decrease of LPUE, biomass landed, and annual revenues declined almost half of the initial LPUE in 2016 (49.96, 59.92, and 41.02% of the decrease, respectively) (Figure 3d). The fishing effort diminished similarly in both areas, with effort declining by 21.48% in the buffer of the CA and 29.9% in that of the NTR. In contrast, the LPUE and annual revenue declined to a much lesser extent in the buffer area of the NTR (35.6 and 32.4%, respectively).

Community diversity metrics

The species richness was similar between BASELINE, NTR, and CA (Table 3). The taxonomic group presenting the highest species diversity was the teleost ($S = 26$–31), followed by crustaceans ($S = 10$–12). Shannon diversity values were slightly higher in the BASELINE ($H' = 2.64$) than in the NTR ($H' = 2.38$). However, the Chao estimator indicated that species richness was higher (97.33 ± 21.86 species) in the NTR than in the CA and in BASELINE (76.63 ± 11.02 and 69 ± 4.65 species, respectively).

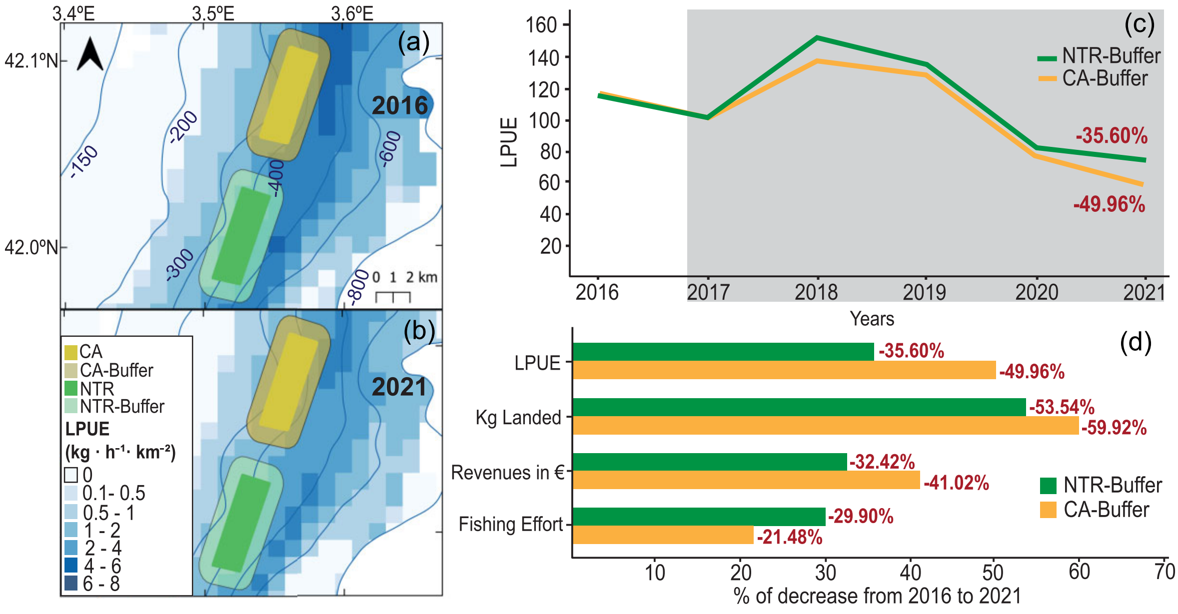

Figure 3. Spillover of Norway lobsters to the buffer area (22 km^2) around the no-take reserve and the control area. (a) Spatial distribution of Norway lobster LPUE (kg·h^{-1}·km-2) in 2016, (b) and 2021, around the NTR and the CA and their buffers. (c) Annual LPUE of Norway lobster between 2016 and 2021 inside the buffer areas of the NTR (NTR-Buffer) and the CA (CA-Buffer). The light grey area indicates the temporal closure. (d) % of decrease from 2016 to 2021 in the NTR-Buffer and CA-Buffer in the annual LPUE, annual kg landed, annual revenues in €, and the total annual fishing effort (time of fishing activity, h).

Table 3. Total number of species, total abundance (Ab, *N* km^{-2}), Shannon diversity (*H*), and Chao index (mean and standard deviation) of megafauna species observed before the closure (BASELINE) and after 4 years in the control area (CA) and the no-take reserve (NTR).

		Total	Teleosts	Echinoderms	Cephalopods	Elasmobranchs	Crustaceans
BASELINE	Species	63	26	2	10	2	23
	Ab	15 294	5 066	22	3 081	1 201	5 924
	H	2.64	2.19	0.69	0.61	0.03	1.87
	Chao	69 ± 4.65					
CA	Species	61	28	2	10	2	19
	Ab	7 351	4 313	1	488	152	2 397
	H	2.09	1.33	0.69	0.37	0.01	1.12
	Chao	76.63 ± 11.02					
NTR	Species	64	31	1	12	1	19
	Ab	8 619	4 375	1	705	202	3 336
	H	2.38	1.59	0	0.54	0	1.65
	Chao	97.33 ± 21.86					

Abundance, biomass, and length–frequency of coexisting demersal species

The assemblages were composed of teleosts, elasmobranchs, cephalopods, crustaceans, and echinoderms. The abundance and biomass of the demersal community differed significantly between BASELINE, NTR, and CA (abundance, Pseudo-$F_{2,97} = 11.47$, adjusted $p = 0.001$; biomass, Pseudo-$F_{2,97} = 16.29$, adjusted $p = 0.001$). For each species, PERMANOVA tests indicated that for abundance and biomass, 6 teleosts, 1 cephalopod, and 3 crustaceans differed among BASELINE, NTR, and CA (Figure 4). The species that only presented fluctuations in the NTR were the teleost *Helicolenus dactylopterus* for both abundance and biomass and the demersal shark *S. canicula* only for biomass (Figure 4a and b). Species that showed fluctuations in time were the teleost *Argentina sphyraena*, *Gadiculus argenteus*, *Molva macrophtalma* (Figure 4c–e), and the crustaceans *Chlorotocus crassicornis*, and *Plesionika heterocarpus* (Figure 4f and g). There were species that presented differences in time and inside the NTR, these were the teleosts *Coelorinchus caelorhincus*, *Phycis blennoides*, the cephalopod *A. veranyi*, and the crustacean *Parapenaeus longirostris* (Figure 4h–k).

Regarding body size, we found that some species presented differences in the mean body size and size distribution patterns among the NTR, the CA, and the BASELINE (Figure 5, Supplementary Table S6). Regarding differences in mean sizes, the species with fluctuations generated by the NTR were the teleost *C. caelorhincus* and *H. dactylopterus* (Figure 5a and b). Fluctuations in time were observed in the teleost *Trigla lyra*, and the cephalopod *A. veranyi* (Figure 5c and d). Species that differed in size over time and inside the NTR were the teleosts *A. sphyraena*, *G. argenteus*, *Micromessistius potassou*, *M. macrophtalma*, and *P. blennoides* (Figure 5e–i), the shark *S. canicula* (Figure 5j), and the crustaceans *C. crassicornis*, *P. longirostris*, and *P. heterocarpus* (Figure 5k–m). As for shifts in body size distribution patterns, tested by Kolmogorov–

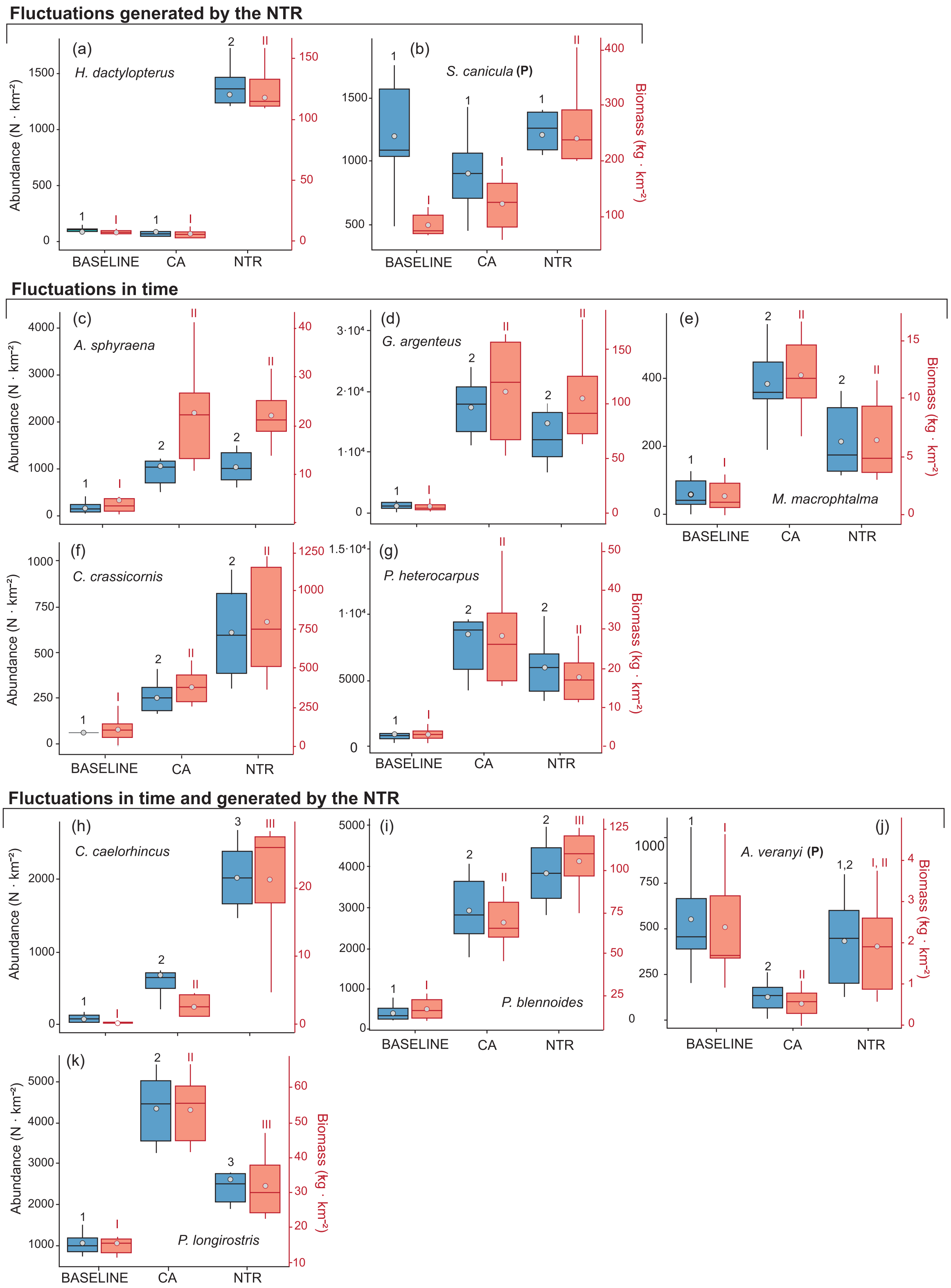

Figure 4. Coexistent species classified according to the effects observed differences among the control area, no-take reserve, and before the closure (BASELINE). Abundance (in blue) and biomass (in red) of Norway lobsters and the statistically significant differences indicated in Arabic numbers for abundance and roman for biomass. Predator species indicated with a P.

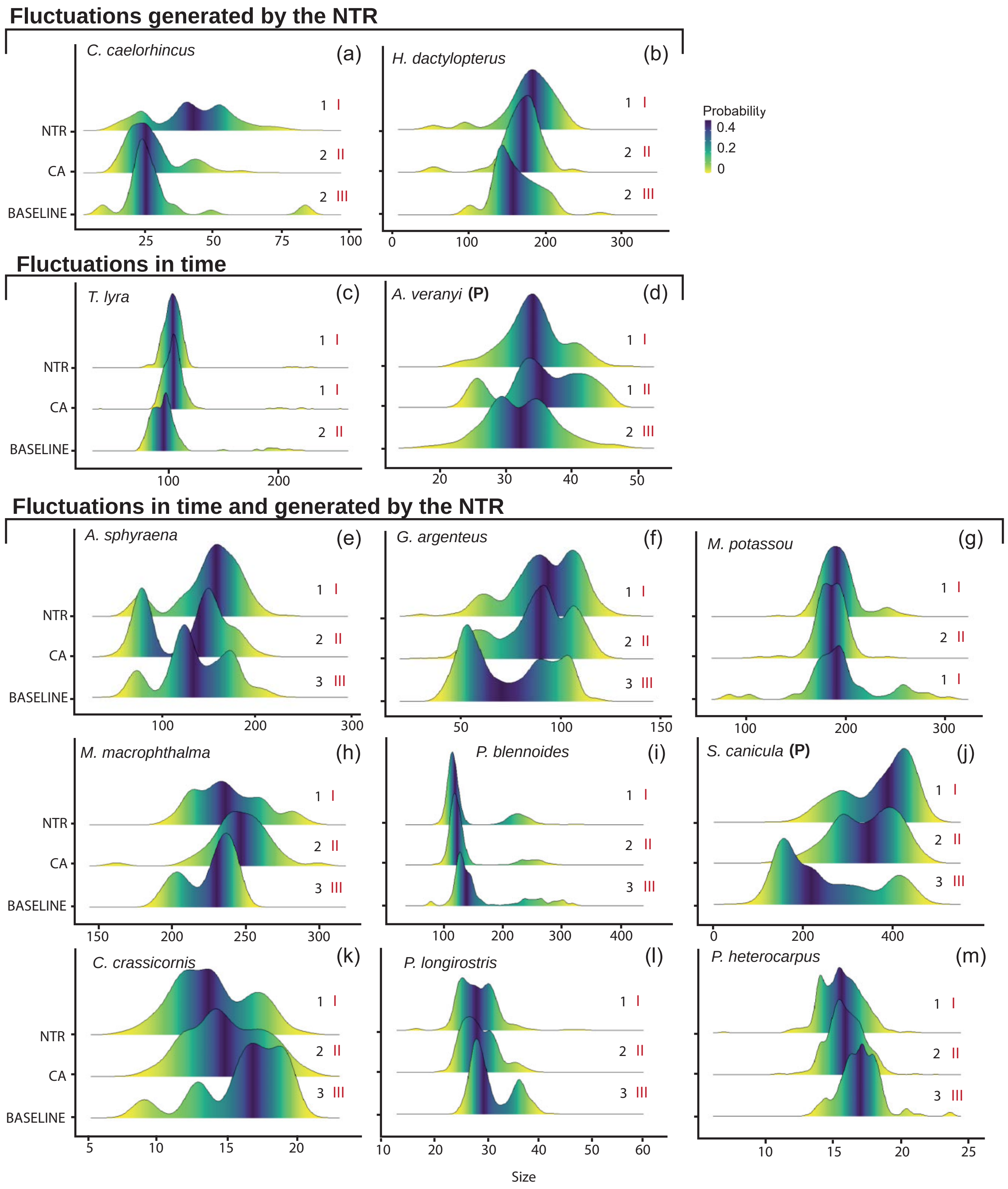

Figure 5. The length–frequency distribution of body length of Norway lobsters coexisting species that showed differences among control area (CA), no-take reserve (NTR), and before the closure (BASELINE) classified in three categories. According to colour degradation, the most probable size to coincide with mean size (CL for crustaceans, TL and AL for teleosts, and ML for cephalopods, in mm) is dark blue. Different Arabic numbers and roman numbers indicate statistically significant differences on mean sizes and size distributions, respectively. Predator species indicated with a P.

Smirnov tests, the species that showed significant differences in distribution among BASELINE, NTR, and CA were the teleosts *G. argenteus*, *M. macrophtalma*, and *P. blennoides*, the cephalopod *A. veranyi*, the elasmobranch *S. canicula*, and the crustaceans *C. crassicornis*, *P. longirostris*, and *P. heterocarpus* (Figure 5).

Regarding the potential predators of Norway lobster (Vigo *et al.*, 2022), the demersal shark *S. canicula* and the cephalopod *A. veranyi* were the species that showed significant fluctuations over time inside the NTR.

Discussion

Using a BACI approach, we assessed the effect of a NTR in the Mediterranean deep-water on three population parameters (abundance, biomass, and size structure) of Norway lobster and coexisting demersal megafauna after four years of protection. Our findings revealed that the Norway lobster showed signs of recovery, showing higher abundance, biomass, and larger individual body size inside the NTR compared to a control (fished) area and the initial baseline state. We also found higher biomasses around the NTR borders than in the surroundings of the CA indicating a positive spillover effect of the NTR. The protection also increased the trophic level and shifted the trophic niche of Norway lobster inside the NTR after four years. At the community level, although community metrics indicated similar diversity and species richness, we found an increase in the population descriptors of three fish species (*C. caelorhincus*, *H. dactylopterus*, and *P. blennoides*) and one elasmobranch (*S. canicula*) that were more abundant and showed higher biomass in the NTR than in the CA and the initial baseline state.

The ceasing of fishing in a deep-water area that was overfished has proven to be an effective management tool to restore the abundance and biomass of Norway lobster. These results corroborate a previous evaluation conducted 2.5 years after the closure using ROV video surveys in both the NTR and the CA (Vigo *et al.*, 2023). Here, we report that the Norway lobster population increased by 60% compared to the baseline state before the closure. Moreover, we observed a decrease in abundance and biomass in the CA during the study period, amounting to about 80% relative to the baseline state, four years before the closure of the NTR.

The NTR also generated a recovery of size structure, achieving large individuals for both males and females in the NTR. Individuals may respond to shifts in size-selective mortality inside the NTR due to fisheries-induced selection (Baskett and Barnett, 2015; Moland *et al.*, 2021). Other lobster species have shown patterns of size-assortative mating more pronounced inside MPAs, such as claw size as a sexually selected trait (Sørdalen *et al.*, 2018, 2020; Moland *et al.*, 2019). The sex ratio was similar between the NTR, CA, and the baseline state, with more males than females before and 4 years later. This can be explained by the activity pattern behaviour of Norway lobster females that hide inside their galleries after the spawning period (Aguzzi *et al.*, 2007). During the spawning season, berried females hide inside their burrows for a long period, which confers them some protection from trawling, and consequently, more males are caught between September and February by fisheries. However, we found a higher abundance of berried females in the NTR that could increase the potential recruitment, more individuals added to the local population (Agnalt *et al.*, 2007; Di Salvatore *et al.*, 2021), and more potential spillover of eggs and larvae. The combination of higher abundance and large-size females could result in a high reproductive output, producing more offspring of better condition (Hixon *et al.*, 2014; Dick *et al.*, 2017). The female population in the NTR may not only provide good recruitment for the local population but also benefit fishers in promoting spillover, exporting more larvae to other habitats where fisheries are still undergoing (McClanahan and Mangi, 2000; Planes *et al.*, 2009; Huserbråten *et al.*, 2013). The export of adults from MPAs to areas adjacent to the reserve has been proven, in many cases, to provide significant benefits to fisheries despite the loss of the MPA's area as a fishery ground (Follesa *et al.*, 2011; Di Lorenzo *et al.*, 2016; Lenihan *et al.*, 2021). According to the biomass fished (LPUE and kg data) around the NTR and the CA, the Norway lobster population has clearly decreased in the recent years. However, we found a mitigation effect around the NTR, probably associated with a spillover of adult individuals from the NTR to the surroundings. The LPUE, although lower than in 2016, was higher at the NTR borders than in the CA. It is important to note that revenues showed a decrease in both areas compared to 2016, with the decreases being more pronounced in the buffer of the CA. Despite the possible higher abundance of Norway lobsters in the buffer of the NTR, it is worth considering the possibility that larger individuals are being also exported outside the reserve, thereby increasing the commercial value of the landings as observed with other lobster stocks (Moland *et al.*, 2013). We suggest that the larger individuals, which potentially fetch higher prices in the market, may be contributing to revenues outside the NTR Protected areas can hold larger and older fish, and in this sense, some studies have even reported that protected areas exported world-record fish catches, supplying trophy-size fish to recreational fisheries (Bohnsack, 1996; Roberts *et al.*, 2001). Indeed, considering the distribution of fishing effort and the behaviour of fishers around the boundaries of the NTR is crucial to understanding the dynamics and fluctuations in the catch per unit effort (CPUE) or LPUE (Smith and Jensen, 2008; Lenihan *et al.*, 2023). The increase in LPUE can be influenced by factors such as a net export of individuals from the NTR (Goñi *et al.*, 2006; 2010) or lower fishing effort within the reserve area. This has been observed in other Mediterranean reserves with other lobster stocks (Follesa *et al.*, 2011; Kleiven *et al.*, 2019). In this study, a general decrease in fishing effort was observed in both areas, with slightly higher reductions observed around the NTR. While continued monitoring of the fishing effort distribution is necessary, based on the available data, we suggest that the increase in LPUE of Norway lobsters around the NTR is primarily due to a net export of individuals rather than solely a result of lower fishing effort within the reserve area. Acknowledging the complexity of factors influencing LPUE, including fishing effort distribution and fisher behaviour, allows for a more comprehensive understanding of the observed changes in catch rates. It is essential to continue monitoring these dynamics and further investigate the contribution of different factors to the observed patterns in LPUE around the NTR. Closing an area to fisheries involves possible shifts not only in single targeted species but also in habitat and ecosystem status (Bourlat *et al.*, 2021; Vigo *et al.*, 2023). Analysing carbon and nitrogen isotope ratios, we observed a trophic niche shift in Norway lobsters inside the NTR after four years of closure. Prey availability and abundance may change the trophic niche and cause diet differences (Vizzini and Mazzola, 2009). Specifically, carbon ratios provide information about the primary energy source (e.g. benthic or pelagic photosynthesis), while nitrogen allows us to distinguish trophic levels and determine the trophic position of consumers (O'Reilly *et al.*, 2002). Our study found that Norway lobsters in the NTR had higher nitrogen stable isotope values after four years of closure, indicating that these individuals consumed trophic resources placed in a higher position in the food web than those in the CA and before closure. The results suggest that the NTR affects not only the abundance and size structure of species, but also the diet composition and trophic biology of individuals (Dell *et al.*, 2015). Norway lobster's diet consists basically of other decapods, other crustaceans (euphausiids and peracarids), and fish (Cristo, 1998; Cristo and Cartes, 1998). In many cases, however, suspended particulate organic matter constitutes a significant part of its diet, particularly among small and medium-sized and berried female Norway lobsters (Santana *et al.*, 2020). Greater food availability and the presence of larger individuals in the NTR may have generated this trophic shift inside the NTR. Future studies could shed light on Norway lobster feeding ecology inside the NTR and examine seasonal variations using stomach contents and stable isotope analyses.

BACI results also revealed that protection did not increase biodiversity inside the NTR, with similar megafauna assemblages found in both evaluated areas over time. However, the species cumulative curves and the Chao estimator allowed us to compare the species diversity at each area, suggesting that with more sampling effort we could have achieved a greater composition of species in the no-take area, indicating a potential higher diversity (Moreno and Halffter, 2000). After 4 years, community metrics (e.g. diversity and species richness) showed similarity of species composition between areas, but we detected significant differences in abundance, biomass, and size structure at species level due to the closure. We have already mentioned the significant changes observed in Norway lobsters inside the reserve attributed to the closure of the area. Observing the different responses among all species, only three teleosts (*C. caelorhincus*, *H. dactylopterus*, and *P. blennoides*) showed an increase in abundance, biomass, or size structure following fishing cessation. These species are commonly fished in the multispecies trawl fishery targeting Norway lobsters in the study area (Sardà, 1998b). As the most widely commercialized scorpionfish species, *H. dactylopterus* may resist fishing pressure due to the dispersal of young individuals to northern areas and the effective reproductive strategy in which viviparity confers high fecundity and enhanced survival for embryos and larvae (Muñoz and Casadevall, 2002; Ribas *et al.*, 2006). The teleosts *H. dactylopterus* and *C. caelorhincus* were the species that better responded in all the parameters (abundance, biomass, larger body sizes). In addition to the direct effect of fishery protection on these species, higher densities are usually found in areas with greater food availability, which may be an indirect driver of the increase in density in the NTR (Massutí *et al.*, 1996; García-Ruiz *et al.*, 2020).

However, it is important to note that many other species experienced shifts in density, biomass, and size structure that cannot be solely attributed to the protection provided by the reserve. Population abundance, biomass, and size of some species may have changed over time due to factors such as oceanographic conditions, which may show a great interannual variability (Bonaduce *et al.*, 2021) and can have significant impacts on marine ecosystems, influencing primary production, species composition, reproductive cycles, and overall health of marine organisms (Bellard *et al.*, ; Bernardello *et al.*, 2012; Bruno *et al.*, 2018). The distribution and abundance of some species can be strongly correlated to sea temperature, such as cold-water species (*C. caelorhincus*, *A. sphyraena*, *G. argenteus*, and *M. macrophtalma*) that suffer physiological stress associated with variations in temperature (Perry *et al.*, 2005; Sabatés *et al.*, 2012). In this study, we did not compare the fluctuations of environmental factors with the response of species over time, though it is a fact that climate change is continuously increasing water temperatures (Van Vuuren *et al.*, 2008). However, we observed greater abundances and biomass of cold-water species in time. This could be due to the fact that temperature can regulate the condition and reproductive strategies of some cold-water species, which produce a higher number of eggs, but of poorer quality, when temperature increases (Dutil and Lambert, 2000; Serrat *et al.*, 2018). The proximity of the Gulf of Lions, one of the coldest areas of the Mediterranean Sea, and the presence of deep cold waters sinking from the surface can indeed act as a climatic refuge for many cold species (Petrenko, 2003; Ben Rais Lasram *et al.*, 2010). These environmental conditions provide a sanctuary from the warming effects of the surrounding Mediterranean waters, offering favourable temperatures and habitat for cold-adapted species. Other species, as is the case with some deep-sea shrimps, may present fluctuations due to changes in their feeding assemblages or some other specificities related to the habitat (Carbonell *et al.*, 2003). Another unexpected response was found with *P. longirostris*, a valuable and highly exploited crustacean that is a short-life species with high reproduction rate (Ribeiro-Cascalho and Arrobas, 1987; Abelló *et al.*, 2002). This crustacean intensively increased in time in the CA, suggesting a general increase of the population due to external factors, possibly temperature (Colloca *et al.*, 2014; Quattrocchi *et al.*, 2020), while in the NTR it decreased with respect to the control. We suggest that limited resources or competitive interactions with other species may have affected the population of *P. longirostris* inside the NTR (Carr, 2000).

The recovery of the Norway lobster population within the NTR did not appear to be affected by predator species (Vigo *et al.*, 2022). The increased abundance of Norway lobsters within the reserve may have implications for the population structure of their predator species. The protection provided by the NTR can result in an increase in predators' density due to the higher abundance of prey or food availability (Coll *et al.*, 2006; Daskalov *et al.*, 2007). This increase in prey availability can also benefit the population growth of Norway lobsters, as they primarily feed on other decapod crustaceans, euphausiids, peracarids, and even fish that can also benefit from the protection provided by the reserve (Cristo and Cartes, 1998; Zacchetti *et al.*, 2022). However, in this study, we observed an increase in the Norway lobster population despite the increase in abundance, biomass, or size structure of two of their predator species (*A. veranyi* and *S. canicula*). These two species showed fluctuations in time with shifts in the mean body size and lower densities in the CA, while higher densities and larger individuals were found within the NTR. Considering that these species are highly mobile, their rapid increase over a period of only 4 years suggests that marine reserves may have more of a benefit for those types of species than would have been expected. It is plausible to suggest that more individuals, including larger individuals, remain within the NTR due to the higher availability of food resources (Laptikhovsky, 1999; Barría *et al.*, 2018; Serrat *et al.*, 2018; Guerra-Marrero *et al.*, 2020). The protection provided by the reserve may contribute to enhanced foraging opportunities and increased food availability, attracting these species and promoting their growth and abundance within the reserve. It is important to note that these dynamics may change over time, and further monitoring is necessary to evaluate the long-term effects on predator–prey interactions within the NTR.

All the factors mentioned have the potential to affect the recovery and resilience of species (Andrello *et al.*, 2015). Furthermore, it is crucial to acknowledge that species' response and adaptation to closure measures can vary, and a 4-year closure period is relatively short to observe clearer signs of recovery for some species. Many species did not present any effect, maybe due to other factors such as their life-history traits or shifts in species relationships that were not controlled in this study, such as predation and competition. Long-lived species, such as elasmobranchs, also influenced by their commercial and exploitable value, may require longer periods of protection to adequately respond due to their relatively low growth rate, late maturity rate, and low fertility rate (Cailliet *et al.*, 2005; Claudet *et al.*, 2006; Kaplan *et al.*, 2019), while other species may respond quickly to protection due to their high fecundity rate such as some crustaceans and teleosts observed in this study (Coll *et al.*, 2011; García-*Rubies et al.*, 2013). It is worth noting that highly mobile species may not be significantly impacted by small- to medium-sized protected areas (Game *et al.*, 2009; Grüss *et al.*, 2011; Pittman *et al.*, 2014; Di Franco *et al.*, 2018), such as the reserve examined in this study. Given these complexities, a comprehensive approach is necessary when assessing the effectiveness of marine reserves. To fully comprehend the observed changes in the species dynamics, factors beyond the closure itself, such as environmental changes and species-specific characteristics, should be considered (Magris *et al.*, 2014).

In conclusion, after only 4 years of protection, this deep-water NTR has proved to be a strong effective management measure for restoring the Norway lobster population as indicated by larger individuals and almost four times the biomass observed in the control even if the MPA size was only about 10 km^2 (see the first description of this MPA in Vigo *et al.*, 2021). This NTR was a pilot closure evaluated to prove that it was an effective measure to recover the Norway lobster population. On the basis of our results, we propose establishing a network of small NTRs focused on recovering Norway lobster stocks as an effective management tool for fishery conservation (Gaines *et al.*, 2010; Grorud-Colvert *et al.*, 2014), obtaining relatively rapid gains over the cost of closing fished areas. The NTR could also serve as a planning unit in terms of size and shape for developing spatial conservation planning methods (e.g. Ball *et al.*, 2009). Long-term monitoring is crucial for evaluating the effects of this NTR on Norway lobster and the co-existing megafauna, as its effects could fluctuate over time (Vandeperre *et al.*, 2011; Merder *et al.*, 2020).

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Supplementary material

The following supplementary material is available at *ICESJMS* online version of the manuscript. The details and information about the experimental fishing surveys conducted in 2017 and 2021 at both the control area and the no-take reserve are provided in Supplementary Table S1. In Supplementary Table S2, there are the details about the Norway lobster individuals collected and analysed for the stable isotopes, and in Supplementary Table S3 the values of UDOI (Utilization Distribution Overlap Index) between areas obtained from the same individuals. In Supplementary Table S4, there are the data gathered from the annual LPUE, biomass, and total incomes at the buffers of the control area and the no-take reserve. Supplementary Table S5 provides the abundance and biomass of all the coexistent megafauna species found in the Norway lobster habitat, and Table S6 provides the body size of the species that presented significant differences between areas.

Conflict of interest

The authors have no conflicts of interest to declare.

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Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

Author contributions

Maria Vigo (Data collection, Methodology, Formal analysis, Investigation, Writing), Joan Navarro (Conceptualization, Data collection, Investigation, Validation, Writing), Guiomar Rotllant (Data collection, Review & editing), Nixon Bahamón (Data collection, Review & editing), Marta Carretón (Data curation, Review & editing), Marta Carretón (Data curation, Review & editing), Juliana Quevedo (Data collection, Review & editing), Alba Rojas (Data collection, Review & editing), and Joan B. Company (Conceptualization, Data collection, Investigation, Validation, Writing)

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ROV-based monitoring of passive ecological recovery in a deep-sea no-take fishery reserve

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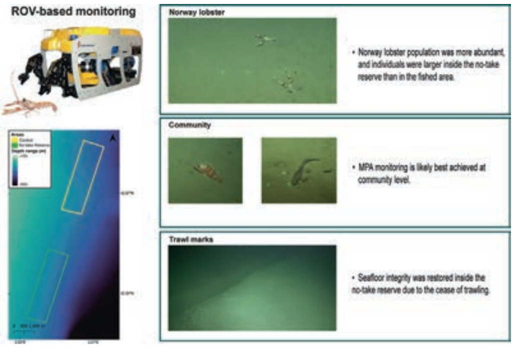
HIGHLIGHTS

- Norway lobster population was more abundant within the no-take reserve.
- Norway lobster individuals were larger within the no-take reserve.
- Seafloor integrity was restored within the no-take reserve.
- MPA monitoring is likely best achieved at community level.
- ROVs are useful non-invasive tools for deep-sea MPA monitoring.

GRAPHICAL ABSTRACT



- Norway lobster population was more abundant, and individuals were larger inside the no-take reserve than in the fished area.
- MPA monitoring is likely best achieved at community level.
- Seafloor integrity was restored inside the no-take reserve due to the cease of trawling.

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ABSTRACT

In the context of marine conservation, trawl fishing activity is the most important ecosystem stressor in demersal Mediterranean waters. Limited management measures in bottom trawling have caused deep-sea stocks of the iconic Norway lobster *Nephrops norvegicus* to decrease over the last decade. This crustacean acts as an umbrella species for co-existing megafauna. Here, we used non-invasive Remote Operated Vehicle (ROV) video-surveys to investigate the status of a pilot deep-sea no-take reserve implemented in the northwestern Mediterranean by quantifying demographic indicators of Norway lobsters and the co-existing benthic community, seafloor restoration, and the presence of marine litter. The results revealed that in the no-take reserve the Norway lobster stock showed higher abundance and biomass, and slightly larger body sizes than in the control area without fishing prohibition. Some taxa, such as the fishes *Helicolenus dactylopterus* and *Trigla lyra* and anemones of the family Cerianthidae, increased in abundance. We also observed that all trawling marks were smoothed and most of the seafloor was intact, clear indicators of the recovery of the muddy seafloor. The accumulation of marine debris and terrestrial vegetation was similar in the no-take reserve and the fished area. On the basis of the results of this study, we suggest that the use of no-take reserves might be an effective measure for recovering the Norway lobster stock, its co-existing megafauna community, and the surrounding demersal habitat. We also suggest that ROV video-survey might be a useful, and non-invasive method to monitor megafauna and seafloor status in protected deep-sea environments.

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1. Introduction

The Mediterranean Sea is a biodiversity hotspot, constituting <1 % of the global ocean surface, but comprising up to 18 % of the world's marine species, 25–30 % of them being endemic (Bianchi and Morri, 2000; Coll et al., 2010; Regato, 2008). Fishing activity is one of the most important ecosystem stressors in Mediterranean waters, altering biodiversity and habitats (IOC-UNESCO, 2021). Fisheries play an important economic and social role in local and regional economies, representing nearly 20 % by weight and 35 % by value of European fishery production (Papaconstantinou and Farrugio, 2000). Although in 2019 the European Commission implemented a global management strategy for the whole western Mediterranean (WestMED initiative, European Commission, 2017a, 2017b), each country independently legislates its own fisheries, applying diverse management measures linked to the reduction of effort, such as a decrease in the number or fishing capacity of vessels, governing bottom otter trawl (trawling, hereafter), or restricting fishing activity seasonally or in particular areas (Aristegui-Ezquibela et al., 2021; Papaconstantinou and Farrugio, 2000).

Beyond the potential effects of global change on marine biodiversity and functioning (Denman, 2008; Levin and Le Bris, 2015; Trindade-Santos et al., 2020), the high-impact bottom trawling that has been used by Mediterranean Sea fisheries for >80 years (Palanques et al., 2006; Puig et al., 2012) is one of the main drivers of ecosystem change in deep-sea Mediterranean demersal communities (Danovaro et al., 2017). The main concern about applying management measures for fishery sustainability in the Mediterranean is related to the multi-specificity of fisheries preventing bottom trawl fleets from catching just the target species, rather than a relatively large number of unwanted species that are discarded (i.e., wasted), which may represent, on average, 25 % of the total catches (Blanco et al., 2023; Gorelli et al., 2016; Sánchez et al., 2004). Bottom trawling is a poorly selective fishing method with a great impact on demersal communities and deep-sea ecosystems. Consequently, most Mediterranean stocks (ca. 62.5 %) are being fished at their maximum sustainable yield or above their maximum reaching unsustainable levels (FAO, 2022; Papaconstantinou and Farrugio, 2000; Tsikliras et al., 2015). Moreover, bottom trawlers disturb and destroy seafloor habitats in their path, including seagrasses, coral reefs, or rock gardens, considered key habitats for multiple species (Stiles et al., 2010; Reed et al., 2007). Bottom trawling can also strongly modify seafloor morphology because of the resuspension and removal of a large amount of sediment by the action of wires, otter doors, sweeps, and nets (Palanques et al., 2006; Puig et al., 2012). As a result, historically intense commercial trawling has acted as a geological force flattening the surface of the continental shelf and slope margins in the Mediterranean, exposing its hardened substrate (Puig et al., 2012).

In the western Mediterranean Sea, the trawl fleet operates at a depth of between 50 and 800 m (Gorelli et al., 2011) targeting Norway lobster *Nephrops norvegicus* at a 300–500 m depth (Sardà, 1998). This demersal decapod is one of the most important demersal stocks for European fisheries, distributed on muddy bottoms along the northeast Atlantic Ocean and the Mediterranean Sea (Aguzzi et al., 2023; Aguzzi and Sardà, 2008; Bell et al., 2006; Ungfors et al., 2013). Nevertheless, due to high fishing pressure and ineffective management measures for the sustainable exploitation of the species, the catches of this iconic European crustacean have been decreasing over the last several years (from 2008 to 2016 there has been a decrease of 19 % in catches in the EU, EUMOFA, 2019; Letschert et al., 2021; Lolas and Vafidis, 2021). The species' dependency upon fragile silt and clay mud habitats, in which Norway lobsters dig their burrows, makes it highly vulnerable to trawling impacts (Campbell et al., 2009). Also, as a marine ecosystem engineer, the Norway lobster's burrowing behaviour increases habitat heterogeneity and provides structures for other co-existing megafauna, acting as an umbrella species (i.e., a key conservation target to protect the whole benthic community; Roberge and Angelstam, 2004).

The establishment of Marine Protected Areas (MPAs), such as legally recognized no-take reserves where fishery activity is prohibited, could be a useful management measure for not only recovering the over-exploited Norway lobster stock, in terms of density and body size, but also promoting the co-existing benthic community (Melaku Canu et al., 2020; Vigo et al., 2022, 2021) and enhancing seabed quality and overall demersal richness (Cabral et al., 2020; Sala-Coromina et al., 2021; Sala and Giakoumi, 2018). The benefits obtained from MPAs could also be observed in adjacent areas, as a result of the spillover of adults and juveniles from the protected area (Lenihan et al., 2021; Sala-Coromina et al., 2021). Management evaluations within no-take fishery reserves have already been carried out on crustacean species, such as the European lobster *Homarus gammarus* and the spiny lobster *Palinurus elephas* (Follesa et al., 2011; Goñi et al., 2010; Padilla et al., 2022; Wiig et al., 2013). In the Mediterranean Sea, there are very few assessments of the use of no-take reserves for the recovery of Norway lobster populations, except for the Pomo Pit area in the Adriatic (Bastardie et al., 2017; Melaku Canu et al., 2020) and a no-take fishery reserve located at a deeper depth (375–400 m) in the northwestern Mediterranean (Order APA/753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753To; Vigo et al., 2021).

Monitoring strategies for the evaluation of the efficacy of no-take reserves for the recovery of Norway lobster stocks are a priority (Lester et al., 2009). Unfortunately, compared to shallow areas (e.g., Linares et al., 2012; Lloret et al., 2006), the monitoring of deep-sea stocks is a technological and operational challenge (Aguzzi et al., 2020). Experimental trawling remains the most common tool to quantify the abundance and biomass of deep-sea stocks (e.g., Fiorentini, 1999; Sánchez et al., 2007; Tuset et al., 2021). However, its use in an MPA is not desirable due to its intrinsic impact on benthic communities and habitats. As an alternative strategy to assess the status of demersal and benthic communities, visual monitoring through the use of Remotely Operated Vehicles (ROVs), Autonomous Underwater Vehicles (AUVs), and other systems is increasingly employed (Benoist et al., 2019; Chimienti et al., 2018; Huvene et al., 2016). In fact, there are regular underwater television (UWTV) surveys that are conducted to provide abundance estimates for Norway lobsters on the functional units (FUs) in the North Atlantic to assess their stocks (Dobby et al., 2021). Video-surveys can provide habitat assessments evaluating anthropogenic impacts at the level of seabed sediment integrity or the presence of marine litter (Bo et al., 2014; Mecho et al., 2020) defined as any persistent, manufactured or processed solid material discarded, disposed, or abandoned (definition by the United Nations Environment Programme; UNEP).

In this study, we used ROV video-surveys to investigate the ecological and morphological status of a pilot no-take reserve implemented in a deep-sea northwestern Mediterranean area 2.5 years after its establishment as well as the situation of a nearby control (fished) area. We followed an ecosystem-based approach, i.e., by quantifying the demographic indicators of abundance, biomass, and body size of Norway lobsters and other co-occurring benthic megafauna, including the main predators of Norway lobsters. We also examined the status of seafloor recovery as a metric for passive recovery from trawling impacts and the presence of marine litter and terrestrial vegetation in the reserve.

2. Materials & methods

2.1. Study area and ROV surveying procedures

This study was conducted in a deep-sea no-take fishery reserve with an area of 10 km^2 (hereafter referred to as no-take reserve), located along the continental margin from 351 to 475 m depth in the northwestern Mediterranean Sea (Fig. 1A). This no-take reserve was established on the northern flank of the Palamós canyon, where deep-sea trawling has taken place for around a century (Puig et al., 2012). In the whole slope region, the sediment is compact silt and clay mud suitable for the excavation of burrows by Norway lobsters (Maynou and Sardà, 1997). This reserve was created in 2020 by the Spanish Government (Order APA/753/2020; https://www.boe.es/eli/es/o/2020/07/31/apa753To) with the main objective of recovering the stock of Norway lobster in this Mediterranean area. However, before the designation as an MPA, fishing activity inside the no-take reserve was ceased in September 2017 through an agreement, i.e., not officially enforced, between two local fishermen's associations (Roses and

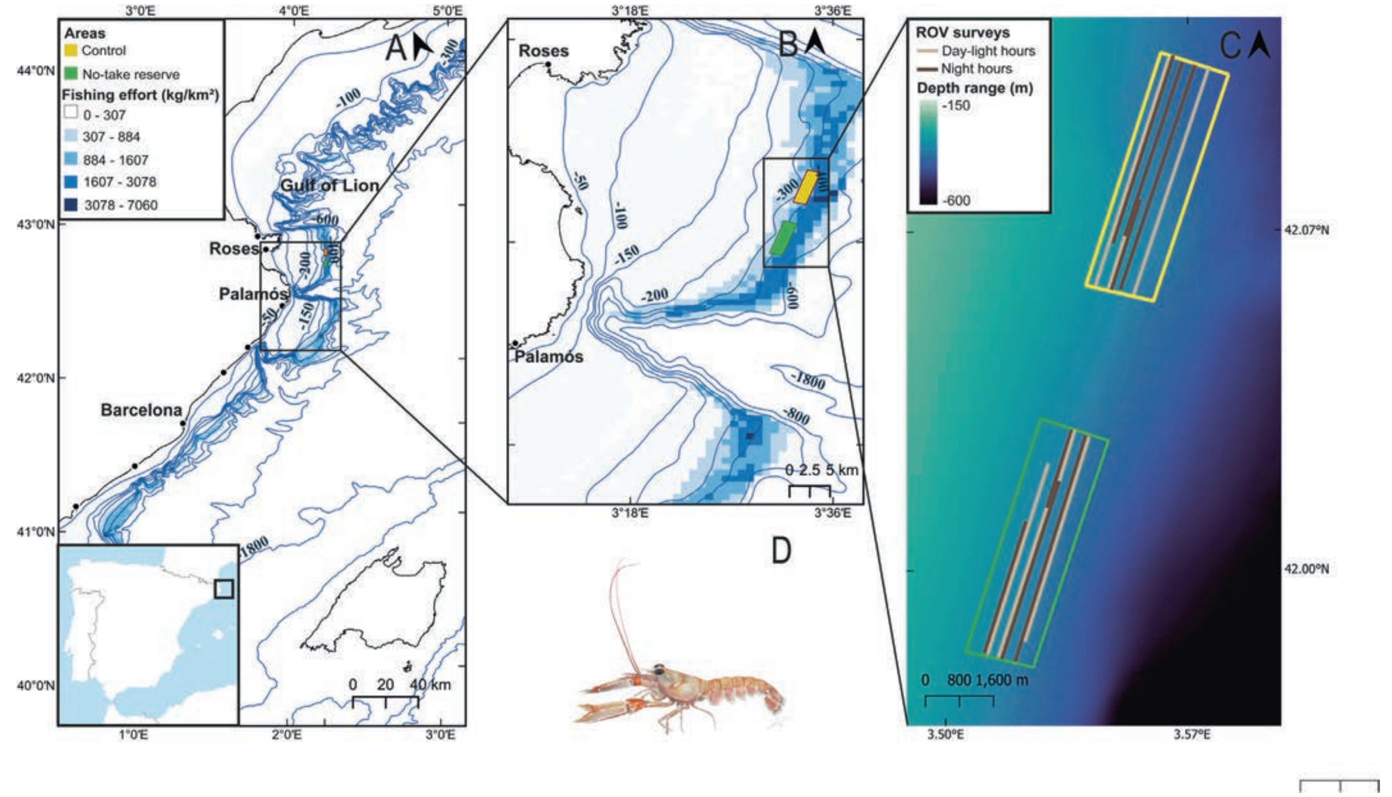

Fig. 1. The study area showing A) the spatial distribution of Norway lobster catches, B) the location of the no-take reserve and the control area, and C) the position of the ROV video-surveys. The spatial distribution of Norway lobster catches accumulated was obtained by combining vessel monitoring system information and official daily landing data in the time period 2005–2018 (European Commission, 2022). D) Norway lobster illustration by Joan Mir-Arguimbau.

Palamós). We used, for comparative purposes, an adjacent control area (i.e., ecologically, geomorphologically and bathymetrically equivalent) where bottom trawling was permitted, having the same dimensions as the no-take zone (Fig. 1B). The no-take reserve has a bathymetric range of 310–475 m and the control area has a range of 290–440 m depth (Fig. 1C).

Just prior to the cessation of fishing in the no-take reserve (August 2017), we conducted 4 experimental fishing surveys in the no-take area and 2 in the control area, using an otter bottom trawl net of a square mesh size of 12 mm. All hauls were of 1 h of duration, with an average speed of 2.5 knots. The swept area (km^2) of all hauls was estimated based on vessel speed (S, in knots), average horizontal opening of the net (BT, in m) and haul duration (H, in h) between the initial and final position of the gear on the bottom (Sparre and Venema, 1998). The preliminary results of these experimental trawling surveys (see Fig. 2) indicated that abundance (control area; mean = 1584.31; SD = 925.89 No.·km^{-2}; no-take reserve; mean = 2789.56; SD = 1446.37 No.·km^{-2}), biomass (control

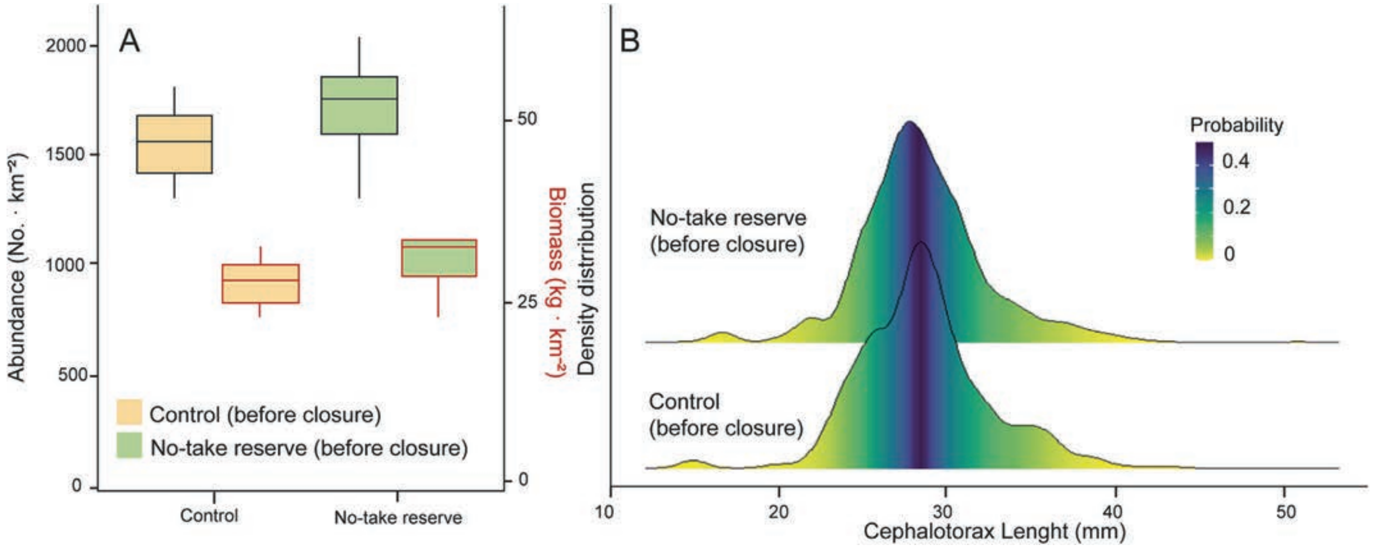

Fig. 2. A) Abundance and biomass of the Norway lobster in the no-take reserve and in the control area in August 2017 as determined by experimental trawl fishing. B) Body size density distribution determined by experimental trawl fishing in August 2017. Based on the color degradation, dark blue indicates the highest likelihood of sizes (CL, mm) coinciding with the mean size.

area; mean = 24.65; SD = 12.54 $kg{\cdot}km^{-2}$; no-take reserve; mean = 42.16; SD = 20.79 $kg{\cdot}km^{-2}$), and size distribution (control area; mean = 23.37; SD = 4.97 mm CL; no-take reserve; mean = 27.30; SD = 4.81 mm) of Norway lobster did not differ between both control area and no-take reserve (Abundance; F1, 5 = 0.31, $p = 0.61$; Biomass; $\chi^2 = 0.86$; $p = 0.35$; Mean size distribution; ($\chi^2 = 0.05, p = 0.48$).

To monitor Norway lobster (Fig. 1D) abundance and biomass in a non-invasive way, ROV video-surveys were performed in both the no-take zone and adjacent control area in February 2020, 2.5 years after the implementation of the no-take reserve. In particular, we conducted six ROV video-survey transects in the no-take reserve (341–376 m depth) and six in the control area (327–424 m depth) (Fig. 1C, Supplementary Material Table A1). These surveys were performed on board the R/V *Sarmiento de Gamboa* with ROV Liropus 2000, a Super-Mohawk ROV. The ROV was equipped with a forward-facing video camera (HD Kongsberg OE14-502) positioned below four Halogen 250 W Deep Sea Power & Light (DSPL) lights. The ROV also had two parallel lasers with 10 cm separation, to provide a reference scale for animal sizing within the camera field of view. Underwater ROV positioning was measured by a High Precision Acoustic Positioning system (HiPAP; 350 P Simrad) with a spatial accuracy of 0.3 % and an error of range of detection <20 cm. This was linked to the Differential Global Positioning System of the R/V.

The ROV video-surveys were continuously recorded and conducted during consecutive 24 h cycles close to the bottom (50–100 cm of altitude above the seabed) at a constant speed of 0.6 $m{\cdot}s^{-1}$ (Ayma et al., 2016; Grinyó et al., 2022; Mecho et al., 2020, 2018). The video-swept area was calculated from the ROV instantaneous velocity each second, multiplied by the width of the image as measured by the laser pointer (approximately 1.5 m width at a constant height of 1.8–2 m). Despite possible bathymetric and swept area differences between surveys, each ROV video-survey conducted was considered a replicate within each. We standardized by adjusting the resulting parameters according to the swept area. We also quantified the presence of other co-occurring megafauna species, marine litter, organic debris such as terrestrial vegetation, and the status and recovery of the seabed by categorizing the trawling impact marks (see below for a more detailed explanation).

2.2. Norway lobster evaluation

To estimate the abundance and biomass of Norway lobsters in the no-take reserve and in the control area, we conducted two complementary approaches: "burrow-system counting" and "animal counting". In the burrow-system approach, we followed the assessment protocols of the Working Group on Nephrops Surveys (ICES, 2016; Dobby et al., 2021), counting all burrow-systems in the control area and the no-take reserve. Burrows of Norway lobster present characteristic features related to the shape and appearance of burrow openings that occasionally number two or three in a system, and are easily identified (e.g., Chapman, 1980; Froglia et al., 1997; Tuck et al., 1994; Supplementary Material Fig. A2). To standardize the counting of burrows from each video-transect, their abundance was standardized by the unit of video-swept seabed surface, obtaining a density estimate as the number of burrow-systems per km^2. We assumed that one burrow-system contained only one Norway lobster as this species is highly territorial and usually only one adult occupies the burrow-system (Johnson et al., 2008; Sbragaglia et al., 2017; Vigo et al., 2021). We also considered that all burrow-systems were occupied, as unoccupied burrows rapidly degrade and collapse (Marrs et al., 1996).

In the animal counting approach, we standardized the number of individuals counted in ROV transects per unit of video-swept area during 24 h cycles. The video-swept area was calculated in m^2 for each minute of video recording (given the constancy of cruising; see above), and then converted into km^2. Therefore, the data were presented as the number of individuals per km^2 (i.e., density). Only in the animal counting approach, we tested for differences considering the abundance of Norway lobsters during daylight hours and then during nighttime hours (considering sunrise at 8 am and sunset at 6 pm).

To test the differences between Norway lobster counting approaches, burrow-system and animal counting, between the control area and the no-take reserve, two-way ANOVA tests were conducted. The test allowed assessing the variance of the abundance of Norway lobsters with two fixed factors ("Area" for the control and no-take reserve, and "Activity" for presence in daylight hours and in nighttime hours). For burrow abundance, we conducted non-parametric Kruskal-Wallis tests in the R software version 4.1.2 (R Core Team, 2021) using the function *kruskal.test*. Statistical analyses were carried out beforehand to test for normality and homogeneity of variances for each variable using the functions *shapiro.test* and *bartlett.test* respectively of the package "stats".

On the basis of the frames recorded in the ROV surveys, we measured the body size of Norway lobsters based on their cephalothorax length (Carapace Length = CL, in mm) using the software ImageJ V. 1.53q (Abràmoff et al., 2004) measuring individuals aligned within the field of view (i.e., whose cephalothorax was seen next to the two laser beams). We estimated the body size of each individual by averaging five repeated measures to minimize measurement bias. Then, a class-size frequency distribution was constructed (using the averaged CL measure for each individual) for both the control area and no-take reserve. We applied one-way ANOVA tests to compare body size between the control area and the no-take reserve.

The body mass (in g) of Norway lobsters was estimated from a length-weight relationship for the species, using a standard allometric model. We averaged the allometric coefficients from 1995 reported by Sardà et al. (1998), in the same area of this study (GSA06), between female and male coefficients for obtaining combined sexes coefficients (Sardà et al., 1998):

$$W = 0.00045\ CL^{3.10}$$

where W is body weight in grams and CL is cephalothorax length (see above). The constants 0.00047 and 3.14 are the coefficients a and b of the allometric model. Weight was calculated from each measure of CL computed for both the control area and no-take reserve, and the average and standard deviation were also estimated. Subsequently, we estimated the biomasses along each video-transect in the no-take and control areas. For this, we converted the previously obtained weight into biomass ($kg{\cdot}km^{-2}$) with the following formula (Morello et al., 2007; Froglia et al., 1997):

$$B = \overline{W} \cdot A/1000$$

where B is the biomass ($kg{\cdot}km^{-2}$), $\overline{W}$ is the mean individual weight (g) from all the individuals that were possible to measure with ImageJ (we were only able to measure individuals aligned within the field of view), and A is the total abundance corrected by swept area ($No.{\cdot}km^{-2}$). We calculated a total of four biomasses depending on the A source: for the two areas, control zone and no-take reserve, and the two approaches, burrow-system and animal counting.

A non-parametric statistical approach was used to determine significant differences between groups for cases in which normality and homogeneity of variance were not met. The Kruskal-Wallis non-parametric test was used to compare estimated biomasses in the control area and the no-take reserve, and between burrow-system counting and animal counting of Norway lobster. To compare estimated biomasses from burrow-systems in different areas, we conducted parametric one-way ANOVA tests.

2.3. Community megafauna taxa evaluation

Taxonomic identification and counting of the co-existing megafauna taxa were performed for each ROV video-survey analyzing the recorded video frames. A video-catalog of best images of the detected taxa that appeared in the area was built as a reference for their classification (Supplementary Material Figs. A3–A9). All these individuals were then classified at the lowest possible taxonomic level according to identification guides (Froese and Pauly, 2022; Grinyó et al., 2022; Lloris, 2015; Fricke et al., 2022; WoRMS Editorial Board, 2022) and by taxonomic specialists from the Institut de Ciències del Mar (ICM-CSIC). Due to the difficulty of correctly assigning cephalopods to particular species, we classified them into three larger taxonomic groups: Superorder Decapodiformes, Order Octopoda, and Order Sepiida. The community (dis)similarity of all co-occurring taxa was calculated via the video-swept area method (see previous section). We also identified the main predators of Norway lobster based on Vigo et al. (2022).

To examine the differences between the control area and the no-take reserve in the composition and abundance of taxa, we generated a nonmetric Multi-Dimensional Scaling (nMDS) ordination analysis in the R software version 4.1.2 (R Core Team, 2021) using the function *metaMDS* of the package "vegan". The abundances were previously square-root transformed to achieve normality, and a Bray-Curtis similarity matrix was calculated. Once we visualized the grouping, we conducted a one-way permutational multivariate analyses with *adonis* from the package "vegan" (PERMANOVA tests; Anderson, 2001) using one fixed factor ('area', with two levels) to test for differences in community (dis)similarity between transects from the control area and the no-take reserve. As for Norway lobsters, we compared all taxa abundances between the control area and the no-take reserve with PERMANOVA and a pairwise multilevel comparison with Bonferroni-based adjusted *p*-values by using the package "pairwiseAdonis" and *pairwise.adonis* (Martinez Arbizu, 2020). Moreover, Shannon's diversity index (H', log 10 base) (Shannon and Weaver, 1948) was calculated to measure species diversity in each community (control area and no-take reserve). To test for differences between areas, one-way ANOVA tests were performed for each biodiversity index.

We constructed two taxa accumulation curves (Thompson and Withers, 2003; Ugland et al., 2003) to record the cumulative number of species in each study area (control and no-take reserve) as a function of the cumulative effort expended searching for them (hours of video recorded by ROV surveys). The taxa accumulation curves allowed us to assess and compare diversity across the two areas and to evaluate the adequacy of the ROV video-surveys in representing the benthic and demersal fauna in each area. We also calculated the Chao estimator in the R software version 4.1.2 (R Core Team, 2021) using *specpool* from the package "vegan" for assessing species richness in the two communities, the control area and the no-take reserve. This estimator indicates how many species or different taxa would be registered if the effort sampling was increased or how many species we did not record with our effort (Béguinot, 2016; Chao, 2006).

2.4. Marine litter and terrestrial vegetation

We classified marine litter as plastic, metal, glass, and the remains of fishing nets (GESAMP, 2021; Mecho et al., 2020; Ramirez-Llodra et al., 2011). We also counted terrestrial vegetation items (such as tree branches) to analyze all organic inputs coming from terrestrial sources (Galimany et al., 2019). The abundance of the different types of litter and terrestrial debris were also standardized by the swept area (km^2). The differences in the abundance of anthropogenic debris between the control area and the no-take reserve were tested using two-way ANOVA tests with two fixed factors ("Area" with two levels for the control and no-take reserve, and "Type of Debris" with five levels). The difference in the abundance of terrestrial debris between the control area and the no-take reserve was also tested with non-parametric Kruskal-Wallis tests in the R software version 4.1.2 (R Core Team, 2021) using the function *kruskal.test*.

2.5. Seafloor integrity and recovery

We examined seafloor integrity in the control area and the no-take reserve by assessing the perturbations of trawling marks (by bottom trawl metal doors and trawl nets). We classified them into six different categories according to the degree of alteration (see description in Table 1, Fig. 3). We recorded the duration of their appearance in each ROV video-survey, classifying them as stated in Table 1, and then a percentage was calculated considering the total time recorded at each transect. Finally, we estimated the overall average and standard deviation of the control area and the no-take reserve.

Table 1
Categories of seafloor impact due to trawling.

Categories	Description
1	Seafloor with no perturbations. No signs of trawling effects.
2	Perceptible trawling marks, probably old trawling marks in recovery.
3	Smoothed door mark from the trawling gear.
4	Flattened seafloor due to the net of the trawling gear.
5	Flattened seafloor with door marks and berming of the muddy sediment.
6	Deeply altered seafloor due to a profound door mark of the trawling gear.

We tested for differences in the variance of presence of each category of alteration between areas and also among all six categories defined in Table 1. We conducted the non-parametric test of Scheirer Ray Hare in the R software version 4.1.2 (R Core Team, 2021) using the function *scheirerRayHare* of the package "rcompanion". The post-hoc tests were performed using multiple comparisons with Dunn's Test using the function *dunn.test* from the package "dunn.test" and "FSA".

3. Results

In total, we recorded 72 h in all the ROV surveys, corresponding to a total swept area of 83.82 km^2 (Supplementary Material Table A1). We covered a similar time and area in the control area (time = 32 h; area = 40.18 km^2) and the no-take reserve (time = 39 h; area = 43.64 km^2).

3.1. Norway lobster evaluation

ROV surveys showed significantly higher numbers of Norway lobsters in the no-take reserve than in the control area, independent of the approach used (burrow-system or animal counting; Figs. 4–5). Regarding the abundance of Norway lobster based on burrow-system counting, although the average number of burrows in the no-take reserve (mean = 7513; SD = 2951 No.·km^{-2}) was higher than in the control area (mean = 4411; SD = 3203 No.·km^{-2}), the difference was not statistically significant ($\chi^2 = 3.10$; $p = 0.07$). With the animal counting approach, during nighttime, we found a similar (Fig. 4A; $F_{1,\ 6} = 23.22$, $p = 0.95$) abundance of Norway lobster in both areas (control area; mean = 1022.94; SD = 954.9 No.·km^{-2}; no-take reserve; mean = 1658.47; SD = 1529.01 No.·km^{-2}). In contrast, during daylight hours, we found that the abundance of Norway lobster in the no-take reserve was significantly higher than in the control area (Fig. 4A; $F_{1,\ 6} = 11.59$, $p = 0.002$).

In relation to the body size of Norway lobsters, we measured 169 out of a total of 299 individuals detected. Testing for differences in body size (CL in mm), we found that individuals from the no-take reserve were significantly larger than the ones from the control area (Fig. 4B; control area; mode = 19, SD = 6 mm; no-take reserve; mode = 23, SD = 8 mm; $F_{1,\ 166} = 14.44$, $p < 0.01$). Moreover, larger-sized individuals were found in the no-take reserve (maximum body size of 51 CL in mm) compared to the control area (maximum body size of 35 mm) (Fig. 4B).

The estimated body mass (g) considering all individuals counted in the two areas was lower in the control area (body mass = 5.51 ± 5.76 g) than in the no-take reserve (body mass = 10.21 ± 12.78 g) (Table 2). Both the burrow-system counting and animal counting approaches showed a higher biomass of Norway lobster in the no-take reserve than in the control area (burrow-system method: $F_{1,11} = 16.88$, $p < 0.01$; animal counting method: $F_{1,18} = 5.14$, $p = 0.03$; Fig. 5). Nevertheless, we found significant differences between the burrow-system and animal counting methodologies. By using the burrow-system approach, the biomass of Norway lobster in both the control area and the no-take reserve was higher than the biomass estimated with the animal counting approach ($\chi^2_{1,30} = 4.23$, $p = 0.04$; Fig. 5A). In contrast, the abundance of Norway lobsters did not differ significantly between burrow counting and animal counting approaches ($\chi^2_{1,30} = 3.95$, $p = 0.05$; Fig. 5B).

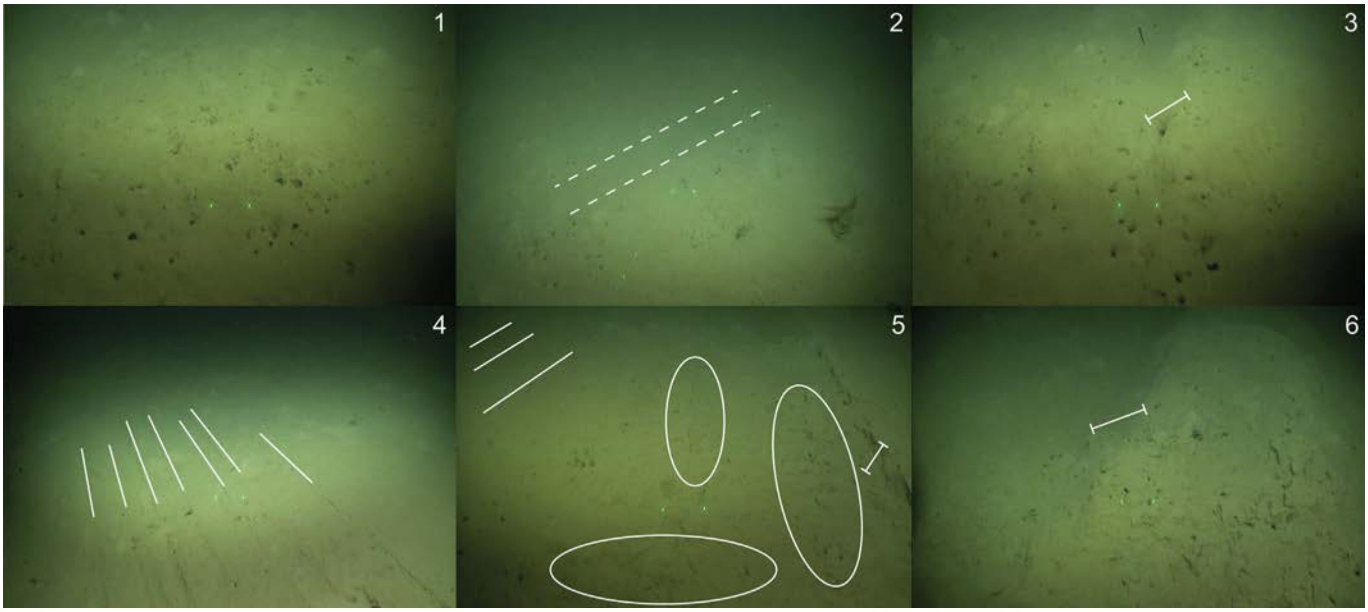

Fig. 3. Trawl mark categories used to evaluate the seafloor state following the descriptions in Table 1. 1: No signs of trawling effects, 2: perceptible trawling marks, 3: smoothed door marks from trawling gear, 4: flattened seafloor due to the trawling gear net, 5: flattened seafloor with door marks and the berming of muddy sediment, 6: deeply altered seafloor due to deep door marks from trawling gear.

3.2. Community megafauna taxa evaluation

We identified a total of 43 taxa from seven major taxa groups: Cephalopoda, Cnidaria, Crustacea, Echinodermata, Elasmobranchii, Porifera, and Teleostei (see Figs. A3–A9 and Table A10 of the Supplementary Material). Diversity indexes showed a similar composition of taxa between the benthic community found in the control area and in the no-take reserve, with Teleostei being the most diverse taxon group in the benthic community followed by Crustacea (Fig. 6A). The Bray-Curtis matrix of distances obtained from the abundances of the demersal community was represented in a nMDS (Fig. 6B). The ordination had a relatively low stress value (0.13) and showed no obvious separation of transects between areas, as was corroborated with a PERMANOVA test (pseudo-$F_{1,18} = 1.61, p = 0.06$).

After comparing the abundance of all identified taxa between the control area and the no-take reserve, we found that only the fishes *Helicolenus dactylopterus* and *Trigla lyra*, and the anemones of the Family Cerianthidae, showed higher abundances in the no-take reserve than in the control area (Table 3; Fig. 6C). The other recorded taxa did not differ in abundance between the control area and the no-take reserve (Table 3). In relation to the predators of Norway lobster, we found that their abundance was similar between the control area and the no-take reserve (Table 3). We did not observe an increase in predators in terms of abundance as a result of the protection provided by the no-take reserve.

The taxa accumulation curves indicated that nearly all taxa were recorded in both areas suggesting a good sampling effort. In the control area, we recorded a total of 40 different taxa, while the Chao estimator was 43, only three more taxa compared with our observations. Similarly,

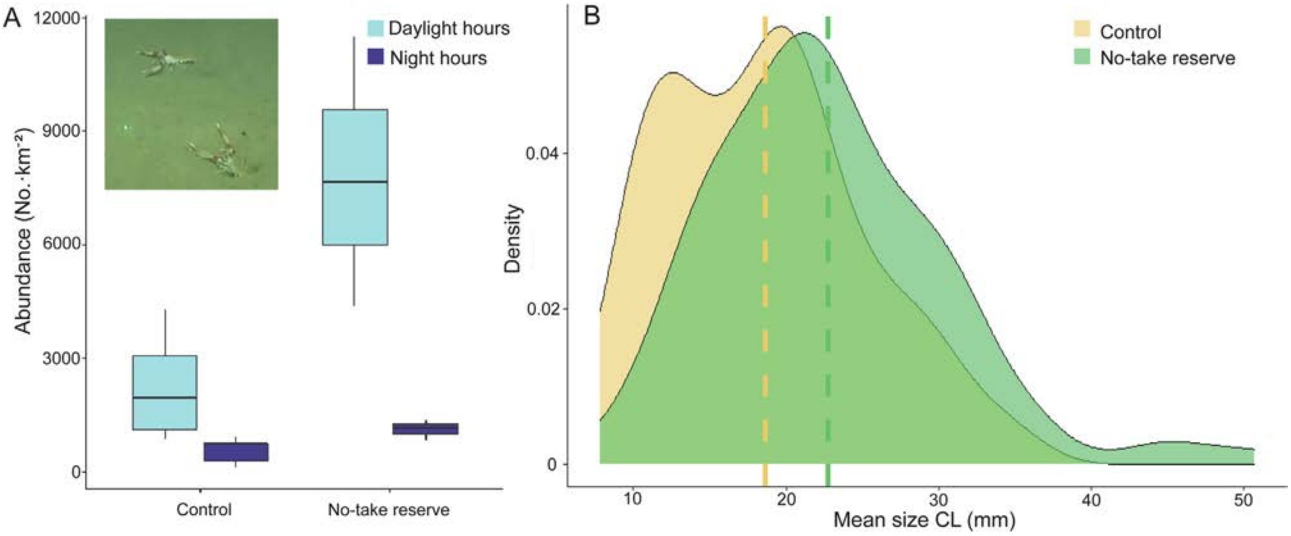

Fig. 4. A) Abundance (animal counting in each transect corrected per the swept area covered) of Norway lobster in the control area and the no-take reserve during daytime and nighttime hours by ROV surveys. The picture shows two individuals of Norway lobster, one outside a burrow and the other inside with only the cephalothorax visible. Box length represents interquartile range, bar length represents range and horizontal lines represent median values. B) Body size distribution of Norway lobsters for the control area and the no-take reserve by ROV surveys. The dashed line represents the individual mean size for each compared area.

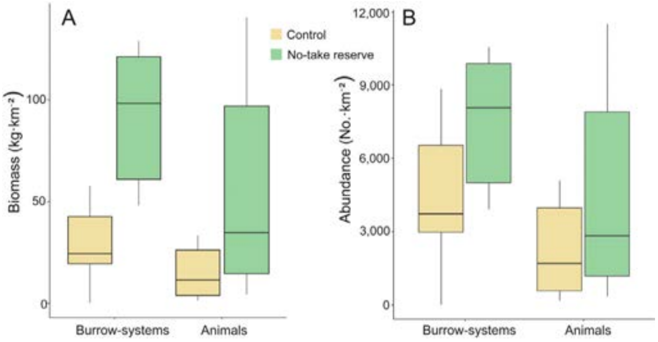

Fig. 5. A) Abundance (counts in each transect corrected per the swept area covered) and B) biomass of Norway lobster calculated with both methodologies (burrow-system counting and animal counting referred in the Figure as "Burrow-systems" and "Animals" respectively) in the no-take reserve and in the control area. Upper and lower 95 % confidence limits are represented by the extent of the vertical bars in the boxplots, indicating the quantiles and the median.

in the no-take reserve, we recorded a total of 43 taxa, while the Chao estimator was 47. In both cases, the saturation curve was reached at approximately 15–20 h of time effort and the estimator indicated that only 3–4 taxa were unrecorded (Fig. 6D).

3.3. Marine litter and terrestrial vegetation

The abundance of anthropogenic debris and terrestrial vegetation debris were similar between the control area and the no-take reserve (Fig. 7A). We did not find significant differences between the control area and the no-take reserve concerning the abundance of anthropogenic debris, ($F_{1,\ 14} = 0.45, p = 0.52$), among types of different debris ($F_{3,\ 14} = 0.72$, $p = 0.57$), or the abundance of terrestrial vegetation ($\chi^2 = 0.04; p = 0.84$). The diversity of anthropogenic debris was higher in the control area (fishing net, glass, metal, and plastic) than in the no-take reserve (plastic and metal) (Fig. 7B).

3.4. Trawl marks

All ROV video-surveys conducted in the control area showed high percentages of seafloor impacted (Fig. 8A). In the no-take reserve, more intact patches (Category 1) showed the highest average percentage (97.24 ± 3.61 %), with the rest of the perturbations being <4 % or not present. In the control area, Category 1 (41.17 ± 27.55 %) and Category 4 (38.21 ± 26.91 %) showed a similar average percentage, followed by Categories 5 and 6 with approximately 10 % coverage in the control area (Fig. 8B). Statistical comparisons showed differences between areas (control area and no-take reserve), categories and the interaction among areas and categories ($H_{1,71} = 13.41$, $p < 0.05$; $H_{5,72} = 28.27$, $p < 0.05$; $H_{11,72} = 22.29$, $p < 0.05$), indicating the presence of more intact patches (Category 1) in the latter and more deeply ploughed patches (Category 6) in the former. The only categories of impact that appeared in the no-take reserve were smoothed door marks (1 ± 1.12) and slightly perceptible trawl marks (1.52 ± 2.62) (Fig. 8).

Table 2
Population parameters of Norway lobster in the control area and the no-take reserve based on ROV surveys. Biomass was obtained from the total density and the mean weight of individuals calculated from an allometric model, which considered the mean size (CL) of individuals. Body mass was calculated from the mean body size of each area of study.

	Control	No-take reserve
Burrow-systems abundance (No.·km^{-2})	4411 ± 3203	7513 ± 2951
Individual abundance (No.·km^{-2})	2227 ± 1849	4518 ± 4248
Body size (CL length, in mm)	19 ± 6	23 ± 8
Body mass (g)	5.51 ± 5.76	10.21 ± 12.78
Biomass from burrow-systems abundance (kg·km^{-2})	28.81 ± 20.92	91.82 ± 36.06
Biomass from animal abundance (kg·km^{-2})	12.27 ± 9.71	46.13 ± 43.37

4. Discussion

Here, we investigated the effects of passive ecological recovery of a deep-sea no-take reserve from the western Mediterranean Sea using non-invasive ROV video-surveys. We examined the recovery state of the overexploited Norway lobster stock and assessed how their densities and biomasses differed in this no-take reserve compared to an adjacent control area in which bottom trawl fisheries operate. The results revealed that in a relatively short period of time (2.5 years) after ceasing trawling activity, the Norway lobster population showed higher abundance, biomass, and larger mean individual size in the no-take area than in the control area. Moreover, we also found that some community species, such as the Teleostei *H. dactylopterus* and *T. lyra* and sessile marine species from the family Cerianthidae, were more abundant in number inside the no-take reserve. We also observed how trawling marks on the seafloor in the no-take reserve were nearly absent.

4.1. Norway lobster recovery

The recovery of overexploited stocks of Norway lobster has been suggested to take between four to six years (Sardà et al., 1998) and some habitats may require at least 10 years to detect signals of recovery (McClanahan and Mangi, 2000). Here, after only 2.5 years, we found that the population of this crustacean in the no-take reserve was recovered in comparison with the control trawled area. This result suggests that MPAs may offer quick benefits in locations near fishing grounds where fishing mortality is elevated and stocks are below sustainable fishing levels (Halpern, 2003; Hart, 2006), corroborating the fact that the Norway lobster stock is being highly overexploited in the study area (Field et al., 2006; Sarda, 1998). The recovery rate of this species depends upon the rate of successful recruitment (Sardà, 1998). Since small juvenile Norway lobsters remain hidden inside burrows during the first year of life (Powell and Eriksson, 2013; Tuck et al., 1994), the present study refers to the population after their first year of life, or those individuals that already exhibit burrow emergence behaviour.

In the last few decades, UWTV surveys have become the primary assessment method used by the WGNEPS focusing on burrow counting, as they are static and relatively constant (Bell et al., 2018; Sardà and Aguzzi, 2012). However, the burrow counting method has uncertainties such as the persistence of empty burrows or exclusion from tunnel occupation by other fish and crustacean species that maintain its structural integrity (Aguzzi et al., 2021). To address this issue, we foresaw an opportunity to improve current stock assessment methods by applying two different approaches to estimate stock abundance and biomass, namely "burrow-system counting" and "animal counting", which showed contrasting results. With the burrow-system approach, we observed similar abundances in the control area and the no-take reserve. Therefore, similar counts in both areas demonstrate that burrows can resist trawling, indicating equivalent numbers/densities of remaining individuals that rebuild the burrow systems after trawling disturbance, assuming that all are occupied only by Norway lobsters, as other species may opportunistically occupy and maintain Norway lobster tunnels (reviewed by Sardà and Aguzzi, 2012). Considering that juveniles initially occupy burrows linked to those of adults (Chapman, 1980; Tuck et al., 1994), the maintenance of high burrow densities could indicate a suitable habitat for good recruitment (Chapman and Howard, 1988; Johnson et al., 2013). Nonetheless, tunnel counts present several levels of uncertainty. Burrows can offer some protection from trawling; however, intense impacts on burrows destroy system integrity (Hiddink et al., 2006; Tillin et al., 2006). We did not measure the size and shape of burrow systems, although we generally noticed that burrow systems from the control area were more flattened and without the muddy mounds characteristic of well-structured systems in the no-take reserve

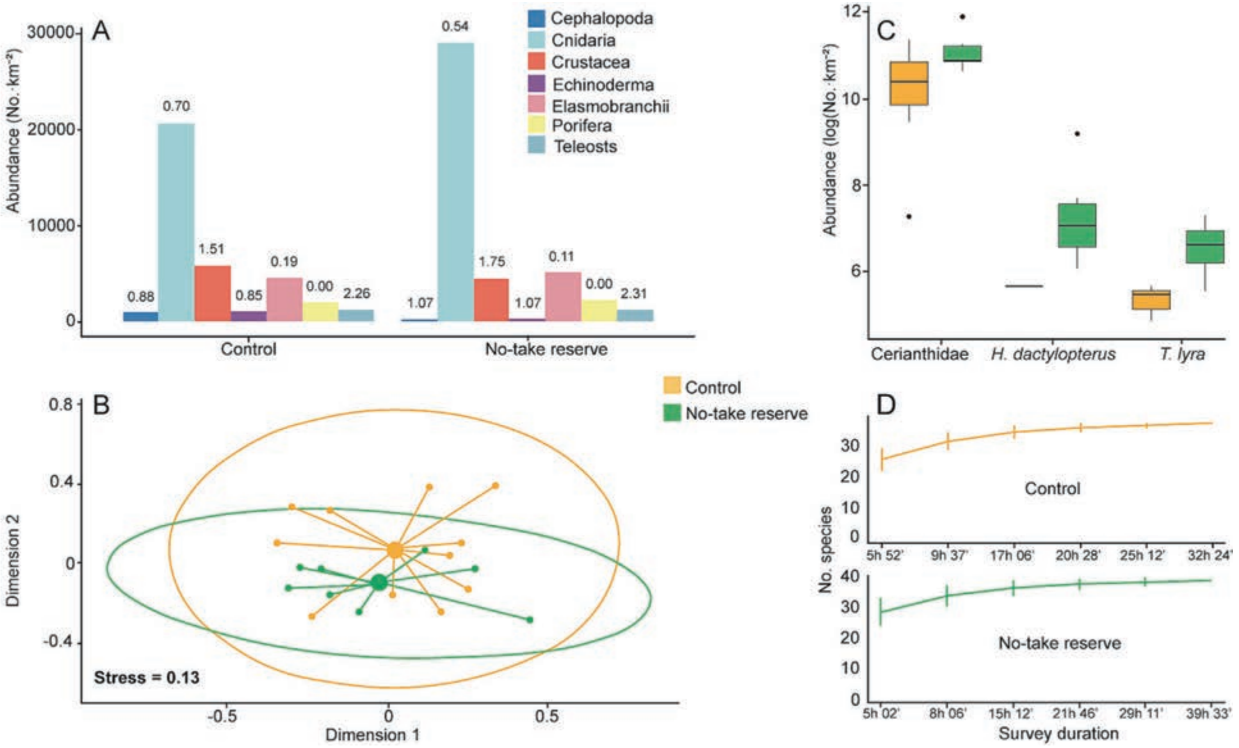

Fig. 6. A) Abundance of all megafauna taxa observed separated into six groups (Cephalopoda, Cnidaria, Crustacea, Echinoderma, Elasmobranchii, Porifera, and Teleostei) indicating the Shannon diversity values from each group in both the no-take reserve and the control area. B) Non-metric multidimensional scaling representation which indicates the similarities in terms of abundance and species composition (counts of all species corrected per the swept area covered in each transect) between the no-take reserve and the control area by overlapping both areas. Ordination ellipses represent 95 % confidence, and spiders connect the species composition variability with the centroid of each area, control area (in yellow) and no-take reserve (in green). C) Violin plots representing the densities of Family Cerianthidae, *Helicolenus dactylopterus*, and *Trigla lyra* individuals in the control area (in yellow) and in the no-take reserve (in green). D) Species accumulation curves for the no-take reserve and the control area, the hours accumulated for each transect are also specified. The error bars represent the standard deviation of the accumulation curve.

(Supplementary Material, Fig. A2). In addition, the stability of burrow systems per se also depends on the composition of the sediment in relation to currents (Campbell et al., 2009). In our case, differences in both habitat variables were not studied (as currents were not measured), since both surveyed areas are just small parcels of a much larger and homogenous slope area (Palanques et al., 2005; Send et al., 1999). In this scenario, we did not observe species other than Norway lobster close to tunnel system entrances in either area. Norway lobster juveniles usually occupy burrows already created by adults to avoid predation (Chapman, 1980).

Here, we suggest a complementary and more reliable approach to counting all individuals of Norway lobster, classifying them according to their activity, as an alternative method of ICES stock assessment by UWTV surveys (Bell et al., 2018). This approach expanded on the results of animal density in relation to behavioral rhythms obtained through UWTV surveys in shallower areas of the Atlantic Ocean (Aguzzi et al., 2021). In regard to the day-night activity of Norway lobsters in deep-sea waters, we observed the limited presence of visible individuals during the night, corroborating how the locomotor activity of Norway lobsters that inhabit deep ecosystems below 300 m in depth is predominant during daylight hours (Aguzzi et al., 2003; Vigo et al., 2021). This result confirms that any video-based fishery-independent assessment of species along the continental slope should be carefully centered on daytime hours to better capture visible animals and to perform their count for calibration with counting burrow systems (Aguzzi et al., 2021).

The abundance of Norway lobster was higher in the no-take reserve compared to the control area. However, we only noticed this significant increase during daylight hours, whereas at night the abundance of Norway lobster was similar: very scarce in both the control area and the no-take reserve. This fact can be explained by their burrowing behaviour, which indicates that the demographic indicators of this species should be evaluated according to their activity patterns which depend on optimum environmental light conditions (Chapman and Rice, 1971). The class-size distribution of the no-take reserve showed a higher mode size with larger sizes absent in the control area. We expect that the ranges of body size distribution and mode will increase in the no-take reserve, proportionally to the years of protection at a relatively fast pace (Babcock et al., 2007; Lester et al., 2009; Moland et al., 2013). It is important to highlight that before the closure, the body size distribution of Norway lobster was similar in both no-take reserve and control area (Fig. 2). However, a long-term monitoring for demographic assessment is crucial to observe these beneficial size shifts in the no-take reserve in comparison to adjacent areas.

Total biomass reflects both size and abundance, resulting in a robust measure for MPA protection (Lester et al., 2009; Soykan and Lewison, 2015). In some cases, MPAs have only a detectable biomass response, and not an abundance response, due to the low pre-MPA harvest of some species or high variability in recruitment (Kaplan et al., 2019). Biomass can increase much more quickly than abundance as a result of the low mortality of older and larger-sized individuals. On the other hand, if biomass is low, but abundance is still high, an increase in recruitment into the area could be indicated (Nalepa et al., 2010). Estimating this demographic variable through mean body size as calculated in the two approaches (i.e., burrow-system and animal counts) indicates how in both cases biomass was higher in the no-take reserve. All the evaluated variables (i.e., abundance, mean body size, and biomass) reflected the positive effects of passive restoration in the no-take reserve. We found the species in the no-take area showed a rapid response to protection from fishing and that it may asymptotically increase until reaching carrying capacity over the years as long as this protection measure lasts. Comparing both counting methods, burrow-system and animal counts, we recommend the second approach as it provides more accurate information.

Table 3

Mean (±SD) of the abundance (No.·km^{-2}) of the megafauna species observed in the control area and the no-take reserve based on ROV surveys. Results of PERMANOVA statistical tests performed are also indicated with the Bonferroni-based adjusted *p*-values. The predators of Norway lobster based on Vigo et al. (2022) are indicated with a (P). The species that showed significant differences in statistical results are in bold.

Species	Control	No-take reserve	Statistical results
Teleostei			
Arctozenus risso	442 ± 202	487 ± 1	Pseudo-F = 0.54 adjusted-*p* = 0.59
Coelorinchus caelorhincus	597 ± 231	397 ± 236	Pseudo-F = 1.08 adjusted-*p* = 0.30
Conger conger (P)	837 ± 453	927 ± 425	Pseudo-F = 1.19 adjusted-*p* = 0.28
Gadiculus argenteus	456 ± 200	718 ± 520	Pseudo-F = 0.06 adjusted-*p* = 0.81
Helicolenus dactylopterus	**280 ± 1**	**2157 ± 2954**	**Pseudo-F = 23.36 adjusted-p = 0.002**
Lepidopus caudatus	407 ± 121	995 ± 834	Pseudo-F = 1.49 adjusted-p = 0.28
Lepidorhombus boscii	4059 ± 4040	4277 ± 1763	Pseudo-F = 1.102 adjusted-*p* = 0.31
Lophius spp. (P)	346 ± 148	241 ± 120	Pseudo-F = 2.20 adjusted-*p* = 0.16
Merluccius merluccius (P)	496 ± 628	281 ± 192	Pseudo-F = 0.22 adjusted-*p* = 0.86
Micromesistius poutassou	177 ± 56	0	Pseudo-F = 2.66 adjusted-*p* = 0.22
Molva macrophthalma	252 ± 80	199 ± 69	Pseudo-F = 2.26 adjusted-*p* = 0.17
Family Myctophidae	964 ± 776	538 ± 668	Pseudo-F = 1.27 adjusted-*p* = 0.19
Ophichthus rufus	0	138 ± 1	Pseudo-F = 1.40 adjusted-*p* = 0.42
Ophisurus serpens	0	166 ± 59	Pseudo-F = 3.25 adjusted-p = 0.17
Phycis blennoides	2183 ± 4144	1786 ± 929	Pseudo-F = 1.25 adjusted-*p* = 0.26
Symphurus nigrescens	272 ± 148	142 ± 4	Pseudo-F = 0.12 adjusted-*p* = 0.85
Trigla lyra	**212 ± 78**	**772 ± 427**	Pseudo-F = **5.65** adjusted-***p*** = **0.017**
Trisopterus capelanus	388 ± 290	255 ± 155	Pseudo-F = 0.02 adjusted-*p* = 0.83
Unclassified	705 ± 244	386 ± 285	Pseudo-F = 0.67 adjusted-*p* = 0.38
Echinodermata			
Astropecten sp.	410 ± 228	363 ± 154	Pseudo-F = 0.31 adjusted-*p* = 0.60
Brissopsis lyrifera	391 ± 1	253 ± 166	Pseudo-F = 4.31 adjusted-*p* = 0.10
Holothuroidea spp.	1683 ± 3097	440 ± 252	Pseudo-F = 0.57 adjusted-*p* = 0.54
Elasmobranchs			
Raja spp.	251 ± 1	138 ± 1	Pseudo-F = 0.05 adjusted-*p* = 1.00
Scyliorhinus canicula (P)	4901 ± 3069	5678 ± 2408	Pseudo-F = 1.57 adjusted-*p* = 0.23
Cephalopods			
Decapodiformes (P)	342 ± 217	226 ± 165	Pseudo-F = 0.92 adjusted-*p* = 0.93
Octopoda (P)	1496 ± 2811	365 ± 256	Pseudo-F = 0.08 adjusted-*p* = 0.90
Sepiidae (P)	475 ± 435	249 ± 106	Pseudo-F = 0.81 adjusted-p = 0.52
Cnidaria			
Arachnanthus oligopodus	16,294 ± 14,046	14,391 ± 10,927	Pseudo-F = 1.62 adjusted-*p* = 0.21
Family Cerianthidae	**34,982 ± 23,279**	**63,745 ± 30,532**	**Pseudo-F = 4.30** adjusted-***p*** = **0.02**
Funiculina quadrangularis	933 ± 874	1059 ± 884	Pseudo-F = 1.27 adjusted-p = 0.22
Crustacea			
Dardanus arrosor	666 ± 163	1034 ± 755	Pseudo-F = 0.05 adjusted-*p* = 0.76
Goneplax rhomboides	731 ± 342	377 ± 247	Pseudo-F = 0.39 adjusted-*p* = 0.66
Brachyura	15,206 ± 13,986	12,155 ± 13,639	Pseudo-F = 1.01 adjusted-*p* = 0.36
Monodaeus couchii	21,471 ± 18,809	13,065 ± 10,831	Pseudo-F = 0.72 adjusted-*p* = 0.44
Munida sp.	1036 ± 754	647 ± 248	Pseudo-F = 0.63 adjusted-p = 0.38
Family Pandalidae	4025 ± 3924	2921 ± 2525	Pseudo-F = 0.89 adjusted-*p* = 0.91
Parapenaeus longirostris	238 ± 1	317 ± 229	Pseudo-F = 4.27 adjusted-p = 0.0
Plesionika heterocarpus	2279 ± 2047	3824 ± 2642	Pseudo-F = 1.51 adjusted-p = 0.16
Processa sp.	2642 ± 1961	2424 ± 2079	Pseudo-F = 0.07 adjusted-*p* = 0.89
Solenocera membranacea	1797 ± 2037	1023 ± 1076	Pseudo-F = 0.43 adjusted-*p* = 0.65
Porifera			
Polymastia spp.	2023 ± 2177	2287 ± 1838	Pseudo-F = 1.59 adjusted-p = 0.23

4.2. Community megafauna taxa recovery

The number of megafauna taxa detected showed similar values in both areas, with a total of 43 and 40 taxa in the no-take reserve and control area, respectively. The ROV video-surveys may not have been able to detect all species of the benthic community, as many different behavioral reactions to ROV presence occur, from stillness to active avoidance (see behavioral classifications in Ayma et al., 2016; Lorance and Trenkel, 2006). We found that two Teleostei species, *H. dactylopterus* and *T. lyra*, showed higher abundance in the no-take reserve than in the control area. These species are commercialized by Norway lobster fishers and therefore may also benefit Norway lobster fisheries outside the reserve. The anemones from the family Cerianthidae that can retract when the gear of bottom trawl fisheries approaches (Hall-Spencer, 1999) may still be vulnerable to trawling impacts (Kenchington et al., 2006). In our study, these species were abundant in both areas although they also showed a higher abundance in the no-take reserve than in the control area.

Sessile species increase the roughness of mud plains and thus can accelerate the restoration of seabed quality by trapping drifting sediment (Buhl-Mortensen et al., 2010; Grinyó et al., 2020). The anemones from the Cerianthidae family may act as a refuge for other species, such as demersal fishes and crustaceans (Shepard et al., 1986). In fact, we observed the co-presence of *H. dactylopterus* and *Munida* spp. with these anemones, indicating higher abundances of both species within the family Cerianthidae patches as previously reported in other areas (Auster et al., 2003; Uzmann et al., 1977; Valentine et al., 1980). The greater abundance of anemones in the no-take reserve could offer more refuges against predation to other fish and decapod crustacean species, resulting in their increased abundance, as reported here for *H. dactylopterus* and also by Grinyó et al. (2020) in the Alboran Sea. Thus, *H. dactylopterus* and *T. lyra* could be

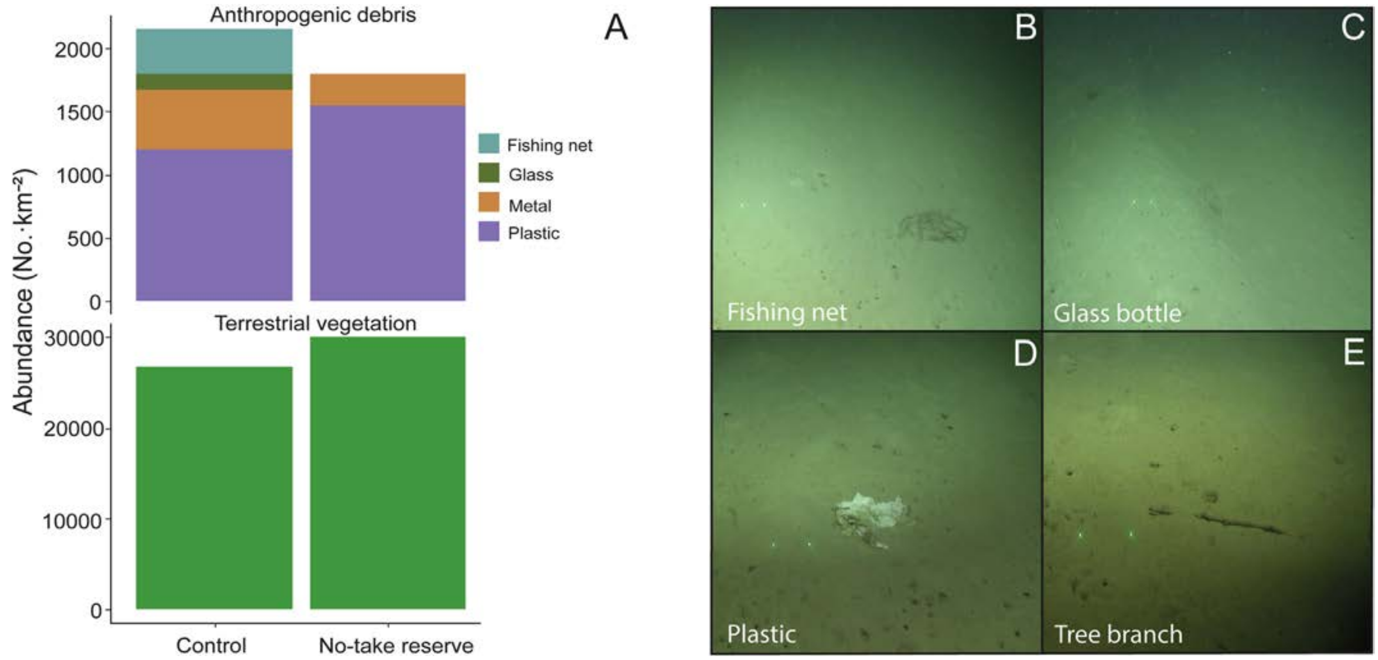

Fig. 7. A) Anthropogenic litter classified as fishing net, glass, plastic, or metal and quantified in both the no-take reserve and the control area; terrestrial vegetation quantified in the control area and the no-take reserve; the plot shows the density of debris from terrestrial vegetation, plastic, and other debris (metal and undefined); examples of B) fishing net, C) glass bottle, D) soft white plastic, and E) tree branch.

defined as key indicators of the effectiveness of a no-take habitat established in Norway lobster grounds, as they are very sensitive to trawling, presenting significant increases in only a short time due to the protection of the no-take reserve. For the remaining species with depleted stocks due to fishing activity, we may likely observe benefits with additional protection (e.g., for species with low fecundity rates and high maturity ages) (Nickols et al., 2019). However, other species may not exhibit benefits because of the small size of the reserve that was designed for the Norway lobster, a crustacean that uses a reduced spatial area (Vigo et al., 2021).

Some MPA assessments consider the species interactions involved, such as predator-prey interactions, evaluating predator densities and biomasses. This approach is crucial even in small MPAs as an incremental shift in predator densities could halt the recovery of an overexploited species and even undermine it (Clements and Hay, 2017), while a lack of predators could also lead to permanent habitat regime shifts (Daskalov et al., 2007). The predators of Norway lobster (Vigo et al., 2022) observed in this study did not present an increase in abundance in the no-take reserve, apparently not influencing the dynamics of their prey, at least during these first years of protection. This result re-enforces the use of reserves as a tool to preserve Norway lobsters compared to the European spiny lobster (*Palinurus elephas*), where juveniles were highly predated by fishes in the MPA (Díaz et al., 2005). One of the success in recovery on Norway lobsters versus the European spiny lobster could be the different habitat, muddy versus rocky substrates. Establishing a network of small no-take reserves should be considered as an effective management tool for fishery conservation of Norway lobster stocks.

Accumulation curves indicate the effectiveness of the monitoring effort, here in terms of hours of video observation. To avoid taxa underrepresentation

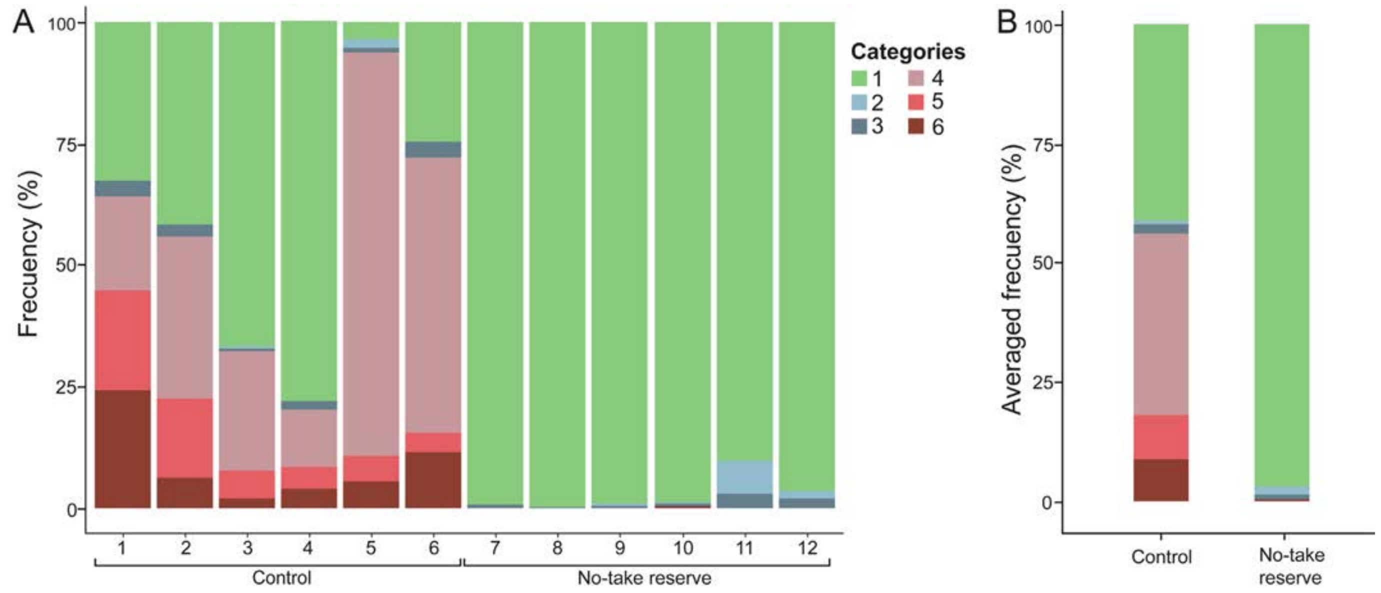

Fig. 8. A) Percentage of trawl mark categories observed via ROV video-survey; B) averaged frequency (%) of trawl mark categories in the control area and the no-take reserve.

in video-based monitoring in NW Mediterranean, we suggest that the minimum ROV video recording time for continental slope, muddy bottom Norway lobster grounds should be 20 h, as indicated by the taxa accumulation curves in the present study. This monitoring indicator, estimated along with data collection during both the daytime and nighttime, could facilitate the monitoring of sessile and motile megafauna in MPAs under restoration.

4.3. Marine litter, terrestrial vegetation, and seafloor recovery

Marine litter and terrestrial vegetation are present in all marine habitats, even in the most remote habitats of the ocean (Pham et al., 2014). We found similar densities between the control area and the no-take reserve in both marine litter and terrestrial vegetation. Most of the marine litter found was plastic, the most abundant form of marine debris, rising globally and with documented impacts on marine ecosystems (Mecho et al., 2021; Sheavly and Register, 2007). In the control area, we also observed fishing nets likely due to recent fishing activities (Galgani et al., 2000; Vieira et al., 2015), which also constitute a major problem as they can cause high fish mortality as a result of “ghost fishing” (Brown and Macfadyen, 2007). Even if trawl fisheries contribute to the removal or displacement of marine litter and terrestrial vegetation, they continuously enter from terrestrial habitats, ships, and other installations at sea. Enclosed areas such as the Mediterranean Sea exhibit some of the highest densities of marine litter (Galgani et al., 2015). The absence of trawling in the no-take reserve did not lead to more accumulation of marine litter nor terrestrial vegetation, as all this debris is continuously distributed, due to hydrography and geomorphological factors of the ocean (Barnes et al., 2009; Galgani et al., 2000), to hotspots of litter accumulation that include shores and the deepest areas in submarine canyons (Corcoran et al., 2009; Pham et al., 2014).

Trawling exerted above the maximum sustainable yield (i.e., overfishing) not only causes stock depletion, but also generates seafloor morphological changes, nutrient cycle alterations, sediment resuspension, and increased bottom-water turbidity (Puig et al., 2012; Pusceddu et al., 2014; Tillin et al., 2006). Here, we reported how the establishment of a no-take reserve helped to recover nearly the full extent of the area from trawling marks in a relatively short time following the termination of this activity. All surveys performed in the no-take reserve indicated only 5 % of the seafloor was altered by trawling marks, with smoother marks already in the process of recovery. In contrast, the control area exhibited >60 % of the seafloor impacted, presenting all categories of trawl marks. The muddy grounds of Norway lobster seem to rapidly recover when trawling fishery activity is stopped. The high density of Norway lobster and other burrowing species such as *Munida* spp. and *Goneplax rhomboides* can produce high bioturbation activity that could also be responsible for surface sediment mixing (to 5–20 cm sediment depth), thereby contributing to the rapid erasure of trawl marks in the no-take reserve (Mengual et al., 2016; Mérillet et al., 2018; Schwinghamer et al., 1998). Nevertheless, although they were not measured in the present study, we believe that the main factors that may be involved in the fast recovery from trawling marks in this area are hydrodynamic parameters such as tidal currents, natural sedimentation, and the deposition of suspended sediments (Friedlander et al., 1999; Linnane et al., 2000). The seafloor state, as we defined it, is a good indicator for measuring the passive restoration of a habitat from trawling. Intermediate approaches to fish stock recovery such as seasonal closure areas may represent too short a time span for the recovery of seafloor habitats (Demestre et al., 2008; Smith et al., 2000).

5. Conclusions

The recovery of overexploited Norway lobster populations and habitats may benefit from applying a passive habitat restoration approach based on total closure of areas for fishing activities. No-take deep-sea reserves require prolonged monitoring that may help to identify potential density-dependent effects on Norway lobster populations in the long-term, inducing an increase in the competition for space. On the basis of our results, we propose establishing a network of small no-take reserves focused on recovering Norway lobster stocks as an effective management tool for fishery conservation, obtaining relatively rapid gains over the cost of closing fished areas. We also suggest the use of ROVs for monitoring marine reserves as an innovative and non-invasive method for evaluating the ecology and seafloor status. Focusing on target species of commercial interest could make the present monitoring procedure feasible in other deep-sea no-take areas worldwide.

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CRediT authorship contribution statement

Maria Vigo- data collection, methodology, formal analysis, investigation, writing.

Joan Navarro- conceptualization, data collection, investigation, validation, writing.

Jacopo Aguzzi- data collection, investigation, validation, writing.

Nixon Bahamón- data collection, formal analysis, review & editing.

José Antonio García- data collection, programming, review & editing.

Guiomar Rotllant- data collection, review & editing.

Laura Recasens- data collection, review & editing.

Joan B. Company- conceptualization, data collection, investigation, validation, writing.

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Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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