UNIVERSITAT DE BARCELONA

Impacto de la pesca y ecología trófica de los tiburones de talla media y grande en el Mediterráneo

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Impacto de la pesca y ecología trófica de los tiburones de talla media y grande en el Mediterráneo

Memoria presentada por

Ignasi Nuez Rodriguez

para optar al grado de doctor por la Universidad de Barcelona

Doctorando

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"En la agreste infancia de la meseta burgalesa pedía a mis buenas niñeras del páramo que me contaran una historia de lobos, y con estas historias me dormía, arrullado por la seguridad de la casa, dulce y confortable".

-Félix Rodríguez de la Fuente-

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ABSTRACT

Sharks and other chondrichthyans are amongst the most threatened organisms on the planet and the interactions with fishing activities, either overfishing or incidental fishing, are the main drivers of their global decline. Generally, sharks occupy high levels in the marine trophic webs and may impose a top-down control over lower trophic levels. Consequently, their disappearance favours the degradation of marine ecosystems. It is therefore necessary and urgent to design and implement conservation measures which can revert the decline of sharks around the world and particularly in the Mediterranean, where the extinction risk of many species is even higher than anywhere else in the world, according to the IUCN's criteria. The development of effective conservation measures needs the broadening and improvement of the actual knowledge regarding shark populations in the Mediterranean, which has been the general aim of the present dissertation. The first chapter focuses on the bycatch (incidental capture) of medium-sized and large sharks inhabiting the Costa Brava (Catalonia, northwestern Mediterranean) through the use of the Local Ecological Knowledge (LEK) gathered by fishermen. Results suggested a decline in the abundance of most of the shark species, largely due to overfishing, being bottom trawling the fishing gear with the highest diversity of captured species. Only the blue shark (*Prionace glauca*), the sixgill shark (*Hexanchus griseus*) and probably the spiny dogfish (*Squalus acanthias*) are still bycaught frequently, while the smoothhounds (*Mustelus* spp.) might have disappeared from the Costa Brava. The second chapter examines the isotopic niche of medium-sized and large sharks in the northwestern Mediterranean through the analysis of stable isotopes of C and N. Results show a high contribution of cephalopods to the diet of all species and reveal medium-sized and large sharks as mesopredators with a unique isotopic niche, different from those of other large predatory fishes and odontocete cetaceans. In the third chapter, the current state of the sixgill shark is analysed in nine Mediterranean countries also making use of LEK. Results showed most of the captures occur in the western and central part of the Mediterranean especially during the warm months and in those gears that operate in deeper waters, particularly in bottom trawling and also bottom longline. Additionally, the study suggests generally low

at-vessel mortality, although further research on post-release mortality is recommended. Finally, the perceived population decline in some countries may be indicative of a regional decline of this species and, as a consequence, a revision of the IUCN conservation status of the sixgill shark in the Mediterranean is advisable. Altogether, the information compiled in this dissertation updates various aspects of the actual state of medium-sized and large sharks, with special emphasis on the sixgill shark and serves as a reference for the development of future measures aimed at protecting and managing shark populations in the Mediterranean.

RESUMEN

Los tiburones y en general los peces condrictios se encuentran entre los organismos más amenazados del planeta, siendo los efectos derivados de la interacción con actividades pesqueras, como la sobrepesca y la pesca incidental, los principales responsables del declive global de sus poblaciones. En general, los tiburones ocupan los niveles superiores de las redes tróficas marinas, pudiendo ejercer un control sobre los niveles tróficos inferiores. Consecuentemente, su desaparición favorece la degradación de los ecosistemas marinos. Es por lo tanto necesario y urgente diseñar e implementar medidas de conservación que reviertan el declive de los tiburones en todo el mundo y particularmente en el Mediterráneo, dónde el riesgo de extinción de muchas especies es más elevado que en las otras partes del mundo, según los criterios de la UICN. El desarrollo de medidas de conservación efectivas pasa por ampliar y mejorar el conocimiento actual sobre las poblaciones de tiburones presentes en el Mediterráneo, que ha sido el objetivo general de la presente tesis. El primer capítulo se centra en la captura incidental de los tiburones de talla media y grande presentes en la Costa Brava (Cataluña, Mediterráneo Noroccidental) mediante el uso del Conocimiento Ecológico Local (LEK) acumulado por los pescadores. Los resultados sugieren un declive en la abundancia de la mayoría de las especies de tiburones, en gran parte debido a la sobrepesca, siendo el arrastre el arte de pesca que captura más diversidad de especies. La captura accidental es aún frecuente sólo en el caso de la tintorera (*Prionace glauca*), la cañabota gris (*Hexanchus griseus*) y posiblemente la mielga (*Squalus acanthias*), mientras que las musolas (*Mustelus* spp.) podrían haber desaparecido de la Costa Brava. En el segundo capítulo, se examina el nicho isotópico de los tiburones de talla media y grande en el Mediterráneo Noroccidental mediante el análisis de isótopos estables. Los resultados muestran una alta contribución de los cefalópodos en la dieta de todas las especies, sitúa a los tiburones de talla media y grande en los niveles superiores de la red trófica, aunque actuando como mesodepredadores y revelan un nicho isotópico distinto al de otros grandes peces depredadores y los cetáceos odontocetos. En el tercer capítulo, se analiza el estado actual de la cañabota gris en 9 países del Mediterráneo,

también haciendo uso del LEK. Los resultados muestran que la mayoría de las capturas de cañabota gris ocurren en la parte occidental y central del Mediterráneo sobre todo durante los meses cálidos y en los artes de pesca de mayor profundidad, especialmente en el arrastre y también el palangre de fondo. Adicionalmente, el estudio sugiere una mortalidad en la embarcación generalmente baja, aunque se recomienda investigar la mortalidad post-captura. Finalmente, el declive poblacional percibido en ciertos países podría ser indicativo de un declive regional de esta especie y, en consecuencia, se aconseja a la UICN una revisión del estado de conservación de la cañabota gris en el Mediterráneo. En conjunto, la información recopilada en esta tesis actualiza diversos aspectos del estado actual de los tiburones de talla media y grande, con especial énfasis en la cañabota gris y sirve de referencia para el desarrollo de futuras medidas enfocadas a la protección y gestión de las poblaciones de tiburones en el Mediterráneo.

ÍNDICE

LISTADO DE ACRÓNIMOS

AMP	Área Marina Protegida
CITES	Convención sobre el Comercio Internacional de Especies Amenazadas de Fauna y Flora Silvestres
CMS	Convenio para la Conservación de las Especies Migratorias
EE. UU	Estados Unidos de América
FAO	Organización de las Naciones Unidas para la Alimentación y la Agricultura
GFCM	Comisión General de Pesca del Mediterráneo
ICCAT	Comisión Internacional para la Conservación del Atún Atlántico
LEK	Conocimiento Ecológico Local (*Local Ecological Knowledge*)
MEDLEM	Monitoreo de Grandes Elasmobranquios del Mediterráneo (*Mediterranean Large Elasmobranchs Monitoring*)
ORP	Organización Regional de Pesca
PSAT	Marca Archivo “Pop-up” por Satélite (*Pop-up Satellite Archival Tag*)
TED	Dispositivo Excluidor de Tortugas (*Turtle Excluder Device*)
UE	Unión Europea
UICN	Unión Internacional para la Conservación de la Naturaleza
ZEE	Zona Económica Exclusiva

INTRODUCCIÓN

1. Tiburones. Marco general.

1.1 *Rasgos característicos y estado actual de las poblaciones de tiburones. Principales amenazas.*

Los tiburones, junto con rayas, pastinacas, peces sierra y quimeras, son organismos vertebrados acuáticos pertenecientes a la clase Chondricthyes (peces cartilaginosos) (Ebert et al., 2021). En la actualidad, se conocen más de 530 especies vivas de tiburones distribuidas en 9 órdenes (Ebert et al., 2021) que, en su mayoría, presentan un cuerpo fusiforme y entre 5 y 7 hendiduras branquiales laterales.

Los tiburones, y los condrictios en general, siguen una estrategia vital conocida como estrategia K, caracterizada por un crecimiento lento, una maduración sexual tardía, una esperanza de vida elevada, una baja fecundidad y una baja capacidad para el incremento poblacional (Pratt & Casey, 1990; Stevens et al., 2000). Este conjunto de características vitales hace a los tiburones muy sensibles a las grandes perturbaciones que comprometen la viabilidad de sus poblaciones, como la sobrepesca, en comparación con los peces teleósteos (Myers & Worm, 2005). Los tiburones de talla grande son altamente sensibles incluso a niveles ligeros de presión pesquera (Ferretti et al., 2010).

La sobrepesca, ya sea como resultado de la pesca dirigida o de la captura incidental es, precisamente, el principal factor responsable del declive de muchas poblaciones de tiburones y rayas a escala global, seguida en menor medida de la pérdida de hábitat, la persecución, el cambio climático y también la contaminación (Dulvy et al., 2014; Gelsleichter et al., 2005). En la actualidad, se estima que un 32,6% de todas las especies de condrictios están categorizadas como amenazadas (Vulnerable, en Peligro o en Peligro Crítico) en la Lista Roja de Especies Amenazadas de la Unión Internacional para la Conservación de la Naturaleza (UICN) (Dulvy et al., 2021). Los tiburones suman un total de 167 de las 391 especies amenazadas que figuran en este listado, lo que representa un porcentaje del 42,7%. Este porcentaje podría ser mayor si las especies categorizadas como con “Datos insuficientes” en la Lista Roja acaban por caer en la categoría de “Amenazadas”, tal como se ha previsto en algunos modelos recientes (Walls & Dulvy, 2021). La sobrepesca no solo representa la amenaza principal que afecta la supervivencia de todas las 391 especies amenazadas; para un 67,3% de estas especies, la sobrepesca es el único motivo de su declive poblacional (Dulvy et al., 2021). La alarmante situación en la que se encuentran los tiburones y sus parientes ha llevado a algunos expertos a afirmar que los condrictios pueden estar enfrentándose a la mayor crisis que han podido experimentar a lo largo de sus más de 400 millones de años de historia (Simpfendorfer & Dulvy, 2017).

El incremento substancial de la presión pesquera en los océanos es un fenómeno especialmente notorio a partir de la segunda mitad del siglo XX, dando como resultado un rápido y acentuado declive de las poblaciones de peces depredadores grandes (Myers & Worm, 2003). Según Costello et al. (2012), los tiburones ya se encontraban en serio declive debido a la pesca en la década de los 70 y, en 2009, la biomasa media de las poblaciones de tiburones capturados por pesquerías habría disminuido entre un 81 y 89% (Costello et al., 2012; Dulvy et al., 2014). En un estudio reciente, se estimó que la abundancia de tiburones oceánicos había disminuido un 70,1% entre 1970 y 2020 (Fig. 4a) (Pacoureau et al., 2021). Mientras que el riesgo de extinción de los atunes y los peces espada se ha conseguido revertir gracias a la disminución de su mortalidad por pesca, los tiburones siguen desplomándose al no contar con medidas de gestión y comercio efectivas que permitan la recuperación de sus poblaciones (Juan-Jordá et al., 2022).

En el estudio de Pacoureau et al. (2021) mencionado anteriormente, las especies de tiburones oceánicos estudiadas presentaban el patrón clásico de desaparición debido a la sobrepesca; primero las especies más grandes, que empezaron a disminuir pronunciadamente antes de 1980, seguidas por el declive de las especies de talla media y finalmente las especies pequeñas. Además, las especies más longevas y con una maduración tardía fueron las que inicialmente disminuyeron más rápido.

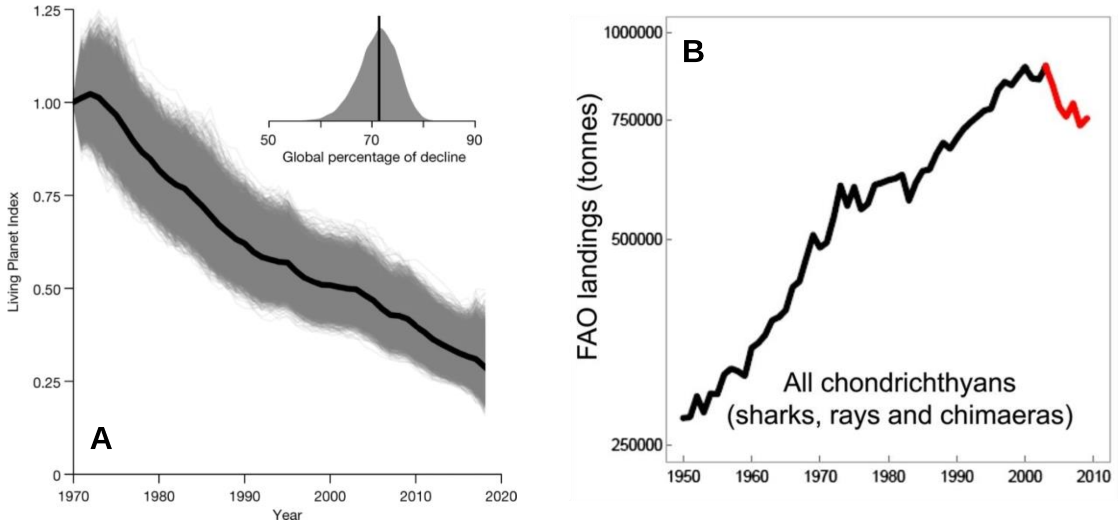


Figura 4. (A) Porcentaje de declive global de las distintas especies de tiburones oceánicos (n=31) entre 1970 y 2020. Figura adaptada de Pacoureau et al. (2021). (B) Desembarques de condrictios reportadas a la FAO desde 1950 hasta 2009. Se observa el pico en 2003 y el subsecuente declive. Figura adaptada de Dulvy et al. (2014).

Los tiburones suelen ser pescados incidentalmente, sobre todo en pesquerías enfocadas a peces teleósteos como el atún o el pez espada (Stevens et al., 2005). No obstante, a menudo se retienen y venden en todo el mundo debido al emergente valor de su carne, aletas, branquias y aceite de hígado (Clarke et al., 2006; Jabado et al., 2015; Cardeñosa et al., 2017; Steinke et al., 2017; Ferretti et al., 2020; Pincinato et al., 2022). Según datos de la Organización de las Naciones Unidas para la Alimentación y la Agricultura (FAO), los desembarques de tiburones y rayas se incrementaron hasta llegar a su pico en 2003 y han disminuido un 20% desde entonces (Fig. 4b) (Dulvy et al., 2014). A principios de los 2000, se llegaron a capturar entre 63 y 273 millones de tiburones en el mundo (Pacoureau et al., 2021).

La desaparición de los tiburones tiene un agravante para el ecosistema marino. Desde un punto de vista ecológico, los escualos tienden a ocupar los niveles intermedios y más altos de las redes tróficas (Myers et al., 2007; Frisch et al., 2016), siendo considerados los primeros como "mesodepredadores" y los segundos como "depredadores apicales". Como tales, ejercen un control sobre niveles tróficos inferiores a través del consumo de presas o la modificación del comportamiento de éstas (Bascompte et al., 2005; Ferretti et al., 2010). Aunque en ecosistemas tropicales no esté tan claro (Roff et al., 2016), se ha demostrado que la pérdida de tiburones en ecosistemas templados puede originar cambios drásticos en la abundancia de otras especies (efecto “cascada trófica”) (Myers et al., 2007; Ferretti et al., 2010), aumentando el riesgo de degradación del ecosistema.

1.2 Prioridades y retos de la conservación de los tiburones.

Aunque el conocimiento de las distintas especies de tiburones es cada vez mayor, aún queda mucho trabajo de investigación por delante. Por ejemplo, identificar los factores claves que inciden en el riesgo de extinción de las especies es de vital importancia si se quieren desarrollar medidas de conservación eficientes. En varios grupos taxonómicos, el riesgo de extinción es el resultado de la interacción entre un factor extrínseco o amenaza y las características vitales y ecológicas de una determinada especie o grupo taxonómico (Dulvy et al., 2014). En un estudio reciente sobre el estado de conservación de tiburones y rayas en el Mediterráneo y el Atlántico Nororiental, Walls & Dulvy (2020) determinaron que, frente a la amenaza de la sobrepesca (factor extrínseco), el tamaño corporal es un rasgo predictivo esencial del estatus de amenaza de la especie (presumiblemente debido a la baja tasa de crecimiento poblacional asociada). En el Atlántico Nororiental, una especie de tiburón de 3 metros de longitud tiene un 73% de probabilidades de aparecer como “Amenazado” en la Lista Roja de la UICN, mientras que esa probabilidad en el Mediterráneo es de un 86% debido a una mayor exposición a la pesca. Así mismo, especies que habitan profundidades menores son más susceptibles a ser pescadas y por lo tanto a estar amenazadas que no especies que viven en aguas profundas (Walls & Dulvy, 2020).

La mejora del conocimiento sobre como interaccionan estas y otras variables con factores extrínsecos como pueden ser la sobrepesca o la pérdida de hábitat es tan recomendable como necesaria. No obstante, esto es solo posible si se posee suficiente información de cada especie. En ese mismo estudio de Walls & Dulvy (2020), 24 de las 67 especies de tiburón del Atlántico Nororiental y 11 de las 40 especies del Mediterráneo, respectivamente, aparecían como "Información Insuficiente" en la Lista Roja de la UICN. Globalmente, el total asciende a 71 de las 536 especies de tiburón que aparecen en la versión más actualizada del listado (Dulvy et al., 2021). A pesar de que muchas presenten un riesgo elevado de extinción, las especies con datos deficientes suelen ser excluidas de las prioridades globales y locales de conservación (Bland et al., 2017). Es por lo tanto importante trabajar con esas especies de las que no disponemos de suficiente información para poder comprender mejor como enfocar los futuros esfuerzos de conservación.

Revertir el declive poblacional de los tiburones es posible si se aplica una gestión de carácter preventivo basada en la ciencia (Peterson et al., 2017; Simpfendorfer & Dulvy, 2017). En un mundo de financiamiento limitado, a pesar de todo, las prioridades para a conservación a menudo se basan en la inmediatez de la extinción, el valor de la biodiversidad o la oportunidad de conservación (Marris, 2007). La Lista Roja de la UICN representa un buen punto de apoyo para guiar las prioridades de conservación de países que disponen de una capacidad limitada para evaluar, gestionar y conservar especies (Pacoureau et al., 2021). Especies globalmente categorizadas como "Casi Amenazadas" o "Vulnerables" podrían soportar aún niveles modestos de presión pesquera si existe una gestión inmediata y concienzuda (Dulvy et al., 2014), mientras que la pesca sostenible de las especies amenazadas no sería ya posible. En su lugar, deberían aplicarse políticas basadas en evaluaciones de los *stocks* o del estatus asignado por la Lista Roja (Peterson et al., 2017). Medidas estrictas como la prohibición de desembarques de las especies amenazadas o la minimización de la mortalidad derivada de la captura accidental son esenciales para frenar el declive y facilitar la recuperación de sus poblaciones de tiburones globalmente (Pacoureau et al., 2021).

Paralelamente, la protección efectiva de los tiburones también radica en censurar y actuar contundentemente ante las prácticas furtivas que tengan lugar en cualquier lugar del mundo, como en el caso del aleteo (*finning*, en inglés). El aleteo, entendido como la actividad de cortar las aletas del tiburón y el posterior arrojo de su cuerpo al mar (no confundir con el procesamiento abordo regulado, el cual puede incluir el corte de aletas a bordo de la embarcación, pero no incluye el descarte del cuerpo (Passantino, 2014)) está globalmente censurado, mientras que el comercio regulado de aletas de tiburón sí es legal en algunos países y también en la UE y los EE. UU.

A pesar de llevar más de dos décadas elevando la concienciación de que los tiburones están en declive, no existe aún un mecanismo global para garantizar el financiamiento, la implementación y el cumplimiento de los planes de gestión pesquera que permitirían la recuperación de las poblaciones hasta niveles en los que nunca más estarían amenazadas (Lack & Sant, 2009; Techera & Klein, 2011). El hecho de que el rango de distribución de muchas especies de tiburones sea muy amplio también dificulta una buena gestión internacional, ya que dichas especies se distribuyen a lo largo y ancho de varias Zonas Económicas Exclusivas (ZEEs en inglés), complicando el desarrollo de medidas de gestión coherentes y efectivas (Dulvy et al., 2014).

La mayoría de gobiernos no disponen a día de hoy de los recursos, experiencia y voluntad política necesaria para conservar de forma efectiva la gran mayoría de tiburones y rayas (Veitch et al., 2012). En cuanto a los diferentes tratados internacionales destinados a la conservación y comercio de la biodiversidad (Ley de la Convención Marítima del 1982, CMS, CITES, Convención de Barcelona, etc.) la realidad demuestra dos cosas; que la gran mayoría de especies de tiburón que se encuentran listadas en los anexos de dichos tratados no cuenta aún con una protección legal efectiva (Dulvy et al., 2014, Lawson & Fordham, 2018; Mancusi et al., 2020) y que el número de especies listadas en aquellos anexos que impiden o regulan el comercio de algunos de los tratados (sobre todo CITES o CMS) es todavía bajo (Fowler et al., 2021). Muchos tiburones podrían ya aparecer en los listados de tratados como CITES, CMS y varias convenciones marítimas regionales y su protección debería ser formalmente considerada como complemento de los planes de gestión elaborados por las distintas Organizaciones Regionales de Pesca (ORPs) (Dulvy et al., 2014).

En la actualidad, existe también un déficit en cuanto a la calidad de la información providente de los desembarques de las capturas de tiburones. Por ejemplo, la identificación y posterior etiquetación de la especie descargada es a veces confusa o incorrecta (Bornatowski et al., 2014; Pazartzi et al., 2019). En la mayoría de registros de captura, las diferentes especies de tiburones aparecen agrupadas, lo que dificulta determinar la presión de pesca que se ejerce sobre una cierta especie (García Núñez, 2008). Los diferentes códigos de aduanas utilizados por los diferentes países dificultan el rastreo de los volúmenes de comercio y también pueden generar imprecisiones en el registro de información. Además, la información compilada sobre los *stocks* transfronterizos puede no ser adecuada si no existe una buena coordinación internacional (García Núñez, 2008). Estos problemas son atribuibles tanto a países en desarrollo que no disponen de planes de gestión pesquera apropiados como a los países del primer mundo (Jacquet & Pauly, 2008; Bornatowski et al., 2013). Toda información recolectada sobre los registros de capturas de tiburones, si cuenta con una buena resolución taxonómica, puede usarse para ayudar a desarrollar medidas de conservación y gestión específicas para los problemas de cada especie (Dulvy et al., 2014). Es por lo tanto necesario que los gobiernos se encarguen también de facilitar una óptima (y sencilla) recopilación de datos de las capturas de tiburones que ocurren en cada país.

2. La pesca en el Mediterráneo.

2.1 Definición y evolución tras la Segunda Guerra Mundial.

El término pesca es usado para designar la actividad que realiza el hombre para capturar peces y otros organismos que viven en el medio acuático (Gazo et al., 1995). Desde los inicios de la humanidad, los peces y otros organismos acuáticos han jugado un papel importante como alimento, pero también como fuente de materiales para la vivienda, ropa, herramientas, etc. En la actualidad, aproximadamente 15 millones de personas de todas las partes del mundo están involucradas en la pesca profesional y el número de personas que dependen indirectamente de este sector es mucho mayor (Sahrhage, & Lundbeck, 2012).

Desde un punto de vista histórico, la pesca se revolucionó con el final de la Segunda Guerra Mundial. La población mundial se recuperó y creció notablemente, lo que conllevó un incremento en el uso de los recursos. Costanza et al. (2007) bautizaron este período (1945-1975) como la “Gran Aceleración”. Es durante este período cuando surgen las pesquerías industriales (Ferretti et al., 2010). En los años 1950 aparece por primera vez el palangre pelágico japonés, destinado a la pesca del atún, que acabó convirtiéndose en el arte de pesca más extendido de todos (Myers & Worm, 2003). Con su expansión aumentaron las capturas de elasmobranquios. A pesar de no disponer de un registro de capturas incidentales durante las primeras décadas después de la aparición del palangre pelágico, Myers & Worm utilizaron el porcentaje de atunes dañados por tiburones como una aproximación de la abundancia de tiburones oceánicos. La evolución de estos valores a lo largo de los años mostró una continua disminución del porcentaje de atunes dañados, hecho que coincide con el declive global en la abundancia de tiburones. A finales de los años 80 y 90, los ya por entonces existentes registros de capturas de tiburones en el Atlántico Noroccidental procedentes de la flota palangrera de los EE. UU. mostraron una disminución en abundancia superior al 70% en la mayoría de tiburones oceánicos (Baum et al., 2003). Las capturas incidentales de estos tiburones también aumentaron a partir de los años 50 debido a la aparición de las redes de deriva, trasmallos modificados capaces de extenderse hasta 50-60 quilómetros y de capturar mayor cantidad de organismos marinos de diferentes tamaños y especies que los trasmallos tradicionales (Richards, 1994).

La intensificación de la pesca también tuvo lugar en las zonas costeras. En el Golfo de Tailandia, por ejemplo, desaparecieron el 60% de los tiburones durante los primeros 5 años de industrialización de la pesca de arrastre (Myers & Worm, 2003) y los datos obtenidos por la flota de palangre pelágico analizados en el estudio de Baum et al. (2003) décadas más tarde constataron disminuciones de entre un 49 y un 89% de la abundancia de tiburones costeros. Tanto los barcos de arrastre como los de palangre pelágico no sólo se volvieron más rápidos y grandes durante la “Gran Aceleración”, sino que también contaban con nuevas tecnologías de posicionamiento, comunicación y búsqueda de peces y eso les ayudó a encontrar y capturar más pescado (Holm, 2012). En consecuencia, la presión en los *stocks* pesqueros se incrementó. Tanto se incrementó que, en el caso de los grandes peces depredadores, se estima que su biomasa habría disminuido hasta un 90% con respeto a la existente en tiempos preindustriales (Myers & Worm, 2003).

La “Gran Aceleración” también se evidenció en el Mediterráneo, donde la abundancia de muchos tiburones disminuyó drásticamente, especialmente las especies de talla grande (Ferretti et al., 2008). En el estudio de Ferretti et al. (2008) llevado a cabo en el Mediterráneo Noroccidental se pueden encontrar algunos casos excepcionales, como el de los tiburones martillo (*Spyrhna* spp.). El último registro de captura o avistamiento de tiburón martillo en aguas costeras se remonta al 1963, mientras que, en aguas pelágicas, las capturas en palangre en 1978 ya eran extremadamente bajas e inexistentes después del 1995. En el Mediterráneo, además del impacto del palangre pelágico sobre las poblaciones de tiburones, el impacto de las redes de arrastre es también considerable, pues las capturas de muchos tiburones en este arte han disminuido considerablemente durante el último siglo (Maynou et al., 2011; Colloca et al., 2020) y muchas especies de elasmobranquios han desaparecido en distintas partes de la cuenca (Ferretti et al., 2010). La pesca de grandes especies pelágicas usando redes de deriva quedó totalmente ilegalizada en enero de 2002 (Tudela et al., 2005).

2.2 Características de la flota pesquera en el Mediterráneo en la actualidad.

En agosto de 2022, la FAO cifró en 78928 el total de embarcaciones que aparecen en el registro pesquero de la Comisión General de Pesca del Mediterráneo (GFCM). Turquía, Grecia e Italia son los países con más embarcaciones de pesca, todos con un número superior a 10.000. España cuenta con un total de 2.344 embarcaciones, que representan el 3% del total de embarcaciones registradas en el Mediterráneo.

Existe una gran variedad de artes de pesca, que se clasifican según la estrategia de pesca utilizada, distinguiéndose a grandes rasgos los que capturan pescado de forma pasiva y los que capturan pescado activamente. Sorprendentemente, los artes de pesca no han cambiado demasiado a lo largo de los años. La mayoría de ellos (sedales y anzuelos, trasmallos, nasas y trampas, redes fijas y arrastradas) están basados en formas primigenias de distintos instrumentos, pero su eficacia se ha ido incrementando a lo largo del tiempo a medida que la experiencia de los pescadores iba en aumento (Sahrhage, & Lundbeck, 2012). Según la última actualización del informe SoMFi de la FAO, los artes de cerco y arrastre pelágico fueron, conjuntamente, los artes de pesca que más capturas desembarcaron en el Mediterráneo entre 2018 y 2020 (un 48,3% del total de desembarques), seguidos del arrastre de fondo y el arrastre de vara (25,3%) (FAO, 2022a). Solo un 18,5% de las capturas desembarcadas correspondió a las embarcaciones artesanales, a pesar de representar el 81,7% del total de la flota del Mediterráneo.

La tendencia del número de total de capturas pesqueras en el Mediterráneo ha ido oscilando desde 1970 hasta 2020, siendo la producción en 2020 (674 mil toneladas) similar a la del 1970 (613 mil toneladas) pero mucho menor que la del 1994 (1.087 mil toneladas) según datos de la FAO (www.fao.org/gfcm/data/capture-production/ar/). El país que más contribuye a la producción pesquera (total de capturas) en el Mediterráneo es Italia (21%), seguido por Túnez (12,9%) y Argelia (12,8%). España se encuentra en quinta posición (9,5%) (FAO, 2022a). El principal grupo de especies capturadas en el Mediterráneo entre 2018 y 2020 fue el de arengue, sardina (la especie más pescada) y anchoa, que tuvo una contribución relativa del 43,6% al total de desembarques, mucho mayor que la del segundo grupo principal de especies capturadas, compuesto por los peces costeros (15%). El grupo formado por tiburones, rayas y quimeras representó un total del 1,7% del total de capturas desembarcadas.

Lógicamente, la extracción de recursos de cualquier medio genera un impacto sobre este. En 2017, menos del 40% de los *stocks* pesqueros del Mediterráneo se encontraban explotados a un nivel sostenible (FAO, 2020) Este porcentaje era menor que el de cualquier otra región del mundo analizada, convirtiendo al Mediterráneo en el mar más sobreexplotado del mundo. En la última actualización del estado de las pesquerías mundiales, los datos de la FAO muestran que el porcentaje de stocks sobreexplotados del Mediterráneo (63,4%) fue inferior al del Pacífico suroriental (66,7%) en 2019 pero, aunque se ha detectado una leve disminución de la sobrepesca, los recursos pesqueros siguen estando altamente estresados (FAO, 2022c). Además, la captura incidental de especies y los descartes continúan siendo un problema añadido a la sobreexplotación de los recursos y ponen en peligro la conservación de varios grupos de animales marinos, incluyendo mamíferos, aves, tortugas y elasmobranquios.

2.3 El Mediterráneo, hogar de una gran diversidad de tiburones.

Descrito como uno de los lugares más ricos del planeta en cuanto a diversidad faunística y florística (Cuttelod et al., 2008), el Mediterráneo es también considerado un punto caliente de diversidad de tiburones (Dulvy et al., 2014). No en vano, alberga alrededor de 49 especies diferentes pertenecientes a 17 familias (Bradai et al., 2018).

A nivel biológico, existen similitudes y también diferencias entre estas especies. Por ejemplo, en cuanto a su estrategia de obtención de alimento, la gran mayoría de los tiburones son depredadores, a excepción de especies zooplanctónicas, como el tiburón peregrino (*Cetorhinus maximus*). En cambio, los tiburones muestran una gran variedad de modos de reproducción; así, encontramos especies ovíparas como la pintarroja (*Scyliorhinus canicula*) o el alitán (*Scyliorhinus stellaris*); ovovivíparas, como la mielga (*Squalus acanthias*) o el marrajo sardinero (*Lamna nasus),* y vivíparas, como el tiburón arenero (*Carcharhinus obscurus*) o la tintorera (*Prionace glauca*) (Serena, 2005). Los tiburones también presentan distintos tamaños, desde especies de talla pequeña como la pintarroja o la pintarroja bocanegra (*Galeus melastomus*), pasando por especies de talla media como la musola (*Mustelus mustelus*) o el cazón (*Galeorhinus galeus*), hasta especies de talla grande, como el tiburón blanco (*Carcharodon carcharias*) o el tiburón peregrino (*Cetorhinus maximus*).

A nivel ecológico, también existen similitudes y diferencias entre especies. En general, las especies tienen una estrategia vital K, mientras que el uso del hábitat difiere entre especies. Así, tiburones como la tintorera (*Prionace glauca*) o el marrajo dientuso (*Isurus oxyrinchus*) se encuentran en la parte superior de la columna de agua y en aguas tanto costeras como oceánicas, mientras que otros tiburones habitan en aguas mucho más profundas. Este es el caso de la cañabota gris (*Hexanchus griseus*), una especie que ha sido parte importante de la presente tesis. Además, no todos los tiburones presentes en el Mediterráneo ejercen el mismo rol ecológico (Albo-Puigserver et al., 2015; Barría, Coll & Navarro, 2015).

2.4 El impacto de la pesca sobre los tiburones en el Mediterráneo.

La continua explotación durante siglos junto con la reciente intensificación pesquera ha llevado a las poblaciones de muchas especies de tiburones al desplome (Cashion et al., 2019), especialmente las poblaciones de tiburones de mayor talla (Ferretti et al., 2008). No en vano, 39 de las 73 especies de condrictios del Mediterráneo evaluadas en la Lista Roja de la UICN se encuentran amenazadas principalmente por la sobrepesca (Dulvy et al., 2016). De esas 39 especies, 23 son tiburones.

En un estudio reciente, Walls & Dulvy (2021) estimaron que el riesgo de extinción de los tiburones en el Mediterráneo y el Atlántico Nororiental era más alto que el de cualquier otro grupo de vertebrados evaluado en la Lista Roja de la UICN y, además, ese riesgo de extinción era mayor en el Mediterráneo que en resto del mundo (Fig. 5). A pesar de la amenaza que supone el Mediterráneo para los tiburones, hasta ahora no se han llevado a cabo suficientes medidas para revertir su declive poblacional, a diferencia del Atlántico Nororiental (Fernandes et al., 2017).

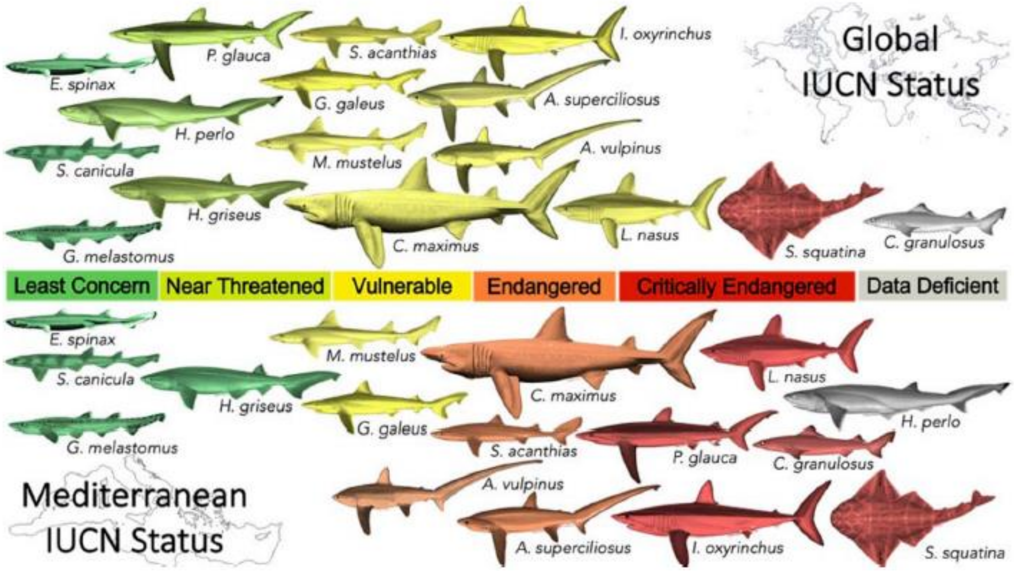


Figura 5. Estados de la lista Roja de la UICN global vs regional (Mar Mediterráneo) de 16 especies de tiburones registradas por la FAO en desembarques realizados en países del Mediterráneo desde 1950 hasta 2014. El riesgo de extinción de al menos la mitad de estas especies es mayor en el Mediterráneo que a nivel global. Figura adaptada de Cashion et al. (2019).

El declive de las poblaciones de tiburones ha comportado también un declive en sus desembarques. No obstante, el esfuerzo pesquero, en general, se ha incrementado (Bradai et al., 2018). Entre 1993 y 1994, el total de capturas de elasmobranquios en el Mediterráneo fue de 20.000 toneladas, frente a las aproximadamente 13.000 que se registran desde el 2014 (FAO, 2022b).

A partir del 2008, Libia y Túnez se convirtieron en los países del Mediterráneo que más tiburones pescan, contribuyendo con más del 70% del total de la producción en todo el Mediterráneo (Bradai et al., 2018). Italia y Turquía eran los países donde se capturaban más tiburones desde 1980 hasta 2008, pero desde 2008 se ha producido un descenso importante en el volumen de capturas de tiburones en los dos países. Los principales órdenes de tiburones capturados hasta 2015 fueron los Carchariniformes y los Squaliformes. Mientras que los desembarques de Squaliformes han ido disminuyendo ligeramente desde finales de los 80, los desembarques de Carchariniformes han disminuido notablemente (Fig. 6).

Si bien es cierto que artes de pesca menores como los trasmallos capturan tiburones incidentalmente (Dudley & Simpfendorfer, 2006; Saidi et al., 2016), al igual que artes puramente pelágicos como el cerco (Gilman 2011; Swimmer et al., 2020), los artes de pesca que representan la principal amenaza para los tiburones son el arrastre y el palangre (Molina & Cooke, 2012; Oliver et al., 2015), que representaron el 35 y el 38% del total de capturas de tiburones en el Mediterráneo desde 2020 hasta 2022 (FAO, 2022a). El palangre pelágico ha sido, precisamente, el gran responsable del marcado declive de los tiburones pelágicos de talla grande en el Mediterráneo (Ferretti et al, 2008).

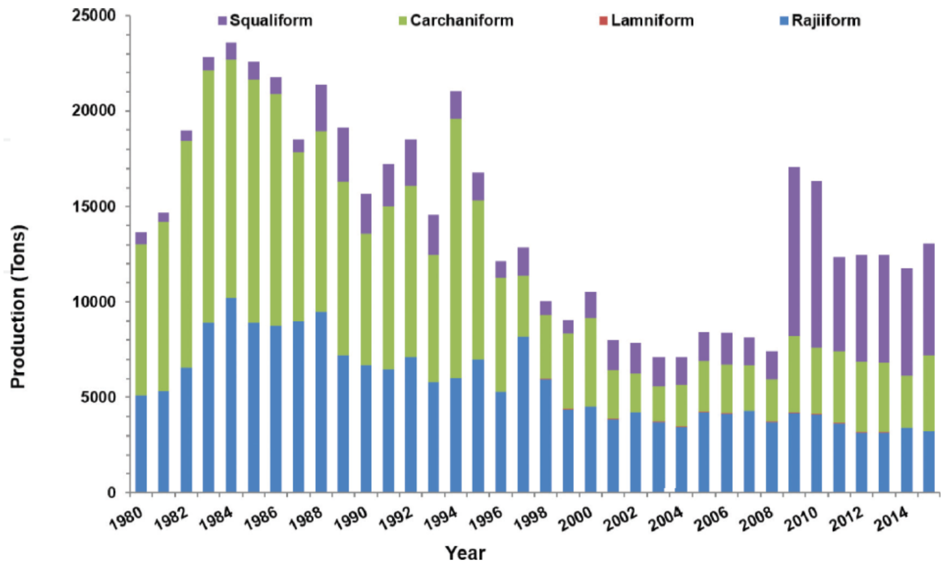


Figura 6. Evolución de los desembarques de algunos grupos de elasmobranquios en el Mediterráneo entre 1980 y 2015. Figura adaptada de Bradai et al. (2018).

Cada vez se dispone de más y mejor información sobre el estado actual de los tiburones del Mediterráneo, pero existe al mismo tiempo un sesgo de información en favor de las especies pelágicas. El principal motivo es que gran parte de la información recopilada sobre los tiburones en el Mediterráneo, sobre todo durante la primera década de los 2000, proviene de las capturas incidentales ocurridas durante la pesca de pez espada o atún por parte de la flota palangrera (Mejuto et al., 2002,2009; Megalofonou, 2005; Ferretti et al., 2008). Estas capturas incidentales están principalmente representadas por la tintorera y, en menor medida, el marrajo dientuso y el tiburón zorro. Gracias a estudios como los anteriormente citados, de estos tiburones conocemos en qué zonas del Mediterráneo y durante qué meses son más abundantes sus capturas, la frecuencia de distribución de tallas, su tendencia poblacional a lo largo de las últimas décadas o incluso el estado en que se encuentran cuando son subidos a bordo de la embarcación. En cambio, el conocimiento sobre algunos tiburones demersales es aún prematuro, sobre todo en el caso de especies de talla grande como la cañabota gris (*Hexanchus griseus*), si bien es cierto que el número de estudios sobre aspectos biológicos y ecológicos de los tiburones demersales del Mediterráneo ha ido en augmento a lo largo de la última década (Ragonese et al., 2013; Navarro et al., 2014; Ramírez-Amaro et al., 2018; Ricci et al., 2021).

2.5 Descripción de las especies estudiadas en la presente tesis.

Los distintos capítulos de la tesis han puesto el foco sobre un total de 8 especies diferentes de tiburones. Estas se dividieron en dos grupos según su longitud total (TL); tres de ellas son tiburones de talla media (90-200 cm TL), mientras que las otras 5 son tiburones de talla grande (>200 cm TL). La talla total (TL) de maduración de la mielga en el Mediterráneo (~90 cm las hembras) (Capapé & Reynaud, 2011) fue usada en esta tesis como referencia para definir la longitud mínima de los tiburones de talla grande. La información aportada a continuación puede consultarse en el documento de la FAO "*Identification guide of vulnerable species incidentally caught in Mediterranean fisheries*" (Otero et al., 2019) y las fotografías en el "*Handbook of the marine fishes of Europe and adjacent waters*" (Iglésias, 2014).

2.5.1. Tiburones de talla media:

- Mielga (*Squalus acanthias*)

Perteneciente a la familia Squalidae. Especie demersal de la plataforma continental y el talud. Puede llegar a alcanzar los 200 cm de longitud total. En el Mediterráneo, figura en el listado de especies del Anexo III del Protocolo SPA/BD. “En Peligro” según la UICN. Capturado incidentalmente sobre todo por artes de arrastre y palangre de fondo.

- Musolas (*Mustelus* spp.)

Género perteneciente a la familia Triakidae. Especies bentónicas, propias de la plataforma continental. Pueden llegar a alcanzar 200 cm de longitud total. En el Mediterráneo, figuran en el listado de especies del Anexo III del Protocolo SPA/BD. “Vulnerable” según la UICN. Captura incidental en los artes de arrastre, trasmallos y palangres.

- Cazón (*Galeorhinus galeus*)

Perteneciente a la familia Triakidae. Especie bentopelágica nerítica. Puede llegar a alcanzar los 195 cm de longitud total. En el Mediterráneo, su pesca y retención está totalmente prohibida al figurar en el listado de especies del Anexo II del Protocolo SPA/BD. “Vulnerable” según la UICN. Capturado incidentalmente sobre todo en los artes de arrastre y palangre de fondo.

2.5.2. Tiburones de talla grande:

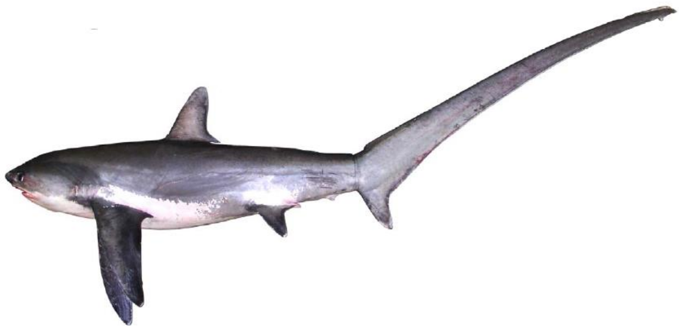
- Tintorera (*Prionace glauca*)

Perteneciente a la familia Carcharhinidae. Especie pelágica, de aguas oceánicas y neríticas. Puede llegar a alcanzar los 400 cm de longitud total. En el Mediterráneo, su captura y venta está permitida. “En Peligro Crítico” según la UICN. Principal captura incidental en los palangres pelágicos.

- Marrajo dientuso (*Isurus oxyrinchus*)

Perteneciente a la familia Lamnidae. Especie pelágica, de aguas oceánicas y neríticas. Puede llegar a alcanzar los 450 cm de longitud total. En el Mediterráneo, su pesca y retención está totalmente prohibida al figurar en el listado de especies del Anexo II del Protocolo SPA/BD. “En Peligro Crítico” según la UICN. Comúnmente capturado incidentalmente en los palangres pelágicos.

- Tiburón zorro (*Alopias vulpinus*)



Perteneciente a la familia Alopiidae. Especie epipelágica, de aguas oceánicas. Puede llegar a alcanzar los 600 cm de longitud total. En el Mediterráneo, su comercialización está prohibida al figurar en el Anexo II de CITES. Figura en el listado de especies del Anexo III del Protocolo SPA/BD. “En Peligro” según la UICN. Capturado incidentalmente sobre todo en palangres pelágicos.

- Cañabota gris (*Hexanchus griseus*)

Perteneciente a la familia Hexanchidae. Especie bentónica, propia del talud continental. Puede llegar a alcanzar los 500 cm de longitud total. En el Mediterráneo, su captura y venta está en general permitida, aunque carece de valor comercial y suele ser descartada. "Preocupación Menor" según la UICN. Principal tiburón de talla grande capturado incidentalmente en el arte del arrastre y, en menor medida, palangres de fondo y trasmallos.

- Tiburón peregrino (*Cetorhinus maximus*)

Perteneciente a la familia Cetorhinidae. Especie epipelágica, de aguas oceánicas. Puede llegar a alcanzar los 1000 cm de longitud total. En el Mediterráneo, su pesca y retención está totalmente prohibida al figurar tanto en el listado de especies del Anexo II del Protocolo SPA/BD como en el Anexo II de CITES. "En Peligro" según la UICN. A veces capturado incidentalmente, sobre todo por las redes de arrastre.

3. La colaboración con el sector pesquero. El Conocimiento Ecológico Local y sus beneficios.

Un método para recopilar información sobre la abundancia y la tendencia poblacional de determinadas especies es recurrir al Conocimiento Ecológico Local (LEK, por sus siglas en inglés) de las comunidades pesqueras locales, entendido como "el conocimiento, la práctica y las creencias acumuladas sobre la relación entre seres vivos (humanos incluidos) con el medio ambiente y que son transferidas culturalmente a las siguientes generaciones" (ver Berkes, Colding & Folke, 2000: p. 1252 para definición). El LEK ha demostrado ser una fuente de información de alta calidad y a bajo coste (Anadon et al., 2009) y numerosos estudios trabajando con pesquerías muestran que la combinación de evaluaciones científicas con LEK puede mejorar las decisiones de gestión (Garcia- Quijano, 2007; Silvano & Valbo-Jørgensen, 2008; Bender et al., 2014; Carothers et al., 2014).

El sistema más comunmente utilizado para obtener LEK son las entrevistas con los pescadores usando cuestionarios estructurados adaptados al propósito del estudio. La duración de cada entrevista es variable, pero ésta debe favorecer el intercambio de información, sobre todo por parte del entrevistado, que en este caso son los pescadores. A lo largo de la entrevista, el pescador responde a las preguntas predeterminadas que más adelante permitirán el análisis de las respuestas. En estudios sobre varias especies de tiburones, las entrevistas se pueden complementar con fotos de las especies objetivo para garantizar su correcta identificación. Cada vez son más numerosos los estudios que hacen acopio del LEK mediante entrevistas a pescadores usando este tipo de cuestionarios y en el Mediterráneo podemos encontrar varios ejemplos (Álvarez de Quevedo et al., 2010; Maynou et al., 2011; Colloca et al., 2020).

Aunque la información recopilada pueda a veces carecer de un alto rigor científico, ya sea porque los recuerdos de algunos sucesos se van difuminando a lo largo de las generaciones o porque la misma información puede no ser suficientemente fiable, el LEK ha resultado ser la única alternativa, por ejemplo, para detectar cambios en la abundancia de especies en un ecosistema (Sáenz-Arroyo et al., 2005; Taylor et al., 2011); obtener datos de especies que se encuentran en países o regiones con escasa información disponible (Peñaherrera-Palma et al., 2018; Almojil, 2021; Leduc et al., 2021), siendo algunas de ellas especies amenazadas a escala global (Leeney & Poncelet, 2015; Haque et al., 2022); evaluar la importancia de ciertas especies para la subsistencia de comunidades locales en países subdesarrollados (Barbosa-Filho et al., 2019; Seidu et al., 2022) e incluso identificar áreas donde la presencia de tiburones no estaba documentada (Rasalato et al., 2010).

4. El análisis de la ecología trófica de los tiburones a través de los isótopos estables.

Tradicionalmente, la dieta de los tiburones ha sido descrita mediante el análisis del contenido estomacal (Ebert, 1994; Cortés, 1999; McCord & Campana 2003). No obstante, al igual que con otros peces depredadores grandes altamente móviles, el estudio del contenido estomacal presenta ciertas limitaciones. Por ejemplo, el número de muestras de individuos de todas las diferentes tallas suele ser insuficiente y el muestreo a lo largo del rango de distribución geográfico del animal suele ser incompleto (Hussey et al., 2011). Esta técnica requiere además la captura y sacrificio del ejemplar y la información dietaria obtenida está únicamente basada en las presas consumidas recientemente (Speed et al., 2012).

Estudios más recientes han optado por un método alternativo basado en el análisis de isótopos estables, principalmente de nitrógeno y carbono (Estrada et al., 2006, Hussey et al., 2011; Carlisle et al., 2012; Curnick et al., 2019). De forma natural, los tejidos de los animales están más enriquecidos en los isótopos pesados, tanto de nitrógeno (^{15}N) como de carbono (^{13}C), que sus presas (Borrell et al., 2011). Como resultado, la abundancia relativa del isótopo pesado de cada uno de dichos elementes aumenta con el nivel trófico (Peterson & Fry 1987; O'Reilly et al., 2002), siendo este incremento mayor en el caso del nitrógeno que en el del carbono. En el músculo de los tiburones, el $\delta^{15}N$ se incrementa ~2,3‰ con respeto a los valores de sus presas, mientras que el incremento de $\delta\ ^{13}C$ es de ~0,9‰ (Hussey et al., 2010a). Típicamente, los valores de $\delta^{15}N$ sirven para determinar el nivel trófico del individuo (Post, 2002; Pinnegar et al., 2002), mientras que los valores de $\delta\ ^{13}C$ sirven para identificar la fuente de materia orgánica que sustenta la red trófica a la que pertenece el consumidor (Peterson & Fry, 1987, DeNiro & Epstein, 1978).

Aunque el análisis de isótopos estables no permite obtener una elevada resolución taxonómica de los distintos grupos de presas consumidas, como sí ocurre en el análisis del contenido estomacal, permite inferir la dieta del animal a largo plazo (Estrada et al., 2003; Fisk et al., 2009), ya que la información obtenida refleja las presas asimiladas a lo largo del tiempo (no sólo ingeridas)

(Estrada et al., 2003; Speed et al., 2012). Además, este tipo de información puede obtenerse con un tamaño muestral mucho más bajo que en el análisis de contenido estomacal. Esto resulta especialmente útil si se trabaja con especies que raramente se capturan (Fisk et al., 2002; Moura et al., 2015) o en las que el porcentaje de estómagos muestreados vacíos puede ser elevado, como en el caso de los tiburones (Cortés & Gruber, 1990; McCord & Campana, 2003; Pethybridge et al., 2011). Finalmente, ciertos tejidos muestreados para el análisis de isótopos estables, como el músculo, pueden obtenerse fácilmente mediante biopsias sin necesidad de causar daño al individuo (Matich et al., 2010), hecho importante si se trabaja con especies amenazadas. Es debido a todas estas características que el análisis de isótopos estables para el estudio de la biología y ecología de los elasmobranquios se ha ido incrementando a lo largo de los últimos tiempos.

No obstante, esta técnica también presenta ciertas limitaciones; el enriquecimiento trófico es variable entre los tipos de tejido muestreado (MacNeil et al., 2005, 2006) e incluso entre individuos de la misma especie (DeNiro & Epstein, 1981). Además, el análisis de isótopos estables depende en gran medida de una referencia isotópica basal fiable (Cabana & Rasmussen, 1996), que puede variar estacional y espacialmente (Popp et al., 2007). Por otra parte, los modelos de mezcla isotópicos precisan de factores de discriminación tróficos específicos, los cuales representan la diferencia entre la composición isotópica de un consumidor y su dieta, para la especie de estudio y el tejido muestreado (Hussey et al., 2010a). En tiburones, el conocimiento sobre los factores de discriminación tróficos es aún pobre (Hussey et al., 2010b) y algunos estudios han empleado el uso factores de discriminación de peces teleósteos para examinar la dieta de los elasmobranquios (Logan & Lutcavage, 2010). El uso de un factor de discriminación inapropiado puede generar una predicción errónea del porcentaje de contribución de las presas a la dieta del consumidor, como constataron Hussey et al. (2010b).

Finalmente, la detección de cambios isotópicos durante períodos de tiempo cortos (meses o estaciones) también resulta difícil en el caso de los tiburones, ya que una renovación isotópica completa en un tejido como el músculo puede tardar más de 400 días en tiburones de talla grande (MacNeil et al., 2006; Hussey et al., 2010b). Esto conlleva que, en el caso de especies que llevan a cabo migraciones a gran escala, los valores isotópicos obtenidos en el momento del muestreo pueden reflejar la composición isotópica de otras fuentes orgánicas con diferente señal isotópica.

OBJETIVOS

A fin de mejorar y ampliar el conocimiento actual de los tiburones en el Mediterráneo, la presente tesis doctoral tuvo dos objetivos principales; el primero consistió en determinar el estado poblacional de los tiburones de talla media y grande en la Costa Brava (Mediterráneo Noroccidental), mientras que el segundo objetivo consistió en examinar el nicho isotópico de los tiburones de talla media y grande presentes en el Mediterráneo Noroccidental. Posteriormente, el primer objetivo se amplió y derivó en análisis del estado actual de una de las especies estudiadas en la Costa Brava, la cañabota gris, en distintos países del Mediterráneo.

En este contexto, la tesis se ha dividido en 3 capítulos, cada uno con sus objetivos:

- En el **capítulo 1**, el objetivo principal consiste en conocer el estado poblacional de las especies de tiburones de talla media y grande presentes en la Costa Brava a través del LEK recopilado mediante entrevistas a pescadores.
- En el **capítulo 2**, el objetivo principal es caracterizar el nicho isotópico que ocupan cuatro especies de tiburones de talla grande (*Alopias vulpinus, Hexanchus griseus, Isurus oxyrinchus y Prionace glauca*) y dos de talla media (*Galeorhinus galeus y Squalus acanthias*) en el Mar Catalán y el sur del Golfo de León (Mediterráneo Noroccidental) mediante el análisis de isótopos estables.
- En el **capítulo 3**, el objetivo principal consiste en usar el LEK para recopilar información sobre el estado poblacional de la cañabota gris (*Hexanchus griseus*), un tiburón de profundidad de gran tamaño y hábitos bentónicos, en la cuenca del Mediterráneo.

Los capítulos 1 y 3 se encuentran ya publicados en revistas científicas con revisión por pares (*Aquatic Conservation: Marine and Freshwater Ecosystems* y *Marine Policy*, respectivamente) y el capítulo 2 se encuentra en proceso de revisión. La estructura y organización de la tesis se presenta en la Figura 7.

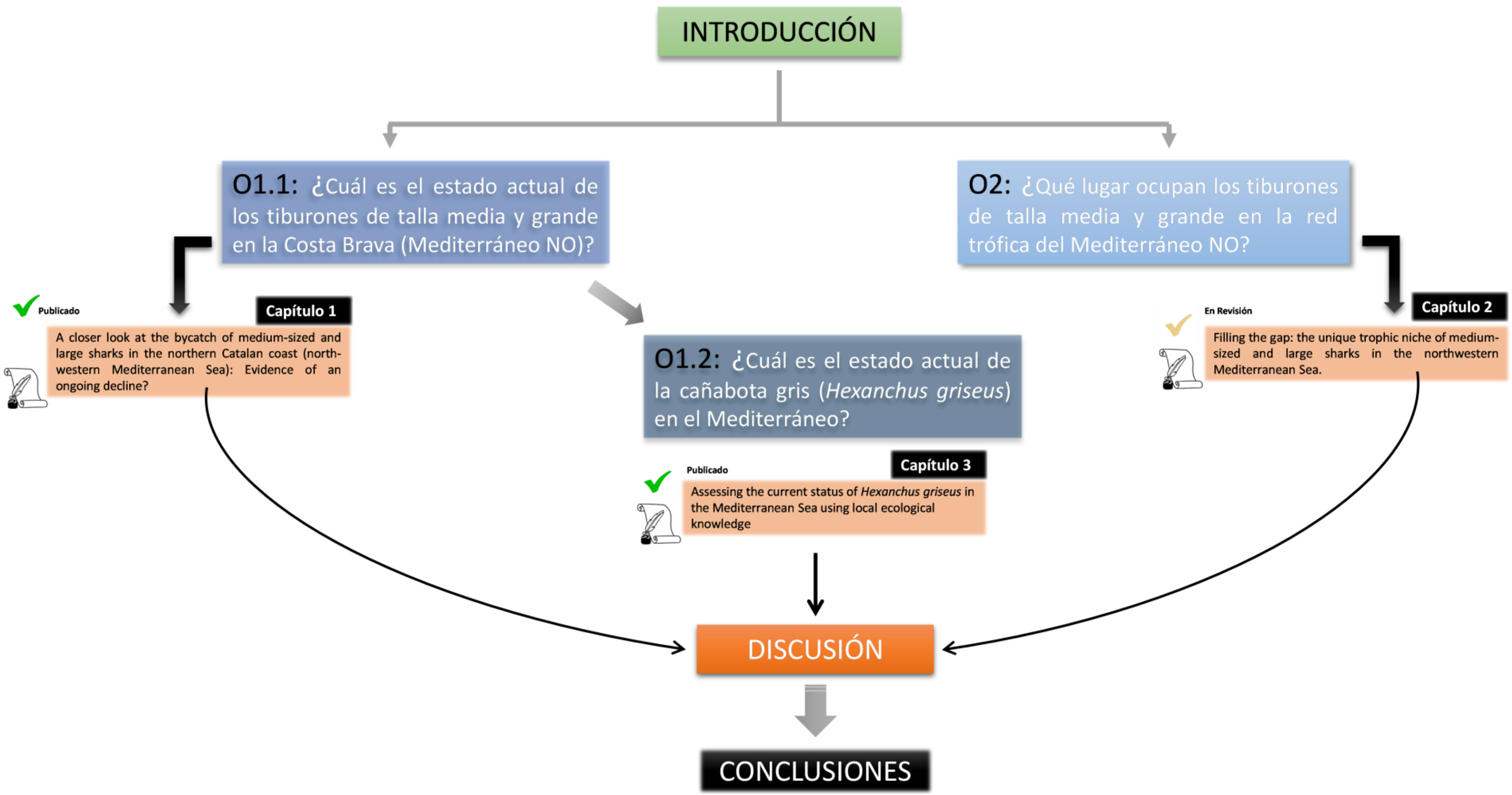


Figura 7. Esquema general de la tesis con los dos objetivos (O) y la organización de los capítulos.

INFORME DE LOS DIRECTORES DE TESIS

Los directores Dr. Manel Gazo Pérez y Dr. Luis Cardona Pascual certifican que la presente tesis doctoral, titulada “Impacto de la pesca y ecología trófica de los tiburones de talla media y grande en el Mediterráneo”, ha sido llevada a cabo por Ignasi Nuez Rodriguez. A continuación, se detalla la contribución que ha realizado el doctorando en cada uno de los tres artículos que componen su tesis, así como las revistas en las que se han publicado y su factor de impacto.

Capítulo 1 “*A closer look at the bycatch of medium-sized and large sharks in the northern Catalan coast (north-western Mediterranean Sea): Evidence of an ongoing decline?*”. 2021. **Nuez, I.**, Gazo, M., & Cardona, L. (2021). A closer look at the bycatch of medium-sized and large sharks in the northern Catalan coast (north-western Mediterranean Sea): Evidence of an ongoing decline? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(9), 2369-2380.

Contribución del doctorando: Contribución al proceso de diseño experimental, realización de encuestas, análisis estadísticos, participación en la interpretación de resultados, redacción del manuscrito original.

El artículo está publicado en la revista *Aquatic Conservation: Marine and Freshwater Ecosystems*, que tiene un Factor de Impacto de 3.258 (2021). La revista se sitúa en la posición 19 / 113 (Q1) en el área de *Marine and Freshwater Biology*.

Capítulo 2 “*Filling the gap: the unique trophic niche of medium-sized and large sharks in the northwestern Mediterranean Sea*.” 2023. Under Review.

Contribución del doctorando: Contribución al proceso de diseño experimental, toma de muestras, realización de los análisis de laboratorio, los análisis estadísticos, participación en la interpretación de resultados, redacción del manuscrito original.

Capítulo 3 “*Assessing the current status of Hexanchus griseus in the Mediterranean Sea using local ecological knowledge*”. 2022. **Nuez, I.**, Giovos, I., Tiralongo, F., Penadés-Suay, J., Cetkovic, I., Di Lorenzo, M., ... & Gazo, M. (2023). Assessing the current status of Hexanchus griseus in the Mediterranean Sea using local ecological knowledge. *Marine Policy*, *147*, 105378.

Contribución del doctorando: Contribución al proceso de diseño experimental. Coordinación de las encuestas, los análisis estadísticos, participación en la interpretación de resultados, redacción del manuscrito original.

El artículo está publicado en la revista *Marine Policy*, que tiene un Factor de Impacto de 4.315 (2021). La revista se sitúa en la posición 16 / 234 (Q1) en el área de *Aquatic Science*, 35 / 228 (Q1) en el área de *Environmental Science* y 50 / 376 (Q1) en el área de *Management, Monitoring, Policy & Law*.

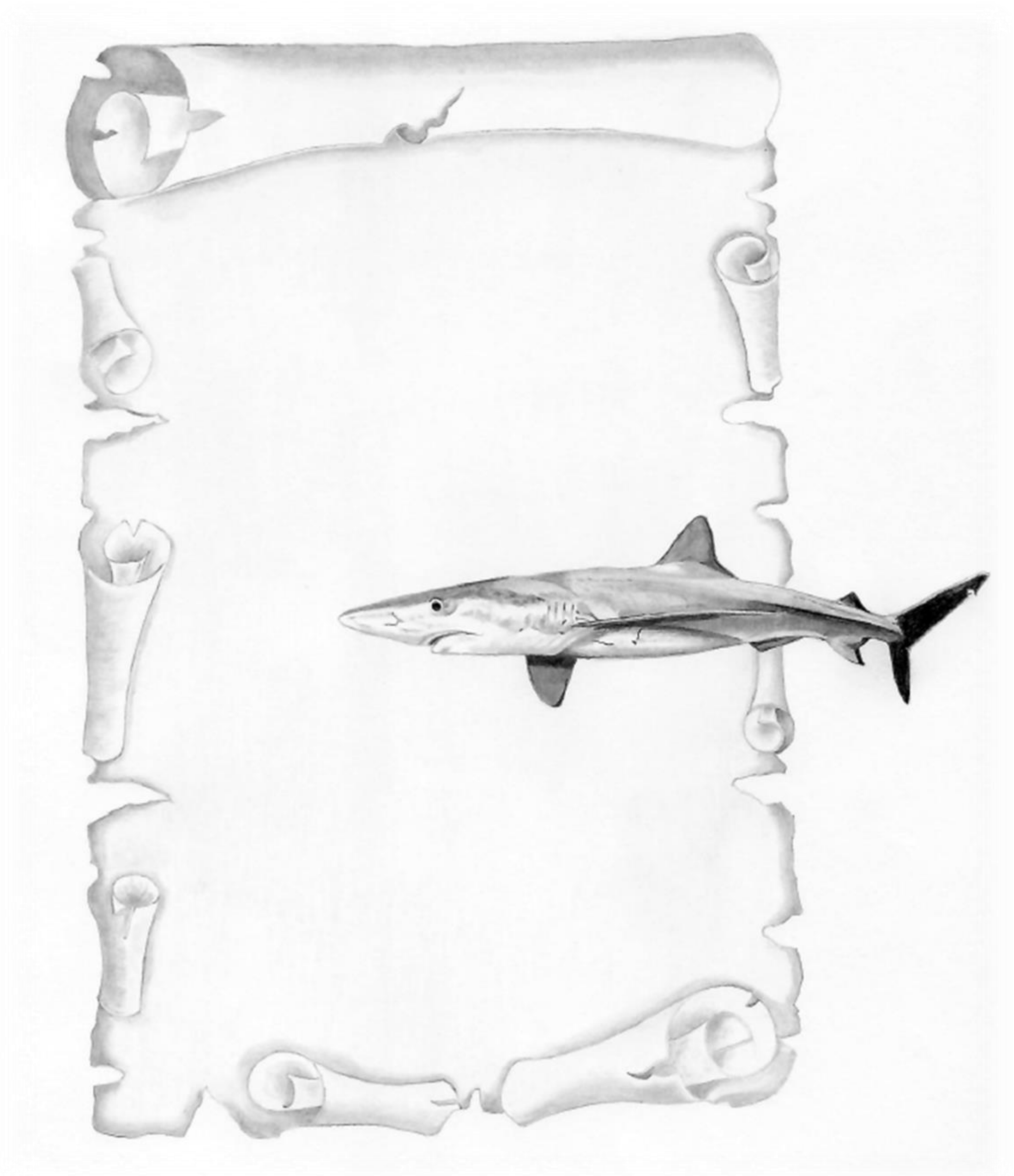
Barcelona, abril de 2023,

Firma de los directores:

Manel Gazo Pérez

Luis Cardona Pascual

Departamento de Biología Evolutiva,
Ecología y Ciencias Ambientales.



CAPÍTULO 1

1. A closer look at the bycatch of medium-sized and large sharks in the northern Catalan coast (northwestern Mediterranean Sea): evidence of an ongoing decline?

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Estado de publicación: publicado en junio de 2021 en *Aquatic Conservation: Marine and Freshwater Ecosystems*.

Abstract

Historically, the Mediterranean Sea supported a rich shark fauna. Presently however, the populations of most shark species have significantly declined, largely due to intense fishing. Interviews to crew members of bottom trawlers, drifting longliners and bottom longliners operating off the Costa Brava (Catalonia, NE Spain) were conducted between October 2016 and July 2017 in order to gather information on the current bycatch rate of several shark species.Interviews covered 41.2% of the fleet and respondents were asked for the bycatch of selected shark species -*Alopias vulpinus*, *Cetorhinus maximus, Galeorhinus galeus, Hexanchus griseus*, *Isurus oxyrinchus*, *Mustelus spp*., *Prionace glauca* and *Squalus acanthias*- in two distinct time periods. Bottom trawlers captured the highest diversity of species (8) followed by bottom longliners (7) and drifting longliners (3). Most respondents (89.7%) declared having captured at least one shark from 2006 to 2016 but only 56.4% declared having captured at least one shark from 2016 to 2017. From 2016 to 2017, the whole fleet captured 89 specimens of *H. griseus* (95% CI=145, 34), 14 of *G. galeus* (95% CI=30, 0), 3 of *A. vulpinus* (95% CI=8, 0), 3 of *I. oxyrinchus* (95% CI=8, 0), 3 of *C. maximus* (95% CI=6, 0) and no *Mustelus spp*. The total bycatch of *P. glauca* and *S. acanthias* was uncertain due to extremely loose confidence intervals. A significant decline was perceived by fishermen in the bycatch of *C. maximus* and *S. acanthias*, whereas the bycatch of *H. griseus* was considered to remain stable. This study suggests a dramatic reduction in the abundance of most of the medium-sized and large sharks of the Costa Brava and the likely disappearance of *Mustelus spp*. from the area. Only *H. griseus, S. acanthias* and *P. glauca* are still being bycaught frequently.

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RESEARCH ARTICLE

WILEY

A closer look at the bycatch of medium-sized and large sharks in the northern Catalan coast (north-western Mediterranean Sea): Evidence of an ongoing decline?

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Abstract

1. Historically, the Mediterranean Sea supported a rich shark fauna. Presently, however, populations of most shark species have significantly declined, largely due to intense fishing pressure.
2. Interviews with crew members of bottom trawlers, drifting longliners and bottom longliners operating off the Costa Brava (Catalonia, NE Spain) were conducted between October 2016 and July 2017 in order to gather information on the current bycatch rate of several shark species.
3. Interviews covered 41.2% of the fleet and respondents were asked for the bycatch of selected shark species—*Alopias vulpinus*, *Cetorhinus maximus*, *Galeorhinus galeus*, *Hexanchus griseus*, *Isurus oxyrinchus*, *Mustelus* spp., *Prionace glauca*, and *Squalus acanthias*—in two distinct time periods.
4. Bottom trawlers captured the highest diversity of species (eight) followed by bottom longliners (seven), and drifting longliners (three). Most respondents (89.7%) declared having captured at least one shark from 2006 to 2016 but only 56.4% declared having captured at least one shark from 2016 to 2017.
5. From 2016 to 2017, the whole fleet captured 89 specimens of *H. griseus* (95% confidence interval (CI) = 145, 34), 14 of *G. galeus* (95% CI = 30, 0), 3 of *A. vulpinus* (95% CI = 8, 0), 3 of *I. oxyrinchus* (95% CI = 8, 0), 3 of *C. maximus* (95% CI = 6, 0), and no *Mustelus* spp. The total bycatch of *P. glauca* and *S. acanthias* was uncertain due to extremely loose confidence intervals.
6. A significant decline was perceived by fishermen in the bycatch of *C. maximus* and *S. acanthias*, whereas the bycatch of *H. griseus* was considered to have remained stable.
7. This study suggests a dramatic reduction in the abundance of most of the medium-sized and large sharks of the Costa Brava and the likely disappearance of *Mustelus* spp. from the area. Only *H. griseus*, *S. acanthias*, and *P. glauca* are still being bycaught frequently.

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KEYWORDS
bycatch, Costa Brava, factors, fishermen, interviews, population, shark

1 | INTRODUCTION

Sharks are amongst the top predators in ocean ecosystems (Dulvy et al., 2008) and potentially exercise a top-down control upon other organisms, thus having a fundamental role in the structure and function of marine communities (Myers et al., 2007; Heithaus et al., 2008; Ferretti et al., 2010). Some estimations indicate that populations of large predatory fish have been reduced by 90% worldwide over the last 50–100 years due to overexploitation (Christensen et al., 2003; Christensen et al., 2014), with sharks being highly sensitive to depletion due to their life strategies (Myers & Worm, 2005). Like most Chondrichthyans, sharks are characterized by K-selected life history traits (Kabasakal, Karhan & Sakınan, 2017), which results in low reproductive potential and low capacity for population increase (Pratt & Casey, 1990). Thus, sharks are more likely to be affected by intense fishing than most teleosts (Castro, Woodley & Brudek, 1999; Stevens et al., 2000). Large sharks in particular can suffer large population declines even with comparatively light fishing pressure (Ferretti et al., 2010). As a result, a large number of shark species are currently threatened worldwide due to bycatch and overfishing (Camhi et al., 2009; Hisano, Connolly & Robbins, 2011; Worm et al., 2013; Dulvy et al., 2014; Simpfendorfer & Dulvy, 2017).

The Mediterranean Sea is considered a biodiversity hot-spot for sharks (Dulvy et al., 2014). Literature published during the 19th century reported abundant populations of species such as *Alopias vulpinus*, *Isurus oxyrinchus*, *Mustelus asterias*, *Mustelus mustelus*, *Prionace glauca*, *Scylorhinus canicula*, *Scylorhinus stellaris*, and *Squalus acanthias* (Peris, 1802; Cisternas, 1867; Navarrete, 1898). The same sources also reported the presence of species currently uncommon such as *Carcharias taurus*, *Cetorhinus maximus*, *Dalatias licha*, *Galeorhinus galeus*, *Odontapsis ferox*, *Oxynotus centrina*, and *Sphyrna zygaena*. Nevertheless, a growing number of studies are reporting a general decline of pelagic sharks in the Mediterranean Sea (Megalofonou, 2005; Ferretti et al., 2008; Fortibuoni et al., 2016; Colloca et al., 2020) and medium-sized and large shark species are seldom reported in the catch list of bottom trawlers operating in the western Mediterranean Sea (Massutí & Moranta, 2003; Massutí & Reñones, 2005), which suggests a severe reduction of the rich shark fauna reported by the 19th century authors (Colloca et al., 2017).

The Mediterranean Sea hosts the highest proportion of threatened species due to unregulated fishing (Colloca et al., 2017). In a recent report published by the IUCN (Dulvy et al., 2016), 39 of the 73 assessed species of Chondrichthyans were found to be regionally threatened in the Mediterranean Sea, with overfishing identified as the main driver of decline and local extinction. Twenty-three of these 39 species were sharks; 12 fell under the category of 'Critically Endangered', six were considered 'Endangered', and five were 'Vulnerable.' Furthermore, 10 species were still listed as 'Data Deficient'. In the Spanish Mediterranean Sea, there remains a paucity of information regarding shark populations (García-Cortés & de la Serna, 2002; de la Serna et al., 2002; Massutí & Moranta, 2003; Massutí & Reñones, 2005), with recent research mostly focusing on the trophic ecology of a few species (Navarro et al., 2014; Albo-Puigserver et al., 2015; Barría, Coll & Navarro, 2015; Barría et al., 2015).

In general, estimating parameters such as abundance or distribution of rare species is time-consuming and requires extensive funding (Anadón et al., 2009). In this context, the local ecological knowledge (LEK) held by fishing communities, taken as "a cumulative body of knowledge, practice and belief evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment" (Berkes, Colding & Folke, 2000: p.1252) has been used to obtain information about abundance and population trends of a wide range of species (Ferguson, Williamson & Messier, 1998; Sáenz-Arroyo et al., 2005; Bender et al., 2014; Damalas et al., 2015; Colloca et al., 2020), as well as other biological and ecological information (Johannes, Freeman & Hamilton, 2000; Silvano et al., 2006; Stacey et al., 2012; Giovos et al., 2019). While some scientists and managers are rather sceptical about its reliability (Shackeroff & Campbell, 2007; Brook & McLachlan, 2008), LEK has proved to be a source of high-quality and low-cost information (Anadón et al., 2009) and numerous studies working on fisheries have shown that combining scientific assessments with LEK can improve management decisions (Garcia-Quijano, 2007; Silvano & Valbo-Jørgensen, 2008; Bender et al., 2014; Carothers et al., 2014).

The purpose of this study was to update the information about the presence of some medium-sized and large shark species inhabiting the Costa Brava, in north-eastern Spain (Figure 1) by means of LEK. Specifically, the aim was to: (i) determine which species are still commonly bycaught by bottom trawlers, bottom longliners, and drifting longliners; (ii) identify the main factors influencing the capture of each species according to the fishermen's perception; and (iii) assess the population trend of each species according to the fishermen's perceptions.

2 | METHODS

2.1 | Study area

The Costa Brava stretches from Portbou (42.435°N 3.174°E) to Blanes (41.651°N 2.778°E), covering up to 60 km of coastline (Figure 1). Its maritime relief is distinctive, with a narrow continental

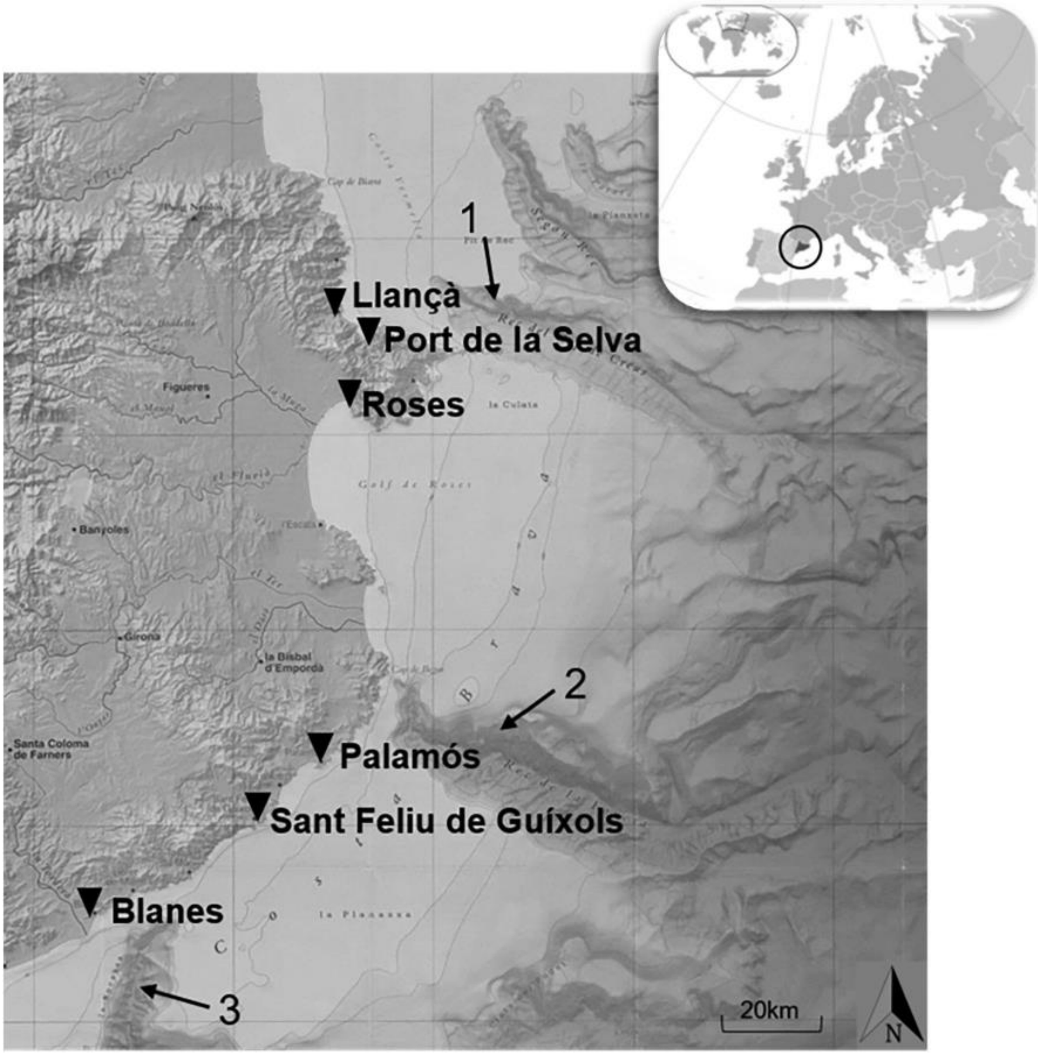

FIGURE 1 Location of the Costa Brava (top, right; source: Google), surveyed ports and topographic representation of the marine relieve of the Costa Brava, along with its three main canyons, Cap de Creus (1), Palamós (2), and Blanes (3). Source: Institut Cartogràfic de Catalunya y GRC en Geociències Marines de la U.B. www.icc.es

shelf and the shelf break found just a few kilometres offshore. The continental shelf and slope are dissected by three submarine canyons (Cap de Creus, Palamós, and Blanes) from north to south (Figure 1). They represent hotspots for marine life and are used as fishing grounds, mostly by the red shrimp (*Aristeus antennatus*) and Norway lobster (*Nephrops norvegicus*) fisheries.

2.2 | Focal species

Information was collected on five species of large sharks (>200 cm standard length (SL): common thresher (*Alopias vulpinus*), basking shark (*Cetorhinus maximus*), bluntnose sixgill shark (*Hexanchus griseus*), shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*) and several species of medium-sized sharks (90–200 cm SL; tope shark (*Galeorhinus galeus*), smooth-hounds (*Mustelus* spp.), and spiny dogfish (*Squalus acanthias*)). A medium size was hereby defined as either equal or bigger than the size at maturity of *S. acanthias* in the western Mediterranean Sea, which is approximately 90 cm SL in females (Capapé & Reynaud, 2011) and therefore allowing us to exclude smaller species like catsharks (*Galeus melastomus* and *Scyliorhinus canicula*).

2.3 | Questionnaire-based survey

Interviews were conducted from October 2016 to July 2017 at six of the 11 fishing ports in the area. These ports were selected because they represented the only ones that were used as a base by either longliners or bottom trawlers. Information was compiled by interviewing fishermen with the aim of covering at least 30% of the fleet of each fishing gear.

The interviews were carried out using a modified version of the questionnaires previously used to assess the bycatch of other species of megafauna in the Spanish Mediterranean Sea (Carreras, Cardona & Aguilar, 2004; Álvarez de Quevedo et al., 2010), which were adapted for sharks. At the start of each interview, the participants were given some identification forms and pictures of each shark species and then responded verbally to a set of questions concerning biological aspects of the species, catch frequency, factors influencing their bycatch, and the population trend of the different species.

Most specifically, fishermen were asked to identify the shark species they had seen and captured and to indicate the month of the year and the fishing grounds where captures of each species had occurred over the last year (2016 to 2017) and throughout the last 10 years (2006 to 2016). Fishermen were also asked to report, as accurately as possible, the number of individuals of each species that had been captured from 2006 to 2016 and from 2016 to 2017 and to say the reason why bycatch of these species took place. Finally, fishermen were asked to give their opinion on the population trend of the focal species choosing from 'increasing', 'stable', or 'decreasing'. For those species under any form of legal protection and whose population numbers were labelled as 'decreasing' in the interviews, potential factors responsible for the decline of these species were divided into three main categories: biological, fishing-induced, and other anthropogenic impacts. The combination of factors was also considered in the analysis and those that did not conform to any of these categories were classified as 'others'.

2.4 | Fishing effort and shark bycatch estimations

The fishing fleet includes three different types of vessels using three different fishing gears (bottom trawlers, bottom longliners, and drifting longliners), so a stratified approach was used to estimate total shark bycatch (Greenwood, 1996). Fishing effort was defined as the number of months in which each vessel operated on an annual basis, as in other studies using the same approach (Carreras, Cardona & Aguilar, 2004; Álvarez de Quevedo et al., 2010). According to Spanish fishing regulations, all bottom trawlers in the region are obligated to cease fishing for 2 months at different times of the year in each port, while longline vessels are not subject to this temporal closure. During the season, every bottom trawler operates from 7 am to 6 pm, from Monday to Friday, with 2–3 tows per day of work.

Total fishing effort with gear z (E_z) was calculated as:

$$E_z = \sum_{i=1}^{i=n} E_{zi}$$

where E_{zi} is the effort from vessels from the ith port operating with gear z.

In its turn, E_{zi} was calculated as follows:

$$E_{zi} = E_{ozi} \frac{n_i}{n_{zi}}$$

where E_{ozi} is the effort reported by the interviewed fishermen from port i operating with gear z, n_{zi} is the number of registered vessels based in port i that used gear z, and n_{ozi} the number of vessels from port i that used gear z and whose crew was interviewed. Total shark catch with gear z (C_z) was calculated as:

$$C_z = C_{oz} \frac{E_z}{E_{oz}}$$

where C_{oz} is the number of sharks caught, as reported by fishermen with gear z; E_z is the total fishing effort with gear z; and E_{oz} is the effort reported by fishermen with gear z. Total shark catch by the whole fleet was the sum of the C_z values of the three gears. The 95% confidence intervals of estimated catch were calculated with the procedure detailed by Greenwood (1996) for stratified sampling.

2.5 | Fishermen's perception on the evolution of shark populations

The questionnaires asked fishermen about their perception on the evolution of the population size of each species, with only three possible answers: increasing, stable and decreasing. A chi-squared test was carried out using IBM SPSS Statistics (Version 24) to assess whether the frequencies of the three possible answers (increase, stable, and decline) differed from those expected by chance (all three answers had the same probability by chance).

3 | RESULTS

3.1 | Fleet coverage and occurrence of shark captures

A total of 42 full interviews were carried out and a minimum coverage of 30% was accomplished for each fishing gear—bottom trawlers (31 interviews; 40.8% of the fleet), bottom longliners (9 interviews; 45% of the fleet), and drifting longliners (2 interviews; 33.3% of the fleet; Table 1). The number of interviews for each fishing gear and fishing port are summarized in Table 1.

Most of the fishermen interviewed (89.7%) declared having captured at least one of the focal shark species from 2006 to 2016, but only half of them (56.4%) had captured any shark from 2016 to 2017 (Table 2). From 2006 to 2016, 'no catches' were reported by only 10.3% of the respondents and capturing more than 10 sharks was the most common answer (28.2%), followed by capturing 100–500 (23.1%), 1–5 (15.4%), 6–10 (12.3%), and more

TABLE 1 Number of surveyed vessels per fishing gear in each port and coverage values

	Bottom trawling	Bottom longline	Drifting longline
Port de la Selva	1 (5)	0 (2)	0 (0)
Llançà	4 (8)	2 (4)	0 (0)
Roses	10 (22)	2 (5)	0 (1)
Palamós	10 (24)	1 (4)	0 (1)
Sant Feliu de Guíxols	0 (0)	0 (1)	1 (1)
Blanes	6 (17)	4 (4)	1 (3)
Total	**31 (76)**	**9 (20)**	**2 (6)**
Coverage (%)	**40.8**	**45.0**	**33.3**
Total coverage		**41.2**	

Note: Numbers in brackets represent the total number of active vessels at the time of the study and were facilitated by each port's captain of the fishermen's association. Coverage values are given per gear and for all surveyed vessels relative to the total number of vessels of the three fishing gears.

TABLE 2 Frequencies of shark captures (top) and range of captured individuals (bottom) from 2016 to 2017 and from 2006 to 2016, according to respondents

		2016–2017 (%)	2006–2016 (%)
	Catches	56.4	89.7
	No catches	43.6	10.3
Captured individuals	0	43.6	10.3
	1–5	38.5	15.4
	6–10	10.3	12.8
	>10	0	28.2
	>50	7.7	10.3
	100–500	0	23.1

Note: All species included. Frequencies are expressed in % in each column.

than 50 sharks (10.3%). From 2016 to 2017, 'no catches' was the most frequent answer (43.6%), followed by capturing 1–5 (38.5%), 6–10 sharks (10.3%), and more than 50 sharks (7.7%).

From 2006 to 2016, bottom trawlers captured all species targeted in this study. Bottom longliners captured seven species but did not capture *Mustelus* spp. *Prionace glauca*, *A. vulpinus* and *I. oxyrinchus* were the only three species captured by drifting longliners. From 2016 to 2017, the average number of sharks captured by the surveyed bottom trawling fleet was 1.7 individuals per vessel per year, whereas 31.1 and 29.5 sharks were captured per vessel per year by the bottom longline and the drifting longline fleets, respectively.

When these figures are extrapolated to the whole fleet, a total of 926 sharks were estimated to have been caught from 2016 to 2017 (Figure 2). *Prionace glauca*, *S. acanthias*, and *H. griseus* clearly dominated the catch, but the only reliable bycatch estimate was that of *H. griseus* (n = 89; 95% CI = 145, 34). Captures of *P. glauca* and *S. acanthias* were so variable that the 95% CI intervals of their estimates were extremely loose (*P. glauca* n = 617, 95% CI = 1288, 0; *S. acanthias* n = 197, 95% CI = 486, 0). The remaining species were rarely captured, which resulted in very low bycatch figures for *G. galeus* (n = 14; 95% CI = 30, 0), *A. vulpinus* (n = 3; 95% CI = 8, 0), *I. oxyrinchus* (n = 3; 95% CI = 8, 0), and *C. maximus* (n = 3; 95% CI = 6, 0). No captures of *Mustelus* spp. were reported. Bottom trawlers captured all the reported specimens of *C. maximus* and about 90% of *G. galeus*, *H. griseus*, and *S. acanthias*. The latter species were also captured sporadically by bottom longliners, while *A. vulpinus* and *I. oxyrinchus* were only captured by drifting longliners. *Prionace glauca* was mainly captured by bottom longliners (70.3%), although drifting longliners (27.7%) and bottom trawlers (1.98%) occasionally captured this shark too (Figure 2).

3.2 | Fishermen's perception on the evolution of shark populations

All gears combined, results show that respondents mainly considered sharks to be suffering a decrease in abundance over time or, to a lesser extent, to remain at a stable number of individuals (Figure 3).

The distribution of answers about the population trends of *A. vulpinus*, *G. galeus*, *I. oxyrinchus*, and *P. glauca* did not depart from that expected by chance (Table 3) and hence fishermen's answers were uninformative. The opposite was true for *C. maximus* and *S. acanthias*, both considered by respondents to be declining more often than expected by chance (Table 3). Likewise, the frequency to which respondents considered that the bycatch of *H. griseus* and *Mustelus* spp. is stable was also higher than that expected by chance (Table 3).

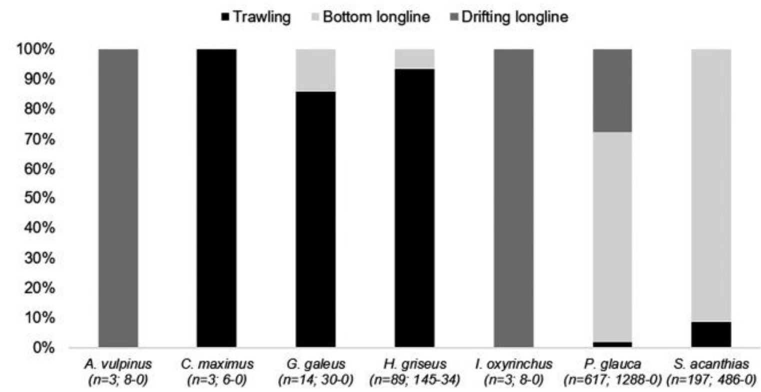

FIGURE 2 Total number of captures of each shark species (n; with 95% confidence interval) extrapolated to the entire fleet operating in the Costa Brava and contribution of each gear from 2016 to 2017

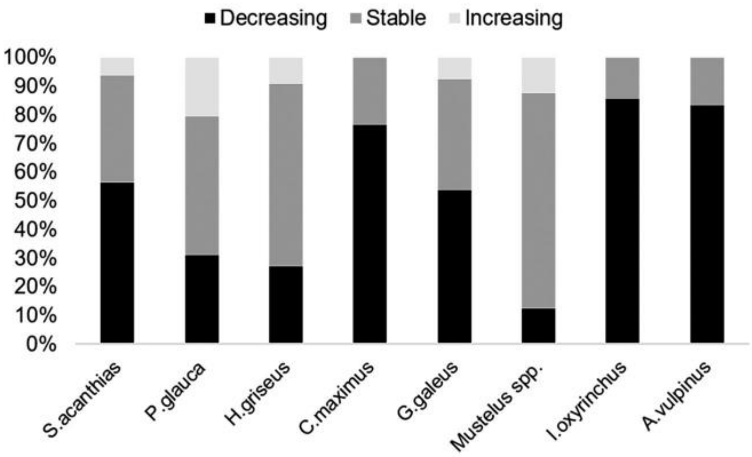

FIGURE 3 Evolution of each species' populations (decreasing, stable, increasing) all gears together. Each trend is illustrated in each column according to its frequency, here expressed in %

TABLE 3 Fishermen's perception on the evolution of shark populations. Level of significance ($P < 0.05$)

Species	Population trend	χ^2	*P*-value
Alopias vulpinus	Decreasing	2.67	0.102
Cethorinus maximus	Decreasing	7.20	**0.007**
Galeorhinus galeus	Decreasing	4.31	0.116
Hexanchus griseus	Stable	10.18	**0.006**
Isurus oxyrinchus	Decreasing	3.57	0.059
Mustelus spp.	Stable	6.25	**0.044**
Prionace glauca	Stable	3.34	0.185
Squalus acanthias	Decreasing	6.13	**0.047**

3.3 | Factors influencing shark captures

Respondents considered overlap between fishing grounds and shark habitat as the main reason for bycatch, followed by the attraction of sharks drawn by the fishing activity (Figure 4). Together, they accounted for the 82.3% of all the answers given by respondents.

At the time of the study, four species were legally protected by Spanish legislation—*A. vulpinus*, *I. oxyrinchus*, *C. maximus*, and *G. galeus*—and each of them were differently affected by each factor (Figure 5). According to respondents, fishing-induced mortality was regarded as the main factor causing the decline in *I. oxyrinchus* (50%), whereas other anthropogenic impacts were identified as the main threat for *A. vulpinus* (66.7%) and *C. maximus* (50%). Finally, biological factors and other anthropogenic impacts, each identified by 30% of the respondents, were considered the two main threats for *G. galeus*.

4 | DISCUSSION

The results reported here indicate that currently only *P. glauca*, *S. acanthias* and *H. griseus* are regularly bycaught by fishermen operating off the Costa Brava, whereas *G. galeus*, *A. vulpinus*,

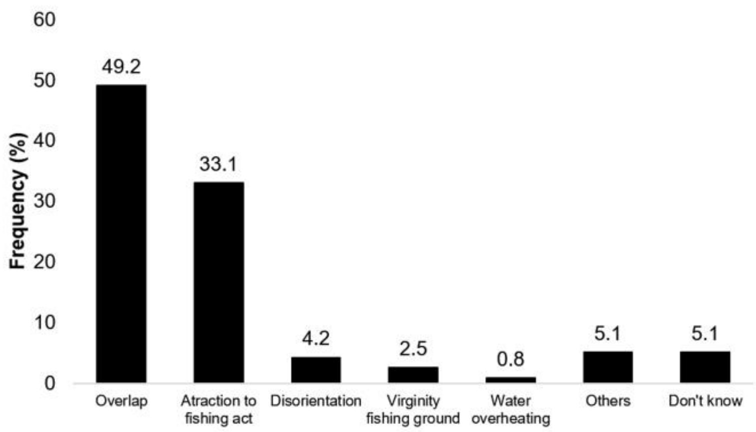

FIGURE 4 Factors affecting shark captures represented with their correspondent frequencies (%) on top of each column

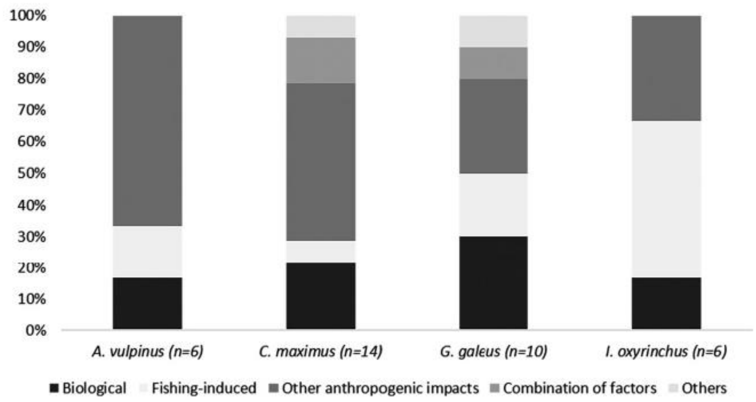

FIGURE 5 Drivers of decline suggested by respondents for each protected species considered in this study (n = number of interviews). Each factor is illustrated in each column according to its frequency, here expressed in %

I. oxyrinchus, *C. maximus* and *Mustelus* spp. are extremely rare. Although interview-derived data might sometimes lack accuracy or be poor if the study is poorly designed (Álvarez de Quevedo et al., 2010), questionnaire-based surveys are one of the most practical methods to assess the bycatch of rare species (Godley et al., 1998). The compilation of data using such a practical low-cost methodology provided the present study with some insight that may pave the way for future species-specific studies and encourage local and regional authorities to develop new conservation strategies in order to tackle the issues facing shark populations off the Costa Brava.

Sharks are highly vulnerable to overfishing and bycatch because of their very low rates of population increase (Camhi et al., 2009). In the Costa Brava, medium-sized and large sharks were regularly captured by fishermen in the 19th century (see Peris, 1802; Cisternas, 1867; Navarrete, 1898), but currently most of them are rarely captured by the fleet. Although the scale of bycatch is also subject to some operational factors such as the characteristics of the fishing gear, the fishing grounds, and the fishing hours (Megalofonou, 2005; Carruthers, Neilson & Smith, 2011; Oliver et al., 2015), it largely depends on shark abundance. Consequently, the decrease in both number and frequency of catches observed in this study might be indicative of an ongoing decline in shark abundance.

This study reveals bottom trawling as the fishing gear responsible for capturing the highest number of the focal shark species. Similar results have been reported in other regions of the Mediterranean Sea (Carbonell et al., 2003; Colloca et al., 2003; Yaglioglu et al., 2015; Bonanomi et al., 2018). Bradai, Saidi & Enajjar (2012) considered demersal species as the most frequently caught by trawlers but also included large pelagic species such as *A. vulpinus*, *P. glauca*, *I. oxyrinchus*, and *C. maximus* as occasional catch. Indeed, 5% of *C. maximus* captures in the Mediterranean Sea are reported from trawl fisheries (Mancusi et al., 2005).

Bottom longline ranked second in number of captured species, with seven reported to be bycaught from 2006 to 2016. Interestingly, *P. glauca* was the most commonly captured species although it is known to spend most of its time near the top of the water column (Stevens, Bradford & West, 2010). The diversity of bycaught species dropped to four from 2016 to 2017, however, and no captures of *Mustelus* spp. were reported from 2006 to 2016 nor between 2016 and 2017. This may suggest that *Mustelus* spp. have been very scarce off the Costa Brava for more than a decade, particularly considering the fact that fishers did acknowledge captures of *S. acanthias*, a species that shares the same habitat.

Conversely, drifting longline only captured pelagic species, namely *P. glauca*, *A. vulpinus*, and *I. oxyrinchus* both from 2006 to 2016 and from 2016 to 2017, even though up to 12 species (including *G. galeus*, *C. maximus*, *Mustelus* spp., and *H. griseus*) are sometimes caught by this gear according a General Fisheries Commission for the Mediterranean report (Bradai, Saidi & Enajjar, 2012).

Concerning the estimation of the total bycatch by the entire fleet of the Costa Brava from 2016 to 2017, captures of *A. vulpinus*, *I. oxyrinchus*, *C. maximus*, and *G. galeus* were very low and the few captures of *A. vulpinus* and *I. oxyrinchus* were restricted to drifting longliners. These two species are pelagic sharks that move close to the surface and have been reported as bycatch in this gear for a long time (Casey & Kohler, 1992; Peristeraki et al., 2008; Cortés et al., 2010; Mejuto et al., 2013). The fact that only a few specimens were captured off the Costa Brava might be further evidence of the severe decline of these large predatory species in the Mediterranean Sea, already reported by Ferretti et al. (2008). Bottom trawlers were involved in all the captures of *C. maximus* reported in this study. *C. maximus* is also a pelagic species found at the top of the water column, but captures of this species can sometimes occur as some individuals get entangled in a trawl net when it is being hauled. *G. galeus* was mainly captured by bottom trawlers but also by bottom longliners. Again, this is as expected for this species, taking into account that this shark usually inhabits waters deeper than those of the three species before-mentioned but shallower than those of bottom-dwelling sharks, such as *H. griseus*, making it susceptible to being caught by both trawl nets and bottom longlines.

Not a single capture of *Mustelus* spp. was recorded by the interviewed fishermen from 2016 to 2017. *Mustelus* spp. have suffered a drastic decline in the Mediterranean Sea not only in abundance but also in terms of spatial distribution, as its distribution range has diminished in recent decades due to heavy fishing according to (Colloca et al., 2017). The absence of captures of *Mustelus* spp. concurs with Colloca's findings and suggests the possibility that populations of these medium-sized sharks might no longer exist in the Costa Brava.

In the case of *P. glauca* and *S. acanthias*, the extremely high variability in all reported captures from 2016 to 2017 meant it was not possible to give a reliable estimation of their total captures. This high variability stems from the fact that only a few vessels reported captures: two for *P. glauca*, which reported having captured 50 and 200 individuals respectively, and one for *S. acanthias*, which reported having captured 90 sharks. Nonetheless, these results reveal that both species still occur in the region, although probably restricted to a few areas.

Hexanchus griseus was the most consistently bycaught shark by the fleet, yet almost exclusively by bottom trawlers. This species is most usually found on the continental slopes in the Mediterranean Sea (Stefanescu, Lloris & Rucabado, 1993; d'Onghia et al., 2004), which are precisely the main fishing grounds of the bottom trawling vessels targeting the red shrimp in the north-western Mediterranean Sea.

Respondents considered populations of *A. vulpinus*, *C. maximus*, *I. oxyrinchus*, *S. acanthias*, and *G. galeus* to be decreasing off the Costa Brava, but regarded populations of *H. griseus*, *Mustelus* spp., and *P. glauca* as stable. Numbers of *P. glauca* were even considered by a few fishermen, especially longliners, to be increasing. However, the distribution of the three possible answers departed from that expected by chance only for *C. maximus*, *S. acanthias* (both considered as decreasing), and *H. griseus*, and *Mustelus* spp. (both considered stable). Although illustrative, this result does not provide any science-based knowledge and could be highly biased. For instance, as of 2020, *P. glauca* is classified by the IUCN Red List of Threatened Species as 'Critically Endangered' in the Mediterranean Sea and shows a remarkable decreasing trend over the last few years contrary to what respondents have suggested in this study. But perhaps the most striking case is that of *Mustelus* spp., as respondents had not captured single specimen in the area for many years and hence considering the species numbers to be stable actually means that it has been rare for a long time.

Overlap between fishing grounds and species distribution has been identified in some studies as a major cause of shark bycatch (Perez & Wahrlich, 2005; Queiroz et al., 2016). Similarly, respondents in this study also acknowledged overlap as the main reason why shark bycatch occurs along with the belief that sharks get attracted to fishing activity.

Even though respondents considered there was no protected species the decline of which could be ascribed to a single factor, some factors did seem to be more relevant in explaining the dwindling numbers of some of these shark species. For example, fishermen perceived fishing-induced factors are greatly responsible for the decline of *I. oxyrinchus*. This coincides with other studies highlighting the dramatic decline of the species in the Mediterranean Sea (Ferretti et al., 2008; Colloca et al., 2017; Colloca et al., 2020), and moderate decline in the Atlantic Ocean (Baum et al., 2003) due to intense fishing. Other anthropogenic impacts, such as changes in water temperature due to global warming, pollution of the marine environment or water impoverishment, represented the main reasons perceived by respondents as to why *C. maximus* and *A. vulpinus* are disappearing. The results obtained for *C. maximus* agree with those of Sims & Reid (2002) and Cotton et al. (2005), who linked the decrease in shark catches with a decrease in the abundance of copepods and sea surface temperature respectively rather than fishing practices and thus differs from other studies that suggest *C. maximus* is mostly affected by overfishing (Stevens et al., 2000). Fishermen also attributed the depletion of *A. vulpinus* to other anthropogenic impacts, thus differing from quite a good number of studies that have considered *A. vulpinus* to suffer from intense fishing pressure (Baum et al., 2003; Ferretti et al., 2008; Goldman et al., 2009). Fishermen did not identify fishing as the main driver of decline for *G. galeus* either, as opposed to findings from other studies that attributed the depletion of this species to a long history of exploitation in target fisheries (Walker et al., 2006; Pondella & Allen, 2008). According to respondents, *G. galeus* seems to be declining for multiple reasons, with biological factors being much more relevant in this than in the other species. Some respondents stated that populations of *G. galeus* were less abundant in the Costa Brava because they had dispersed to other areas, yet no study has ever attributed the disappearance of

G. galeus in a given area to migration to the best of our knowledge. In conclusion, although fishermen often acknowledge that sharks decline as a result of interaction with fisheries, they still blame other actors. This perceived decreasing population trend of most of them stands pretty much in line with the general decrease in the frequency of shark bycatch in the whole Mediterranean Sea reported by Maynou et al. (2011), who stated that shark bycatch had diminished since the early 1940s, coinciding with the intensification of the fishing activity.

The results reported in this study support the need that some action is taken to protect all the medium-size and large shark species occurring off the Costa Brava, and not only the few species that are currently legally protected. Reducing bycatch by means of operational changes or the designation of marine protected areas (MPAs) are the only real alternatives, given the absence of directed fisheries and the often misidentification of sharks in fish markets.

Creating and implementing effective conservation strategies that could bring about biological benefits while considering socio-economic implications should be done by including the fishing sector in the decision-making process, not only for their knowledge in the field but also because many of the fishermen interviewed in this study were aware of the value of sharks as a functional group and were willing to collaborate for the simple purpose of preserving the ecosystem. Fishermen could, for instance, be trained in catch-and-release practices since sharks are sometimes still alive when bycaught. A proper handling and release of an individual might avoid post-release mortality and this could be of great importance especially for threatened species. Some studies with recreational anglers pointed out their positive attitude towards ensuring shark survival (Shiffman & Hammerschlag, 2014; Mcclellan Press et al., 2016). Equipping nets with Turtle Excluder Devices has proved to be an effective way of reducing elasmobranch bycatch (Belcher & Jennings, 2011; Raborn et al., 2012; Garstin, Oxenford & Maison, 2017). In the Costa Brava, a few bottom trawlers have actually started using artisanal bycatch reduction devices to avoid captures of *C. maximus* and *H. griseus*, but their effectiveness is yet to be established. Future research opportunities could be focused on assessing the impact of bycatch reduction devices in the bycatch rates of sharks by trawl nets and also exploring alternative devices that might be used by longline gears to reduce bycatch of pelagic sharks such as *A. vulpinus*, *I. oxyrinchus*, and *P. glauca*.

The designation of MPAs is a powerful approach to tackle the problem of biodiversity loss (Davidson & Dulvy, 2017) given the consequent range of benefits for marine wildlife (García-Charton et al., 2008). Amongst other top consumers, sharks have been used as focal species to designate MPAs given their population traits and distribution (Hooker & Gerber, 2004). Unfortunately, the limitation on data regarding spatial distribution of many shark species might lead to certain MPAs not being as effective in protecting sharks as they should be. Therefore, it is highly important to have reliable information for a given species when identifying areas of ecological importance and again fishermen could contribute to this by broadening the data baseline for many sharks. In a recent study, Giménez et al. (2020) assessed the usefulness of some current MPAs concerning the protection of certain species of demersal elasmobranchs and concluded that only a small part of them was actually relevant for the demersal shark community, since the majority of them were distributed outside the existing MPAs. This conclusion is also relevant for the species studied here, as current MPAs are too small to protect viable populations.

In any case, keeping a synergistic relationship with the fishing sector can for instance engage fishermen in providing continuous data on any kind of megafauna. This has proved to be fruitful in the past in some fisheries (Ticheler, Kolding & Chanda, 1998; Obura et al., 2002; Yochum, Starr & Wendt, 2011). Data on shark abundance or distribution would be of high value especially in areas like the Costa Brava, where the status of some sharks is still far from being well-known. Fishermen could not only provide data on protected species when these got bycaught, but also on commercial species such as *H. griseus*, *Mustelus* spp., *P. glauca*, and *S. acanthias*, which are not regulated under a TAC/quota management scheme in the Mediterranean Sea. This constant flow of information coming from fishermen could help monitor the population status of such species as well, making it easier to detect changes in abundance over time and therefore allowing scientists and managers to develop conservation measures to reverse any detected decline.

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SUPPORTING INFORMATION

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CAPÍTULO 2

2. Filling the gap: the unique trophic niche of medium-sized and large sharks in the northwestern Mediterranean Sea.

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Abstract:

The Mediterranean Sea is considered a biodiversity hotspot and hosts a broad diversity of shark species. Unfortunately, many shark populations have suffered a long story of overexploitation and their abundance has strongly declined over the last decades. This is especially noticeable in medium-sized and large sharks. A few studies have addressed the trophic role of sharks in the northwestern Mediterranean Sea, yet little is known about their ecological niche. In this study, the isotopic niches of six medium-sized and large shark species (*Alopias vulpinus*, *Galeorhinus galeus, Hexanchus griseus*, *Isurus oxyrinchus*, *Prionace glauca* and *Squalus acanthias*) from the northwestern Mediterranean Sea were determined and compared with those of sympatric predatory teleosts and marine mammals. Overall, $\delta^{13}C$ and $\delta^{15}N$ values were similar amongst all the shark species except for *G. galeus*, whose high $\delta^{15}N$ values suggested that the three analysed individuals had recently moved from a distinct area with a different isotopic baseline and hence excluded from further analysis. The mixing models identified cephalopods as the dominant prey of the other five shark species and revealed that those medium-sized and large shark species filled a unique isotopic niche. The trophic position of sharks was similar to those of predatory teleosts and small dolphins but lower than that of larger dolphins, pilot whales and beaked whales. The high contribution of cephalopods to the diet of sharks in the northwestern Mediterranean Sea might be indicative of fish scarcity and deserves further research.

Filling the gap: the unique trophic niche of medium-sized and large sharks in the northwestern Mediterranean Sea.

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Highlights

- The isotopic niches of six medium-sized and large shark species were assessed.
- Their trophic positions suggested they act as high-level mesopredators.
- Cephalopods were the dominant prey group in the diet of five sharks.
- The position of sharks in the $\delta^{13}C$-$\delta^{15}N$ biplot revealed a unique isotopic niche compared to fishes and cetaceans.

Abstract

The Mediterranean Sea is considered a biodiversity hotspot and hosts a broad diversity of shark species. Unfortunately, many shark populations have suffered a long story of overexploitation and their abundance has strongly declined over the last decades. This is especially noticeable in medium-sized and large sharks. A few studies have addressed the trophic role of sharks in the northwestern Mediterranean Sea, yet little is known about their ecological niche. In this study, the isotopic niches of six medium-sized and large shark species (*Alopias vulpinus*, *Galeorhinus galeus, Hexanchus griseus*, *Isurus oxyrinchus*, *Prionace glauca* and *Squalus acanthias*) from the northwestern Mediterranean Sea were determined and compared with those of sympatric predatory teleosts and marine mammals. Overall, $\delta^{13}C$ and $\delta^{15}N$ values were similar amongst all the shark species except for *G. galeus*, whose high $\delta^{15}N$ values suggested that the three analysed individuals had recently moved from a distinct area with a different isotopic baseline and hence excluded from further analysis. The mixing models identified cephalopods as the dominant prey of the other five shark species and revealed that those medium-sized and large shark species filled a unique isotopic niche. The trophic position of sharks was similar to those of predatory teleosts and small dolphins but lower than that of larger dolphins, pilot whales and beaked whales. The high contribution of cephalopods to the diet of sharks in the northwestern Mediterranean Sea might be indicative of fish scarcity and deserves further research.

Keywords: sharks, diet, isotopes, cephalopods, niche, Mediterranean.

Introduction

Trophic interactions largely determine the ecological role of species in ecosystems (McCann et al., 1998). Sharks are considered high-level mesopredators or apex predators (Heithaus et al., 2008; Ferretti et al., 2010; Frisch et al. 2016) and might have played important roles in the dynamics of natural marine ecosystems (Myers et al., 2007; Heithaus et al., 2008; Ferretti et al., 2010; Dulvy et al., 2014). However, evidence for a strong top-down effect of sharks in many current human-impacted marine ecosystems is elusive (Newman et al. 2006; Roff et al. 2016). One possible explanation is that shark populations have been largely reduced due to bycatch and overfishing (Camhi et al., 2009; Hisano et al., 2011; Worm et al., 2013; Dulvy et al., 2014 and 2021; Simpfendorfer & Dulvy, 2017) to the point that they are now functionally extinct in several marine ecosystems (Myers et al. 2007; Heithaus et al. 2014). Examples of local extinctions driven by such intense fishing pressure include the Galapagos shark (*Carcharhinus galapagensis*) in the equatorial Atlantic Ocean (Luiz & Edwards, 2011), one species of whaler shark (*Carcharhinus obsolerus*) in Southeast Asia (White et al., 2019) or the Ganges shark (*Glyphis gangeticus*) in the Indian Ocean (Haque and Das, 2019).

Major population declines have also been reported for sharks inhabiting the Mediterranean Sea (Ferreti et al. 2008 et al. 2010; Graham et al., 2010; Colloca et al., 2017; Moro et al. 2019; Nuez et al. 2021) and their ecological relevance is thought to have decreased considerably (Piroddi et al., 2015). Nonetheless, little is known about the role of sharks in coastal and pelagic food webs relative to teleost fishes (Hussey et al., 2011) and just a few studies have focused on the trophic ecology of sharks in the Mediterranean Sea (Valls et al., 2011; Navarro et al., 2014; Albo-Puigserver et al., 2015; Barría, Coll & Navarro, 2015; Barría et al., 2018; Di Lorenzo et al., 2020).

Stomach content analysis has been the traditional approach to describe the diet of marine predators (Cortés, 1999; Lowe et al., 1996; Joyce et al., 2002; McCord & Campana 2003; Baldwin et al., 2008; Torres-Rojas et al., 2010). However, this method requires large sample sizes to accurately quantify diet composition (Wetherbee & Cortés 2004), which can be extremely difficult when some species are hardly being captured (Nuez et al., 2021). The stable isotope analysis (SIA) of nitrogen and carbon has emerged as an alternative approach to assess some aspects of shark trophic ecology, because it requires small samples than can be collected from live specimens, although it lacks the high taxonomic resolution of stomach content analysis (Peterson & Fry, 1987). Nevertheless, SIA offers some advantages over stomach content analyses because the dietary information obtained from stable isotope analysis represents assimilated, not just ingested prey and the stable isotope ratios of consumer tissues provide an indication of the long-term diet, at least over the time needed to synthesize the analysed tissue (Peterson & Fry, 1987: Post, 2002). During the ingestion of food and excretion of wastes, there is an enrichment of the heavy isotopes (^{15}N or ^{13}C), a process known as fractionation (Olive et al., 2003). Predators therefore have a higher proportion of N and C heavy isotopes than their prey (Domi et al., 2005). However, $\delta^{13}C$ values only increase by 1‰ from prey to predator (Peterson & Fry, 1987; Hobson & Welch, 1992), which is small compared to the variability between marine primary producers (France, 1995). On the other hand, $\delta^{15}N$ values tend to increase by 2-4 ‰ at each trophic level (Caut et al., 2009; Hussey et al., 2010) and thus they are often used to determine the trophic level of an organism (Post 2002; Pinnegar et al., 2002). Metabolically active tissues, such as liver, have higher turnover rates than those less metabolically active (such as cartilage, fin and muscle) (Tieszen et al., 1983) and the slow growth rates of most elasmobranchs compared to teleosts (Garcia et al., 2008) indicate that the white muscle of sharks integrates long-term feeding habits, making it one of the most commonly sampled tissues in elasmobranchs (Hussey et al., 2012). As well as that, a muscle sample is relatively easy to obtain nonlethally from a shark (Matich et al., 2010) and this might be of considerable importance when sampling threatened species (Dulvy et al., 2008). On these grounds, SIA has been used to examine individual feeding behaviour (Matich et al., 2010), assess trophic position (MacNeil et al., 2005; Revill et al., 2009; Borrell et al., 2011; Hussey et al., 2011; Speed et al., 2012; Cardona et al. 2015) and study resource partitioning between sympatric species (Papastamatiou et al., 2010; Kinney et al., 2011; Albo-Puigserver et al. 2015; Borrell et al. 2021), among others.

The aim of this study was to examine the trophic niches of 6 species of medium-sized and large sharks inhabiting the northwestern Mediterranean Sea (*Alopias vulpinus*, *Galeorhinus galeus, Hexanchus griseus*, *Isurus oxyrinchus*, *Prionace glauca* and *Squalus acanthias*) using SIA and compare them with those of predatory teleosts and marine mammals from the same area. Given the set of morphological, behavioural and ecological traits that characterise most species of medium-sized and large sharks around the world, we hypothesised that the isotopic niche of the 6 focal shark species would be different from that of predatory teleosts and marine mammals.

Materials and methods

1. Study area

This study was conducted in the Catalan Sea and the southern part of the Gulf of Lions (northwestern Mediterranean Sea) (Figure 1). The Catalan Sea stretches from the Cap de Creus, near the Spain-France border, to the Ibiza Channel and is a highly productive marine area due to the supply of nutrients transported by the Rhone and Ebro rivers and also the Liguro-Provencal-Catalan current along the continental slope (Estrada 1996). Three submarine canyons located in Cap de Creus, Palamós and Blanes are also representative for being hot-spots of marine life. The Gulf of Lions is also a nutrient-rich and very productive area in the western Mediterranean Sea on account of the nutrient discharges from the Rhone River (Navarro et al., 2014).

2. Focal species

Information was collected on four species of large-sized sharks (i.e., with total length (TL)>200 cm): common thresher (*Alopias vulpinus*), bluntnose sixgill shark (*Hexanchus griseus*), shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*) and two species of medium-sized sharks (TL between 90-200 cm): tope shark (*Galeorhinus galeus*) and spiny dogfish (*Squalus acanthias*). A medium size was hereby defined as either equal to or bigger than the size at maturity of *S. acanthias* in the western Mediterranean Sea, which is approximately 90 cm TL in females (Capapé & Reynaud, 2011).

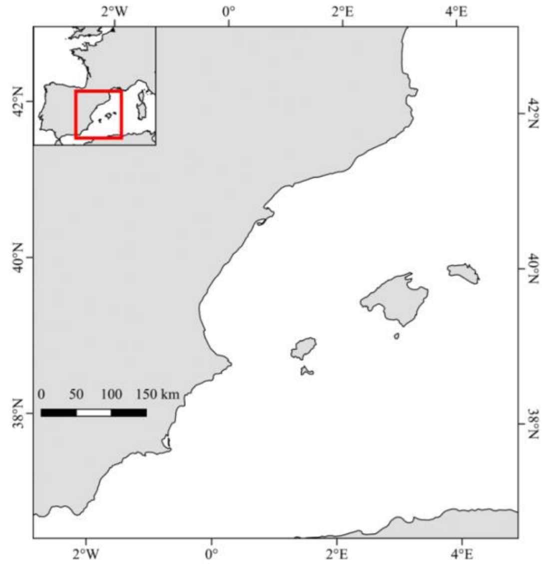

Fig 1. Map of the study area (Catalan Sea and southern part of Gulf of Lions, northwestern Mediterranean Sea).

3. Sample collection

Shark samples were collected opportunistically from May 2017 to April 2019 by observers on board fishing vessels or at the landing ports. White muscle tissue was extracted from behind the first dorsal fin of each shark using a 6 mm disposable biopsy punch. Muscle samples of several potential prey species were also collected and the selection of these species was based on previously published research on elasmobranch diet assessment in the Mediterranean Sea. In their study carried out in the western basin, Barría, Coll & Navarro (2015) found that most of the studied shark species fed on various taxonomic groups. Pelagic teleosts and cephalopods represented the two most important prey groups in the diet of *A. vulpinus*, *G. galeus*, *H. griseus* and *P. glauca* and, together with small crustaceans, constituted the diet of *S. acanthias*. On the other hand, little research has been published on the diet of *I. oxyrinchus* in the Mediterranean Sea, with the only insights coming from the Eastern basin confirming the presence of cephalopods in the stomachs of some individuals (Kabasakal, 2002; Tunçer & Kabasakal, 2016).

Therefore, the potential prey species that were considered in the present study included crustaceans (*Aristeus antennatus* and *Sergia robusta),* fishes *(Auxis rochei, Engraulis encrasicolus, Euthynnus alletteratus, Merluccius merluccius, Sarda sarda, Sardina pilchardus, Trachurus mediterraneus* and *Xiphias gladius)* and cephalopods (*I. coindetii* and *L. vulgaris*)*.* All samples were subsequently stored and frozen at -20°C at the laboratory.

4. Stable isotopes analysis (SIA)

Samples were first freeze-dried, powdered and then a portion of each sample was kept in Eppendorf tubes. Since lipids are depleted in ^{13}C relative to proteins and carbohydrates (Post et al., 2007) and so the higher the tissue lipid content, the more negative the $\delta^{13}C$ value of the organism (Li et al., 2016), a lipid extraction protocol was used. Elasmobranchs also retain n urea ($CO(NH_2)_2$) and trimethylamine oxide (TMAO; C_3H_9NO) in their tissues for osmotic balance (Li et al., 2016). These compounds are depleted in ^{15}N compared to protein and can affect the $\delta^{15}N$ discrimination between predator and prey (Hussey et al., 2014). Therefore, we also removed urea from all our shark tissue samples.

For the lipid extraction, samples were rinsed with a chloroform-methanol (2:1) solution and were hand-shaken for 3m first, then placed in the agitator for 2h. After that, all samples were decanted, suspended in 2:1 chloroform-methanol again and left to agitate for 24h. Each sample was then decanted to remove as much solvent as possible (where lipids concentrate) and was re-dissolved in 2:1 chloroform-methanol and put back to agitate, first for 2h with the follow-up decantation and re-suspension and then for 24h. This process was repeated a total of three times. All samples were afterwards re-dried overnight to eliminate the excess of solvent and then we proceeded to remove the urea by combining them with ultrapure rinse water. Samples were then agitated for 2h, decanted, re-suspended in rinse ultrapure-water and left to agitate overnight. We also collected white tissue samples from a set of different fish species which represent the potential prey of all target shark species in the study area. Lipids were also removed from the fish samples following the same procedure as that of the shark samples.

Once lipids and urea had been removed, the latter only from shark tissue, all samples were taken to the Scientific and Technological Centres (CCIT) of the University of Barcelona for the corresponding SIA. Between 0.23 and 0.30 mg of each shark and fish sample was taken and packed into tin capsules. Capsules were combusted at 900°C using an AE-IRMS Elemental Flash 1112 continuous flow isotope ratio mass analyser connected to a Delta C isotope ratio mass spectrometer. Carbon isotope ratios were reported relative to Vienna Pee Dee Belemnite limestone (VPDB) and nitrogen relative to atmospheric nitrogen, though secondary calibrated standards.

Stable isotopes are given using the conventional d notation where:

$$\delta\ ^{13}C \text{ or } \delta\ ^{15}N\ (‰) = (R_{sample}/R_{standard} - 1) \times 1000$$

where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ in the sample and the reference standards, respectively. Analytical precision was 0.4‰ and 0.25‰ for $\delta^{15}N$ and $\delta^{13}C$ values, respectively.

5. Statistical analysis

The estimated trophic position (TP) for each shark species was estimated using the equation from Post (2002)

$$TP = TP_{baseline} + (\delta^{15}N_{elasmobranch} - \delta^{15}N_{baseline}) / 2.29,$$

with 2.29 being the diet-tissue discriminating factor (TDF) estimated by Hussey et al. (2010) for lipid extracted muscle samples in sharks. An appropriate baseline to estimate shifts in the relative trophic position within a single ecosystem is the use of species with a well-understood trophic position (Post, 2002). Accordingly, we used *S. pilchardus* and *E. encrasicolus* as the baseline for TP estimations. In our study area, their trophic level ($TP_{baseline}$) is 3 (Albo-

Puigserver et al., 2016) and their mean δ^{15}N value (δ$^{15}N_{baseline}$) is 9.1‰ (Cardona, unpublished results).

Diet reconstruction using stable isotope analysis relies largely on the use of adequate diet-tissue discriminating factor (TDF). Here, we use the TDF values derived experimentally by Hussey et al. (2010) for *Carcharias taurus* and *Negaprion brevirostris* to assess the trophic position of other several shark species.

The Bayesian mixing model SIMMR version 0.4.1 (Stable Isotope Mixing Models in R) (Parnell et al. 2016) was used to calculate the relative contribution of the potential preys to the diet of each shark species. The data used to run the model were: δ^{13}C and δ^{15}N individual values of shark samples; mean and standard deviation of δ^{13}C and δ^{15}N values calculated for the potential food sources and the isotopic enrichment (TDF) for carbon and nitrogen from prey to predator (2.29±0.2‰ for δ^{15}N and 0.90±0.3‰ for δ^{13}C) (Hussey et al. 2010). In order to assess the accuracy of our estimates, we used the blackmouth catshark (*Galeus melastomus*) as a control species for the model. This abundant small shark relies largely on mesopelagic decapod, squids and fishes in the Mediterranean Sea (Fanelli et al., 2009; Albo-Puigserver et al., 2015; D'Iglio et al., 2021) so mixing models using the above-reported TDF should recover a similar diet make up.

To construct the biplot of stable isotope ratios of sharks, predatory teleosts and cetaceans from the northwestern Mediterranean Sea, different TDF values were used according to the type of organism. TDF values from Sweeting et al. (2007) were used for fish (*Euthynnus alletteratus, Sarda sarda, Xiphias gladius*) (Δ^{15}N = 3.20‰; Δ^{13}C = 1.50‰), values from Borrell et al. (2012) were used for mysticetes (*Balaenoptera physalus*) (Δ^{15}N = 2.82‰; Δ^{13}C = 1.28‰) and values from Giménez et al. (2016) were used for odontocetes (*Delphinus delphis*, *Grampus griseus*, *Globicephala melas*, *Stenella coerueroalba*, *Tursiops truncatus*, *Ziphius cavrirostris*) (Δ^{15}N = 1.57‰; Δ^{13}C = 1.01‰).

Results

We sampled 35 individuals from 6 species (Table 1). Shark individuals ranged from 74.5 to 440.0 cm in TL. *Alopias vulpinus* had the longest mean TL (440.0 ± 24.9 cm; n=2), followed by *H. griseus* (202.9 ± 60.0 cm; n=11), *P. glauca* (135.9 ± 37.5 cm; n=14), *G. galeus* (113 ± 5.8 cm; n=3), *I. oxyrinchus* (97 ± 4.2 cm; n=2) and *S. acanthias* (76 ± 2.3 cm; n=3).

G. galeus had the highest mean δ^{15}N value (16.9 ± 1.1 ‰), followed by *A. vulpinus* (12.8 ± 0.1 ‰), *I. oxyrinchus* (12.3 ± 0.9 ‰), *H. griseus* (12.2 ± 1.0 ‰), *P. glauca* (12.0 ± 0.7 ‰) and *S. acanthias* (11.8 ± 0.1 ‰) (Table 1). On the other hand, *P. glauca* had the lowest mean δ^{13}C value (-17.3 ± 0.4 ‰), followed by *S. acanthias* (-17.2 ± 0.1 ‰), *A. vulpinus* (-16.9 ± 0.1 ‰), *H. griseus* (-16.6 ± 1.3 ‰), *G. galeus* (-16.5 ± 1.0 ‰) and *I. oxyrinchus* (-16.5 ± 0.4 ‰). *Galeus melastomus* had a mean δ^{15}N value of 10.1 ± 0.5 ‰ and a mean δ^{13}C value of -18.7 ± 0.5 ‰. These results were in line with those obtained by other researchers in the western Mediterranean Sea (Valls, Rueda & Quetglas, 2017; Barría, Navarro & Coll, 2018) and thus helped validate the other values of the focal species.

Species	n	Total length (cm)		δ15N		δ13C			
		Mean	SD	Mean	SD	Mean	SD	TP	SD
A. vulpinus	2	440.0	24.9	12.8	0.1	-16.9	0.1	4.7	0.1
G. galeus	3	113.3	5.8	16.9	1.1	-16.5	1.0	-	-
H. griseus	11	202.9	60.0	12.2	1.0	-16.6	1.3	4.4	0.4
I. oxyrinchus	2	97.0	4.2	12.3	0.9	-16.5	0.4	4.5	0.4
P. glauca	14	135.9	37.5	12.0	0.7	-17.3	0.4	4.3	0.3
S. acanthias	3	75.8	2.3	11.8	0.1	-17.2	0.1	4.2	0.1

Table 1. Mean and standard deviation (SD) of total length, $\delta^{15}N$, $\delta^{13}C$ and trophic level (TP) of each species.

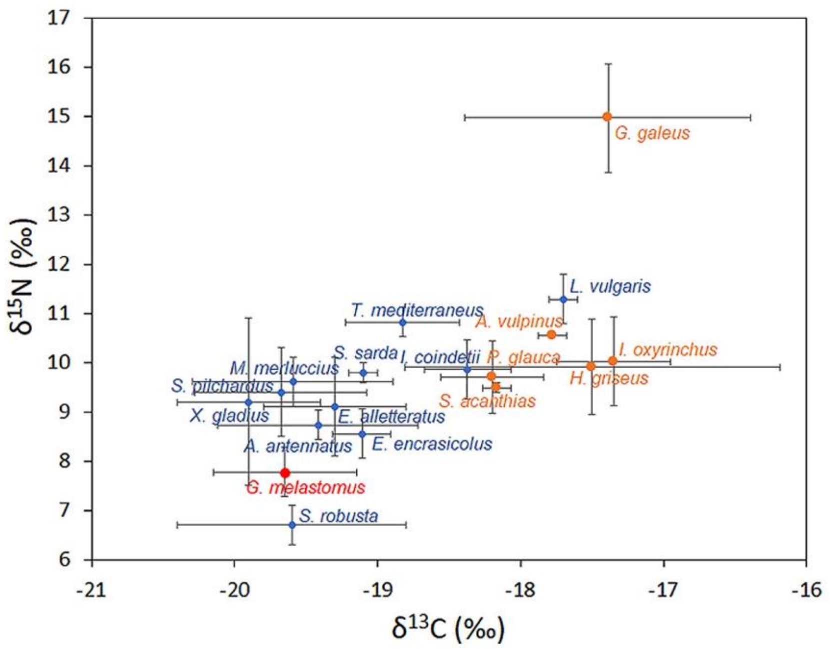

Fig 2. $\delta^{15}N$ and $\delta^{13}C$ values of the diets of sharks from the northwestern Mediterranean Sea corrected for TDF (orange) and their potential prey species (blue).

After correcting for TDF, the bivariate isotopic ratios of the sharks analysed laid close to the values of the two squid species considered, except those of *G. galeus* (Figure 2). The extremely high $\delta^{15}N$ values of the three specimens of this species suggested that they were recent immigrants from an area with an enriched ^{15}N baseline. Accordingly, this species was not considered in further analyses.

For the two species with the highest number of samples, no correlation between TL and $\delta^{15}N$ values was found for neither *H. griseus* ($r=0.040$; $p=0.907$) nor *P. glauca* ($r=-0.072$; $p=0.807$). There was also no correlation between TL and $\delta^{13}C$ values neither for *H. griseus* ($r=0.084$; $p=0.807$) nor for *P. glauca* ($r=0.320$; $p=0.264$) (Figure 3).

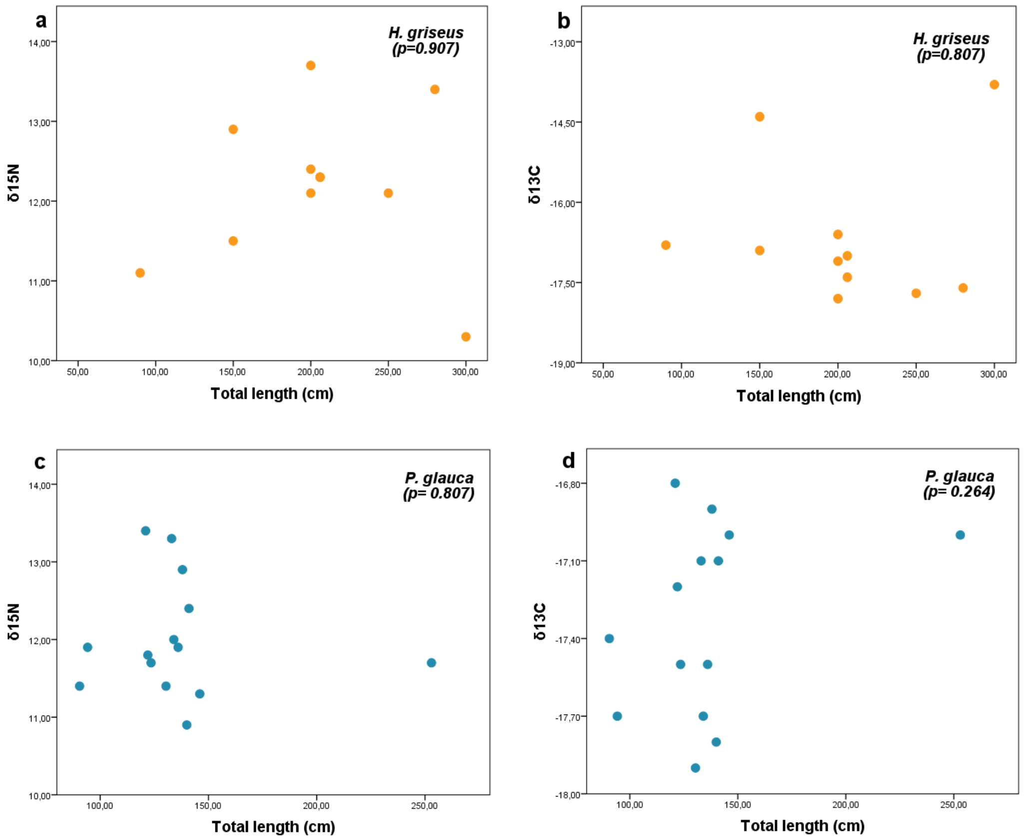

Fig 3. Relationships between the $\delta^{15}N$ and $\delta^{13}C$ isotopic values of *H. griseus* (a, b) and *P. glauca* (c, d) and their total size. *Hexanchus griseus* (orange), *P. glauca* (blue).

The results of the SIMMR revealed that *G. melastomus* had a diet based on decapod crustaceans, with small pelagic fishes as secondary prey (Figure 4b). This result agrees with previous information (see discussion) and suggests that SIMMR likely provides reliable information about the diet of the focal shark species. According to SIMMR, cephalopods were the main prey for all the mid-size and large shark species studied, although differences existed in the relative contribution of teleost fishes to the diet. Whereas *A. vulpinus*, *I. oxyrinchus* and *S. acanthias* solely relied on cephalopods (Figure 4a), mid-size pelagic fishes were also relevant for *H. griseus* and *P. glauca* (Figure 4c and d) (see Supplementary Figure 1). After correcting for the appropriate TDF of each taxonomic group, the $\delta^{13}C$-$\delta^{15}N$ biplot revealed that all focal sharks occupied a unique isotopic niche, different from that of predatory teleosts (*E. alletteratus*, *S. sarda* and *X. gladius*) and odontocete cetaceans (Figure 5).

The highest mean TP was that of *A. vulpinus* (4.7 ± 0.0), followed by *I. oxyrinchus* (4.5 ± 0.4), *H. griseus* (4.4 ± 0.4), *P. glauca* (4.3 ± 0.3) and *S. acanthias* (4.2 ± 0.1) (Table 1).

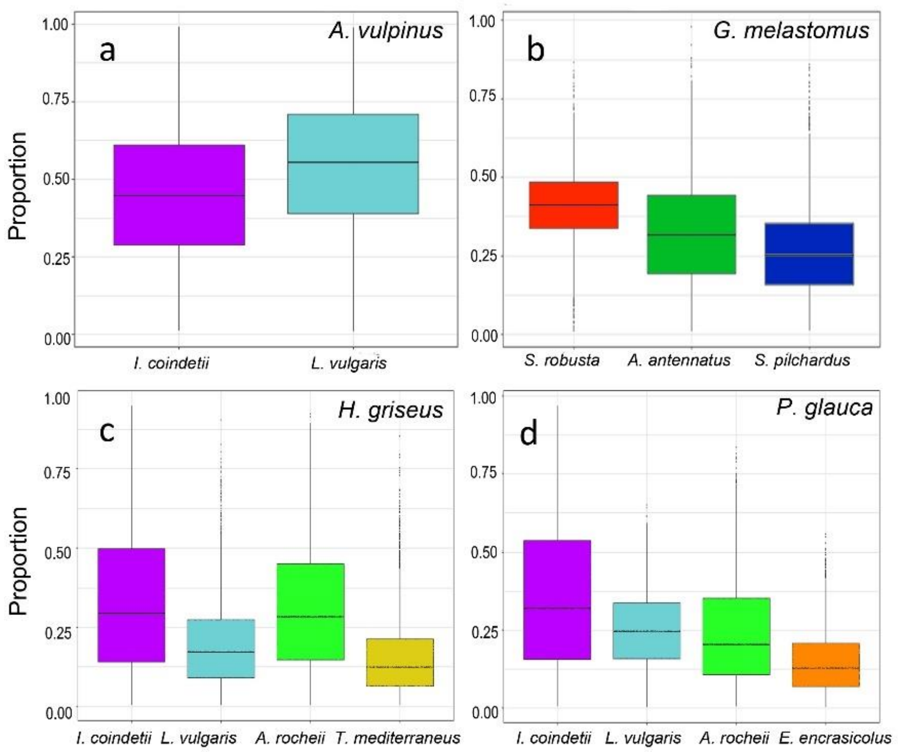

Fig 4. Contribution of potential prey to the diet of *A. vulpinus* (a), *G. melastomus* (b), *H. griseus* (c) and *P. glauca* (d) according to the Stable Isotope Mixing Model in R (SIMMR).

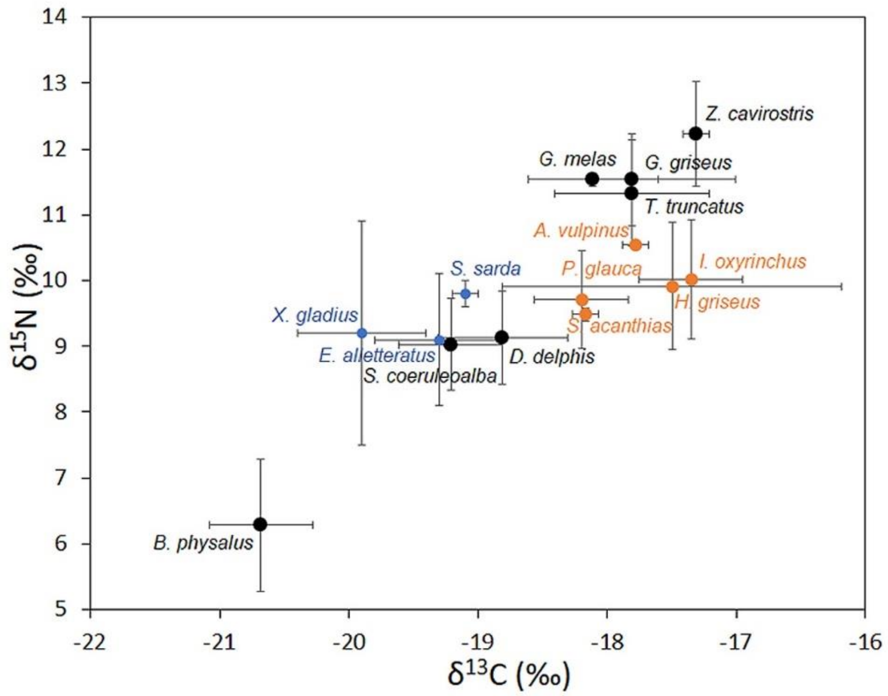

Fig 5. $\delta^{15}N$ and $\delta^{13}C$ values of sharks (orange), predatory bony fishes (blue) and cetaceans (black) from the northwestern Mediterranean Sea.

Discussion

Most shark species are currently very scarce in the northwestern Mediterranean Sea (Ferretti, 2008; Nuez et al., 2021; Walls & Dulvy, 2021), which makes it difficult to collect a large number of samples. Currently, *Hexanchus griseus* and *P. glauca* are the only two large species regularly caught by fishermen in the study area (Nuez et al. 2021) and this explains their larger sample size. Most of the other species proved to be extremely inaccessible as their captures were rare and also because some of them -*A. vulpinus*, *G. galeus* and *I. oxyrinchus*- are protected in Spanish waters through the Spanish List of Species Under Special Protection (LESPRE), meaning they cannot be either retained on board or taken to port. Moreover, *G. galeus* and *I. oxyrinchus* are also listed in Annex II of the SPA/BD Protocol of the Barcelona Convention (UNEP/MAP, 1995). Consequently, the sample size of these species was low.

On the contrary, the much smaller *G. melastomus* is a common bycatch of bottom trawlers operating on the continental slope of the western Mediterranean (Alomar & Deudero, 2017; D'Iglio et al., 2021) and its diet has been accurately described by means of stomach contents analysis (Fanelli et al., 2009; Albo-Puigserver et al., 2015). TDF values are critical in dietary studies based on stable isotope analysis and some kind of validation is required. Here, we used *G. melastomus*, because of its high availability and previous knowledge of its diet, to assess the validity of the TDF values reported by Hussey et al. (2010). The similarity between the diet composition of *G. melastomus* emerging from SIMMR and that previously revealed by gut content analysis in the same area (Fanelli et al., 2009; Albo-Puigserver et al., 2015) confirmed the suitability of the TDF values from Hussey et al. (2010) and indicated that the diet composition of the remaining species emerging from SIMMR were not artefacts caused by the use of highly biased TDF values. This is particularly important when considering the high reliance on squid of most of the species studied here.

Alopias vulpinus, I. oxyrinchus and *S. acanthias* showed similar $\delta^{15}N$ values and squid-dominated diets in the study area, although *A. vulpinus* and *I. oxyrinchus* came out slightly on top of the group. The relevance of squid in the diets of *A. vulpinus* and *I. oxyrinchus* has been reported previously throughout stomach content analysis, both in the Atlantic and the Pacific, although their relative contribution compared to teleost fishes was variable (Stillwell and Kohler, 1982; Preti et al., 2004; MacNeil et al., 2005; Maia et al., 2006). For instance, Stillwell and Kohler (1982) and Maia et al. (2006) clearly showed cephalopods were a secondary prey category for *I. oxyrinchus* in the Atlantic Ocean, where teleosts dominated the diet. In another study also carried out in the Atlantic, Estrada et al. (2003) used SIA to assess the trophic position of several large sharks and reported differences in the contribution of cephalopods to the diet of *I. oxyrinchus* between inshore and offshore waters, with cephalopods being more important than teleosts offshore. Stillwell and Kohler (1982) had already reported this higher importance of cephalopods in the diet of *I. oxyrinchus* in offshore waters. Estrada et al. (2003) also suggested a cephalopod-rich diet for *A. vulpinus*, agreeing with Cortés (1999), while Preti et al. (2004) found that the squid species *Loligo opalescens* was second in importance in the diet of *A. vulpinus* after *Engraulis mordax,* with *L. opalescens* being considerably more prevalent in the cool-water period than in the warm-water/transitional period. Conversely, many studies have reported teleosts to be the most abundant prey group in the diet of *S. acanthias,* with the contribution of cephalopods ranging from negligible (Avsar, 2001; Demirhan et al., 2007: Gül & Demirel, 2021) to important (Henderson, Dunne & Flannery, 2002; Barría, Coll & Navarro, 2015).

Hexanchus griseus and *P. glauca* differed from the former three species by a higher relevance of mid-size pelagic fishes in their diets. As well as *A. vulpinus* and *I. oxyrinchus*, *P. glauca* is a large pelagic shark and a good number of previous dietary studies from different parts of the world show that it feeds mainly on teleosts, with cephalopods contributing little (McCord and Campana, 2003) to moderately (Clarke et al., 1996; Lopez et al., 2010; Barría, Coll & Navarro, 2015) to its diet. However, Cortés (1999) found the overall contribution of cephalopods was much higher, representing around 50% of the diet. The results of the present study were fairly similar and highlighted the large contribution of cephalopods (60%) to the diet of *P. glauca*, with teleost fishes accounting for the remaining part (40%).

As opposed to the pelagic habits of *P. glauca*, *H. griseus* is a deep-sea shark. In its diet assessment in the waters off South Africa, Ebert (1994) found that this shark feeds on cephalopods, teleosts, other chondrichthyans and marine mammals and the contribution of every prey group to the diet varied according to the individual life stage. Here, cephalopods represented the main prey group for *H. griseus* <120cm TL but their importance in the diet decreased as sharks grew bigger, being a secondary prey group in sharks between 120 and 200 cm TL and having minor importance in sharks >200 cm TL. In the Mediterranean Sea, several studies analysing stomach contents highlighted the high contribution of teleosts to the diet of *H. griseus* and also reported chondrichthyans to be a common prey group for this species (Barrull & Mate, 2000; Kabasakal, 2004; Celona et al., 2005). In their study of the diet of *H. griseus* in the Central Mediterranean, Celona et al. (2005) also found cephalopods in several stomachs and they represented the second most important food source for *H. griseus* after teleosts, a fact that coincides with findings of Barría, Coll & Navarro (2015) using SIA. The results of the present study showed a very similar isotopic niche for *H. griseus* and *P. glauca*, with cephalopods and teleosts representing approximately 60% and 40% of their diet respectively. These percentages are similar to those previously obtained by Barría, Coll & Navarro (2015) analysing stomach content but differ from their SIA results, which showed that teleosts had a much higher contribution than cephalopods to the diet of *H. griseus*. However, as in the present study, cephalopods and teleosts were also the only prey groups in the diet of this shark.

The high relevance of squids in the diet of *A. vulpinus, H. griseus, I. oxyrinchus*, *P. glauca* and *S. acanthias* analyzed here might result from two independent factors: ontogenetic dietary changes and scarcity of small pelagic fishes. Ontogenetic diet changes are common in sharks (Wetherbee and Cortes, 2004; Bethea et al. 2006; McElroy et al 2006) and cephalopods have been reported to prevail in the juvenile diet of certain species (e.g. Ebert 1994). Juveniles and immatures dominate shark catches in the Mediterranean Sea (Megalofonou et al., 2009), probably because adults are scarce as a consequence of the high mortality rates they experience (Ferretti et al. 2008). This explains why most individuals of the larger species analyzed here were relatively small: no *I. oxyrinchus* was larger than 100 cm TL, no *P. glauca* was larger than 200 cm TL except for one individual and only two *H. griseus* were larger than 200 cm TL (253 and 280 cm TL each). The prevalence of squids in their diets could be a consequence of their small size, yet $\delta^{15}N$ or $\delta^{13}C$ values were uncorrelated with total length in the samples of *H. griseus* and *P. glauca* and hence no ontogenetic change was evident within the considered range (100-250 cm).

The second potential explanation for the high reliance of Mediterranean sharks on squids could be a sharp decline in the abundance of small pelagic fishes in the western Mediterranean Sea during the past decades, as a result of the combined effects of overfishing and global warming (Coll et al. 2019). Cephalopod landings have also decreased, but this has happened more recently (Colloca et al. 2017). Previous research suggests that cephalopods usually do better in heavily fished ecosystems than teleosts (Caddy and Rodhouse, 1998). If so, the relative availability of squids as prey for sharks might have increased in the western Mediterranean Sea. Gómez-Campos et al. (2011) and Cardona et al. (2015) have also suggested a decreasing contribution of small pelagic fishes to the diet of other predators in the western Mediterranean Sea, though detailed, focalized studies are missing.

The unusual isotopic niche of *G. galeus* most likely has a different explanation, as it lays outside the regional isospace. Analyses of stomach contents in previous studies outside the Mediterranean Sea suggest that the medium-sized *G. galeus* mainly forage on benthic but also pelagic teleosts (Morato et al., 2003) and additionally on cephalopods (Lucifora et al., 2006). Those findings are also similar for this shark in the Mediterranean Sea (Barría, Coll & Navarro, 2015). However, the isotopic ratios of *G. galeus* in this study laid well outside the polygon delimited by the potential prey. Compared to liver or plasma, shark muscle has a low turnover rate (MacNeil et al., 2005; Logan & Lutcavage, 2010) and isotopic equilibrium may take up to 488 days to be reached, according to findings of MacNeil et al. (2005). Since only shark muscle was sampled in the present study, the extremely high mean $\delta^{15}N$ values of *G. galeus* compared to the other sharks might be a result of muscle not having reached a near or complete equilibrium isotopic state with the new environment, a consequence of the relatively little time spent by *G. galeus* in Mediterranean waters. In fact, *G. galeus* is known to undertake long-distance movements: some specimens tagged off the coast of England have been recaptured in the north of Iceland (Stevens, 1990) and several females tagged in the northeastern Atlantic have been recently recaptured in the Mediterranean Sea, proving an existing connectivity between the two areas (Colloca et al., 2019; Thorburn et al., 2019). There is not a clear reason for what drives *G. galeus* to enter the Mediterranean Sea but the presence of both gravid females and juveniles off the coast of Tunisia (Capapé & Mellinger, 1988) might indicate the Mediterranean basin might be a breeding area for this shark. Genetic data would help determine population connectivity across the Atlantic Ocean and the Mediterranean Sea (Colloca et al., 2019). In any case, the unusual values reported here suggest non-equilibrium with local sources and this prevents further speculation on the trophic ecology of *G. galeus*.

When the whole shark assemblage was compared with pelagic predatory teleosts and odontocete cetaceans, little overlap was observed in their isotopic niches. The predatory teleosts *E. alletteratus*, *S. sarda* and *X. gladius* and two species of small delphinids (*D. delphis* and *S. coeruleoalba*) had similar or lower $\delta^{15}N$ values than those of sharks but were highly depleted in $\delta^{13}C$ values. On the other hand, sharks and the largest odontocete cetaceans (*G. griseus*, *G. melas*, *T. truncatus* and *Z. cavirostris*) had very similar $\delta^{13}C$ values, although the latter had higher $\delta^{15}N$ values. The three fish species prey mainly on small pelagic teleosts, although *X. gladius* also feeds on demersal fish (Navarro et al., 2011). The diet of the small delphinids is also dominated by fish, although they also consume squids (Borrell et al. 2021). Conversely, cephalopods prevail in the diets of *G. griseus, G. melas* and *Z. cavirostris* (Astruc, 2005; Blanco, 2006; Bearzi et al., 2011; Borrell et al. 2021). Mediterranean squids are always enriched in ^{13}C compared to small pelagic fishes (e.g. Cardona et al. 2012; this study), which explains why teutophagous odontocete cetaceans are more enriched in ^{13}C than ichtyophagous fishes and delphinids and reinforces the hypothesis that sharks rely heavily on squids. *Tursiops truncatus* seems to be the only anomaly since it mostly relies on fish but is also highly enriched in ^{13}C (Blanco et al., 2001; Pedà et al., 2015).

Sharks have been commonly regarded as apex predators (Stevenson et al., 2007; Hussey et al., 2011) which usually feed at trophic position 4 or higher (Cortés, 1999; Estrada et al., 2003; Speed et al., 2012; Hussey et al., 2015). Nonetheless, this is not always true (Frisch et al., 2016; Bond et al., 2018). The results reported here indicate that sharks are currently at a similar trophic position to predatory teleosts and that some cetaceans occupy a higher trophic position than sharks in the northwestern Mediterranean Sea.

In conclusion, this study shows medium-sized and large sharks i) would be functioning at least as high-level mesopredators in the northwestern Mediterranean Sea; ii) occupy a unique isotopic niche that is not shared with either cetaceans or predatory teleosts. Further research on the apparently high contribution of cephalopods to the diet of sharks in the northwestern Mediterranean Sea is necessary, since it poses the question of whether cephalopods had historically been the predominant prey group in times when fish stocks had not yet been overexploited or instead their high consumption was an adaptative response to fish scarcity.

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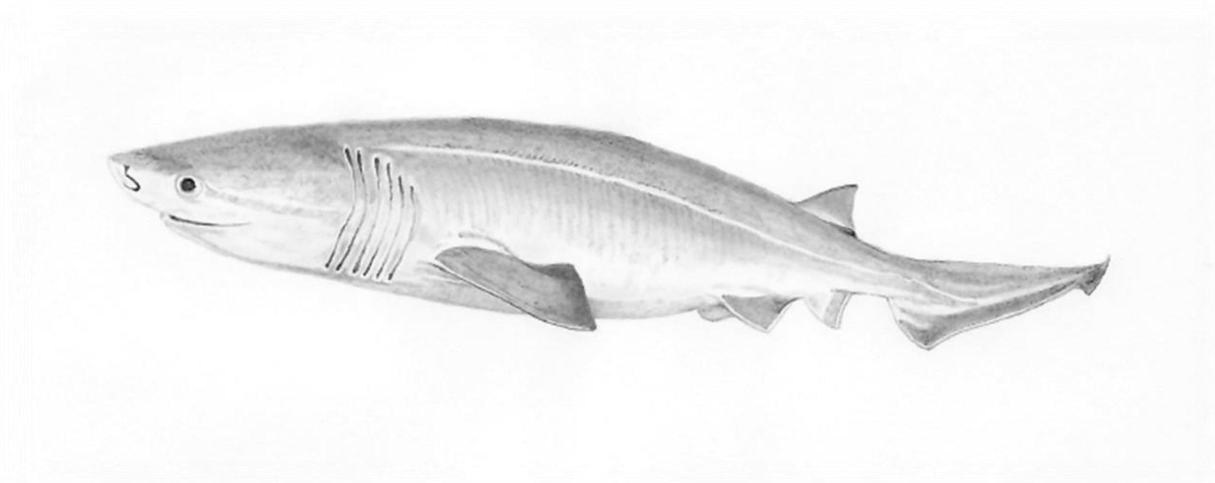

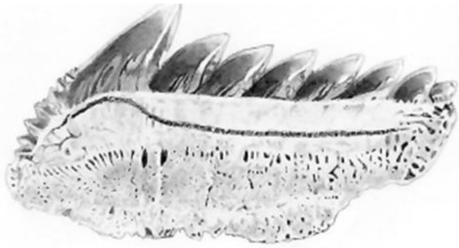

CAPÍTULO 3

3. Assessing the current status of *Hexanchus griseus* in the Mediterranean Sea using local ecological knowledge.

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Abstract:

Fishermen from 9 countries distributed throughout the Mediterranean Sea were interviewed between May and December 2019 with the aim of compiling information about the current impact of fisheries on a large deep-water shark species, the bluntnose sixgill shark (*Hexanchus griseus*). A total of 382 professional fishermen belonging to 6 different gears (bottom trawling, bottom longline, drifting longline, trammel nets, gillnets and polyvalent) took part in the study. Bottom trawlers were the most interviewed fishermen (n = 148) and the best fleet coverage was obtained for bottom longline (38.89%). Results showed most captures of *H. griseus* occur in the Western and Central Mediterranean Sea, particularly during the warm months of the year and most commonly by bottom trawlers and bottom longliners. At-vessel mortality (AVM) was rather low in all gears but a slightly higher degree of individual mortality is suggested in trammel and gillnets. The population trend of *H. griseus* in the Mediterranean Sea could not be inferred from the interviews as answers were highly variable, but the overall trend in some countries may suggest this species is showing signs of population decrease. The results of this study are mostly aligned with the latest IUCN assessment but also recommend reviewing the current status of *H. griseus* in the Mediterranean basin. Further empirical research on post-release mortality would also be advisable to implement measures that help reduce this source of mortality.

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1. Introduction

Sharks and their relatives are possibly facing the largest crisis of their 420-million-year history [77]. Despite playing a key role in the structure and function of marine communities [52,66], many shark populations have severely declined due to intense fishing worldwide [33,54,96]. It has been estimated that the median population biomass of sharks captured by fisheries had declined between 81% and 89% since fishing began [25] and large sharks in particular can suffer strong population declines even with light fishing pressure [43]. These declines have raised worldwide concern over the status of sharks and their survival greatly depends on science-based legislation, which can establish sensible catch quotas for commercial species and effective protection for those species of concern [69]. Nonetheless, catch quotas are not applied everywhere. This is the case of the Mediterranean Sea, where indirect measures to control fishing effort do not exist except for the bluefin tuna (*Thunnus thynnus*), the only fish species regulated by a Total Allowable Catch (TAC) [21].

The Mediterranean Sea represents a hot spot for elasmobranchs but they are exposed to multiple threats such as habitat loss and degradation, pollution, eutrophication, climate change, invasion by alien species and most importantly, intense fishing [20,67]. Most elasmobranchs inhabiting the Mediterranean Sea are demersal and many of them are the bycatch of demersal fisheries, particularly bottom trawling [88], though some species can also be caught by longlines [13,49] and nets operating in shallower waters [86]. Demersal sharks share the same life traits as their pelagic counterparts; they also follow a K-selected life history strategy, characterised by slow growth, late sexual maturity, long life spans, low fecundity and a low capacity for population increase [71,82]. Detailed studies on the distribution and abundance fluctuations of demersal sharks tend to be focused on the most common species [88], such as the small-sized *Scyliorhinus canicula* and *Galeus melastomus* [17, 30,51,75], while little information is compiled about other larger species [22].

The Bluntnose sixgill shark (*Hexanchus griseus*) is a common shark in the Mediterranean Sea and is the biggest member of the Hexanchidae family, reaching up to 500 cm total length (TL) [39]. In Southern African waters, males mature at about 310 cm TL and females are mature at 420 cm TL [35], while in the Mediterranean Sea this species is believed to reach maturity at a slightly smaller size. This was first suggested by Capapé et al. [16] and later reported by Vella & Vella [93], who estimated the maturity size for males and females at about 270 and 400 cm TL. *Hexanchus griseus* is a deep-water species living over insular, continental shelves and upper slopes [24] which can be found at depths of up to 2500 m [64], even though it has also been reported at 200 m from the surface off southern Sicily and between Tunisia and Malta [42]. It is also a common bycatch species that is mainly captured by both bottom and mid-water trawlers but also by gillnets, trammel nets, longlines, handlines and traps [78]. Mislabelling is not rare in this species and this shark is sometimes sold under the common names of other sharks [48]. *Hexanchus griseus* is currently assessed as "Least Concern" in the Mediterranean Sea by the International Union for Conservation of Nature (IUCN), though the fact that it can get caught by this wide range of fishing gears, in addition to counting on little international protection, makes monitoring its population trend important for its preservation, especially under the current degree of fishing pressure [78] and also considering this is a highly migratory species, according to the 1982 Convention on the Law of the Sea [89]. Species that can move over long distances are more likely to move through different jurisdictional boundaries [53], getting exposed to being caught by fisheries in the process and so complicating conservation efforts. It is without a doubt reasonable to prioritize conservation measures aimed at protecting and preserving threatened species, but neglecting non-threatened species can bring about undesirable scenarios that could have been avoided. Unfortunately, this was the case for the blue shark (*Prionace glauca*) in the Mediterranean Sea, a shark that had been assessed as "Vulnerable" in 2006 [19], "Near Threatened" in 2009 [81] and changed to "Critically Endangered" in 2016 [32].

A practical method to obtain high-quality and low-cost information [2] about the abundance and population trends of a given species is using the Local Ecological Knowledge (LEK) held by communities, taken as "a cumulative body of knowledge, practice and belief evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment" ([10]: 1252). Integrating LEK in the management of marine resources often leads to increased participation, compromise, responsibility and empowerment of stakeholders [9,55]. Therefore, the combination of LEK with scientific assessments has the potential to improve management schemes [8,23,45, 76].

To this end, this study aimed at compiling new up-to-date information about the abundance and population status of *H. griseus* in the Mediterranean Sea using fishermen's LEK from 9 different countries. Most specifically, the study focused on looking into several features related to captures of *H. griseus* in every sampling port from each country as well as analysing the fishermen's impressions regarding the population trend of this species. Finally, the results obtained in the study were used to discuss the suitability of the IUCN's latest Mediterranean assessment for *H. griseus* [78] in the present.

2. Material and methods

2.1. Study area

The study was conducted by researchers from a total of 9 (Albania, Cyprus, France (South), Greece, Italy, Libya (East), Montenegro, Spain (Northeast) and Tunisia) of the 21 countries that have coastline in the Mediterranean Sea, allowing the study to cover part of the Western, Central and Eastern basin along with a part of the Adriatic Sea (Fig. 1). Countries were selected according to their location in the basin, fleet volume and composition and total landings. Given the fact that in most cases there was only one researcher per country, only certain ports of each country were sampled except in Montenegro, which was the only country sampled in its totality. In Italy, all sampled ports were in Sicily except for one, the fleet of which operated in the Tyrrhenian Sea, whereas the fleet of the remaining sampled ports operated mostly in the Ionian Sea and the Tyrrhenian Sea. No Italian ports were sampled in the Adriatic Sea. Altogether, the ports sampled in this study fell within the GFCM geographical subareas 6, 7, 9, 10, 13, 14, 16, 18, 19, 21, 22 and 25.

2.2. Questionnaire-based surveys

Interviews with local fishermen were conducted from May to December 2019 and were often conducted at various ports within each country. Consequently, most of the GSAs featured in this study comprised more than one sampling port. However, GSAs 9 and 10 (Italy) and GSA 14 (Tunisia) only featured one port.

Considering the depth distribution of *H. griseus*, the range of fishing gears that can capture this species according to Capapé et al. [15] and Soldo et al. [78] and also the expertise of all the participating researchers, bottom trawling, bottom longline, trammel nets and gillnets were selected as the target fishing gears of this study. In many countries, some fishermen switch gears throughout the year, most usually alternating between small longlines and trammel nets or gillnets. These vessels were also considered a target and regarded as "polyvalent vessels", a term used by the GFCM to define "*all the vessels using more than one gear, with a combination of passive and active gears, none of which exceeding more than 50 per cent of the time at sea during the year*". In various Mediterranean countries, bottom longline, trammel nets and gillnets are used by Small Scale Vessels (SSV) as well. According to the EU definition, SSV have an overall length of less than 12 m and do not

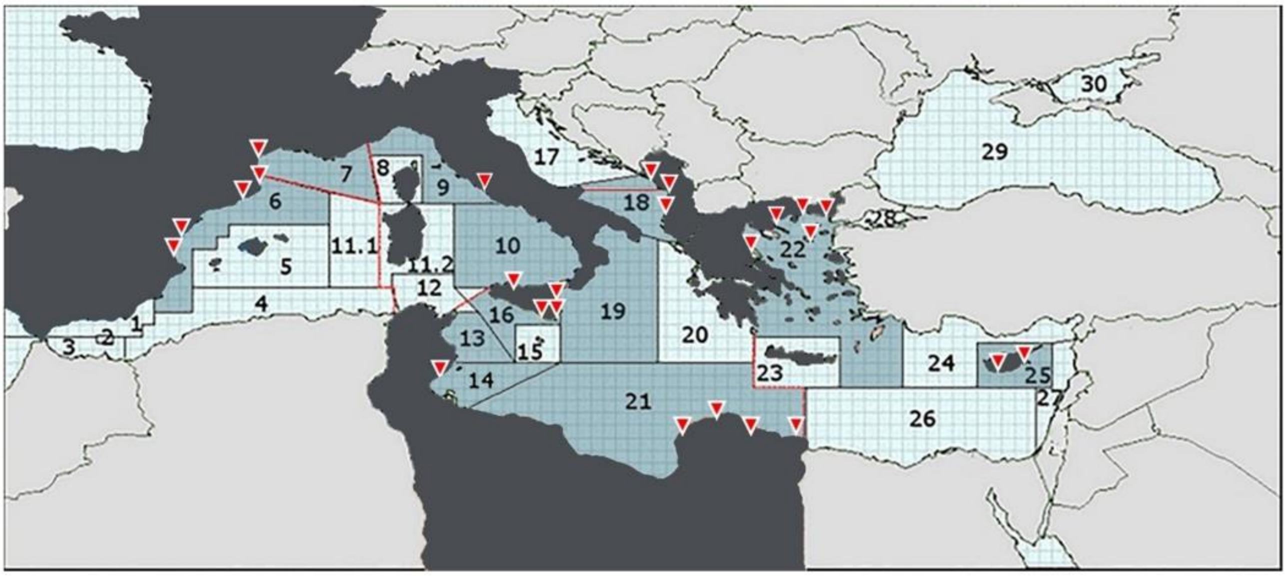


Fig. 1. Map of the Mediterranean Sea including all General Fisheries Commission for the Mediterranean Geographical subareas GSAs. All countries participating in the study are featured in black and GSAs including at least one sampling port are featured in grey. Sampling ports are shown as red pins in every country. Since some sampling ports were very close to each other, some pins represent more than one of these ports.

use towed fishing gear [38]. Although SSV can also switch gears throughout the year, the interviewed SSV in this study were not considered as such but rather the data was analysed according to the fishing gear, that is bottom longlines, trammel nets, gillnets and more than one gear (polyvalent).

The interviews were carried out using modified surveys adapted for the target species (see Annex 1). This methodology has proved to be effective in assessing the occurrence and accidental captures of other species of marine megafauna in the Spanish Mediterranean Sea [1,18, 68], Italy [23] and Greece [87]. Before the beginning of the interview, the fishermen were given some identification forms and pictures of *H. griseus* as well as the other two Hexanchidae present in the Mediterranean Sea (*H. nakamurai* and *Heptanchias perlo*). The questionnaire started with a demographic part and information regarding the fishing gear and then proceeded with a set of questions concerning biological aspects of the species, bycatch frequency, seasonality of reported captures, capture condition at the moment of being taken aboard, regarded as at-vessel mortality (AVM) and also their perception about population trend. Each interview lasted an average of 30 min, though their duration was also subject to the fisherman's availability at the moment of interviewing. Questions were laid out in a relaxed way to allow each interviewee to feel as comfortable as possible and facilitate the flow of information.

In order to assess bycatch frequency, respondents of each fishing gear were asked to report the number of *H. griseus* that had been captured both from 2018 to 2019 and from 2007 to 2017, trying to be as accurate as possible to check if the abundance and distribution of captures from 2018 to 2019 followed a similar pattern to that from 2007 to 2017. When reporting captures, respondents were always asked to give exact numbers. If exact numbers could not be obtained, respondents had to give an approximate number or interval. Nonetheless, a few answers had to be registered as "several", "a lot" or "too many". In those cases, "several" was counted as $n = 5–10$ and both "a lot" and "too many" were counted as $n > 10$. Regarding the seasonality of captures, respondents were asked to indicate the time of the year (months) they had captured *H. griseus* from 2018 to 2019 and from 2007 to 2017. A Chi-squared test [26] was carried out using IBM SPSS Statistics (Version 24) predictive analytics software to check whether captures were distributed similarly between the times of the year when the water column is stratified (May to October) and non-stratified (November to April). A Chi-square test was also used to check whether the probability of capturing *H. griseus* was due to a change in fishing effort (number of fishing months) between these two times of the year for the fishing gears that captured most individuals (bottom trawling, bottom longline and trammel and gillnets).

To assess AVM, respondents who had caught *H. griseus* at least once from 2007 to 2019 were asked whether the captured individuals were alive at the moment of either hauling the nets or pulling up the hooks. Five frequencies were given: "always", "often", "sometimes", "hardly ever" and "never". Similarly, the respondents' perception of the population trend of *H. griseus* was obtained by asking them to choose one of the following categories according to their impressions: "increasing", "stable", "decreasing" or "severely decreasing".

2.3. *Hexanchus griseus* bycatch estimations

The bycatch rate of *H. griseus* for gear z (Tz) was computed as in FAO [40]:

$$Tz = \frac{Nz}{Dz}$$

where N_z is the number of *H. griseus* caught by interviewed fishermen of gear z from 2018 to 2019 and D_z is the number of interviewed vessels of gear z.

The estimation of total *H. griseus* bycatch (C_z) was calculated as,

$$Cz = \sum Tz \cdot Doz$$

where D_{oz} is the total number of registered vessels of gear z in all sampled ports of each country.

2.4. Methodological considerations

Given that the questionnaires were only conducted by one researcher in most countries and that adjustments were made to the economic considerations, researchers were encouraged to use their expertise and critical thinking to sample the most relevant ports and gears, trying to conduct as many interviews as possible.

In regional studies that tackle marine wildlife conservation, other factors that might not need to be contemplated at a smaller scale come into play. Although some countries are culturally very much alike, each country also has its own culture and particular mindset. Fishermen might for instance be more collaborative in certain countries than in others depending on the attitude of the researcher. Others might only decide to collaborate if they can be economically rewarded and, on some occasions, their knowledge of a fixed and pressing issue may predispose them to a higher level of engagement and cooperation. This predisposition of fishermen to collaborate is also highly related to the bond that the researcher has forged with them in other previous studies. Lastly, political and socio-economic issues can also compromise the course of a study by fostering instability, which might restrict mobility around different sampling locations.

For the purpose of the study, the official current fishing fleet statistics of every sampled port were obtained in all countries except for Libya. Since its only existing fleet counting dates back to the early 2000 s, this study excluded that source of information from the analysis as it would not be portraying the current state of the fleet. Instead, this study made use of an alternative estimation of the fleet volume provided by a local fisheries researcher who personally took a census of all active vessels of every gear in all sampling locations.

3. Results

3.1. Fleet coverage

382 professional fishermen from a total of 47 ports were interviewed. Of these 47 ports, 2 were in Albania and in Cyprus, 4 in S France, 8 in Greece, 7 in Italy, 9 in E Libya and in NE Spain, 5 in Montenegro and 1 in Tunisia. Italy was the country with the most interviews (144) from its sampled ports, followed by NE Spain (79) and Greece (50) (Fig. 2). Tunisia was fourth with a much lower number of interviewed fishermen compared to the first three countries (29), closely followed by Montenegro (22), Cyprus (19), E Libya (15), Albania (14) and, with the lowest number of interviewed fishermen, S France (10).

When split into all the fishing gears, bottom trawling (BT) had the highest number of interviewed fishermen, with a total of 149 (Fig. 3). Trammel nets (TN) had a total of 102 interviewed fishermen, followed by polyvalent vessels (PV), with 56 interviews, bottom longline (BL) (40), gillnets (GN) (22) and drifting longline (DL) (13).

Italy had the highest number of interviewed bottom trawlers (64), followed by NE Spain (43), Albania (14), Tunisia (12), Greece (8), Montenegro (6), Cyprus and E Libya (1 each) (Fig. 3). Italy was also the country with the most interviewed bottom longliners (14), followed by Greece (11), NE Spain (10) and Tunisia (5). Four drifting longliners were interviewed in Tunisia, followed by NE Spain, Cyprus and E Libya (3 interviews each). The highest number of interviewed trammel net fishermen was in Italy (65), followed by NE Spain and Greece (16 each), Tunisia (3), Cyprus and Montenegro (1 each). Greece had the highest

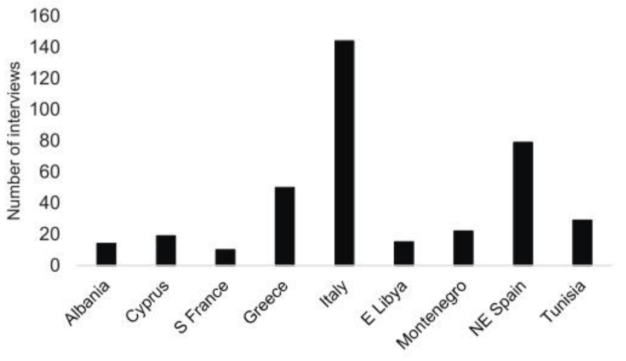


Fig. 2. Number of interviewed fishermen in the sampling ports of each country.

number of interviewed gillnet fishermen (15), followed by NE Spain (3), Montenegro (2), Italy and Tunisia (1 each). Finally, the highest number of interviewed fishermen using more than one gear (polyvalent) was that of Cyprus (14), right before Montenegro (13), E Libya (11), S France (10), NE Spain and Tunisia (4 each).

For the fleet coverage analysis, trammel nets and gillnets were merged into the same category and regarded as TGN, which also included the few remaining polyvalent vessels that either did not use trammel and gillnets or combined these nets with other gears, excluding traps. For further analysis, trammel and gillnets were also kept together as TGN but the remaining polyvalent vessels were treated as another category, named “other polyvalent vessels”.

For all the sampled ports in all countries, the highest fleet coverage was achieved in BL (38.89%) (Table 1). DL and BT had a total coverage of 25% and 18.72% respectively, whereas the fleet coverage for TGN (2.99%) was really low. BT had the highest fleet coverage in Cyprus (50%) and NE Spain (41.35%), followed by Montenegro (37.50%), Italy (26.78%), Albania (16.28%), Greece (7.84%), E Libya (7.14%) and Tunisia (4.72%) (Table 2). NE Spain and Italy were first and second in fleet coverage of BL, though with a much higher difference (71.43% and 18.42% respectively) and were followed by Greece (3.96%). Cyprus and NE Spain were the only two countries where the fleet coverage for DL could be obtained, and it was 33.33% for Cyprus and 20% for NE Spain. TGN had the highest coverage in S France (32.26%) and Italy (30.95%), followed by Montenegro (14.95%), NE Spain (14.84%), E Libya (3.77%) and Greece (2.15%).

3.2. Captures of *Hexanchus griseus*

According to respondents, a total of 2109 *H. griseus* were captured from 2007 to 2017 and these captures were distributed amongst 12 GSAs. GSA 6, which represents almost 2/3 of the Spanish coastline, was the geographical subarea with the most captures of *H. griseus*, with a total of 926 reported individuals (Fig. 4, top). The second GSA with the most captures of *H. griseus* was GSA 16 (Southern Sicily) (n = 292), followed by GSA 19 (Ionian Sea; n = 263), GSA 22 (Aegean Sea; n = 211), GSA 9 (Ligurian Sea and North Tyrrhenian Sea); n = 155), GSA 21 (off Libya) and GSA 25 (off Cyprus) (n = 73 each), GSA 10 (South and Central Tyrrhenian Sea; n = 70), GSA 14 (off Tunisia; n = 36), GSA 18 (Adriatic Sea; n = 8), GSA 13 (also off Tunisia; n = 3) and GSA 7 (Southern France; n = 1).

When divided by GFCM subregions, the highest number of captures of *H. griseus* from 2007 to 2017 was found in the Western basin (n = 1152). The Central basin represented the second subregion with the most captures (n = 667) and the Eastern basin hosted the lowest number of captured *H. griseus* from the three basins (n = 284). Only 8 captures were found in the Adriatic Sea.

From 2018–2019, a total of 218 *H. griseus* were captured in 10 GSAs. GSA 6 was again the GSA with most captures (n = 52), followed by GSA 16 (n = 37), GSA 19 and 21 (n = 33 each), GSA 9 (16), GSA 25 (n = 14), GSA 22 (n = 13), GSAs 10 and 14 (n = 8 each) and GSA 18 (n = 5) (Fig. 4, bottom). No captures of *H. griseus* occurred either in GSA 7 or GSA 13.

The Central basin gathered most of the captures of *H. griseus* (n = 111) from 2018 to 2019. The Western basin was second in number of captures (n = 76), followed by the Eastern basin (n = 27) and the Adriatic Sea (n = 5).

From 2007–2017 and for all sampling regions, bottom trawling was the fishing gear with most captures of *H. griseus* (n = 782), followed closely by bottom longline (n = 689), trammel and gillnets (n = 515), drifting longline (n = 92) and other polyvalent vessels (n = 31), (Fig. 5). Bottom trawling also had the highest number of captured *H. griseus* from 2018 to 2019 (n = 91), followed by trammel and gillnets (n = 67), drifting longline (n = 37), bottom longline (n = 21) and other polyvalent vessels (n = 2).

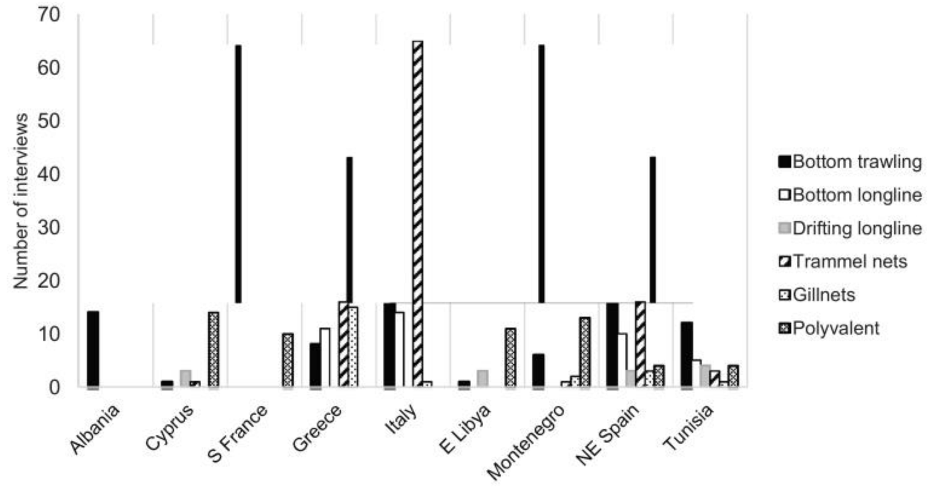


Fig. 3. Number of interviewed fishermen of each fishing gear in the sampling ports of each country.

Table 1
Number of interviewed fishing vessels of every gear in all sampled ports relative to the total fleet volume of the ports and the corresponding percentage (%). (BT=Bottom Trawling; BL=Bottom Longline; DL=Drifting Longline; TGN=Trammel and Gillnets + other polyvalent). [1]5 BL vessels from Tunisia were not included in the table since there was not enough information concerning the total fleet volume to obtain an accurate estimation. [2]4 DL from Tunisia and 3 DL from E Libya were not included in the table since there was not enough information concerning the total fleet volume to obtain an accurate estimation.

	BT	BL[1]	DL[2]	TGN
Interviewed	149	35	6	180
Total	796	90	24	6005
%	**18.72**	**38.89**	**25**	**2.99**

Table 2
Summary of the total fleet coverage of each fishing gear and for all the sampled ports in every country. Values are expressed in %. (BT=Bottom Trawling; BL=Bottom Longline; DL=Drifting Longline; TGN=Trammel and Gillnets + other polyvalent). [1]5 BL vessels from Tunisia were not included in the table since there was not enough information concerning the total fleet volume to obtain an accurate estimation. [2]4 DL from Tunisia and 3 DL from E Libya were not included in the table since there was not enough information concerning the total fleet volume to obtain an accurate estimation.

	BT	BL[1]	DL[2]	TGN
Albania	16.28	–	–	–
Cyprus	50	–	33.33	20.90
S France	–	–	–	32.26
Greece	7.84	3.96	–	2.15
Italy	26.78	18.42		30.95
E Libya	7.14	–	–	3.77
Montenegro	37.50	–	–	14.95
NE Spain	41.35	71.43	20	14.84
Tunisia	4.72	–	–	0.48

3.3. Seasonality

June (35.31%) and July (30.56%) were the months when most captures of *H. griseus* occurred. The lowest frequency of captures was found in December, January and February (14.24%) (Fig. 6).

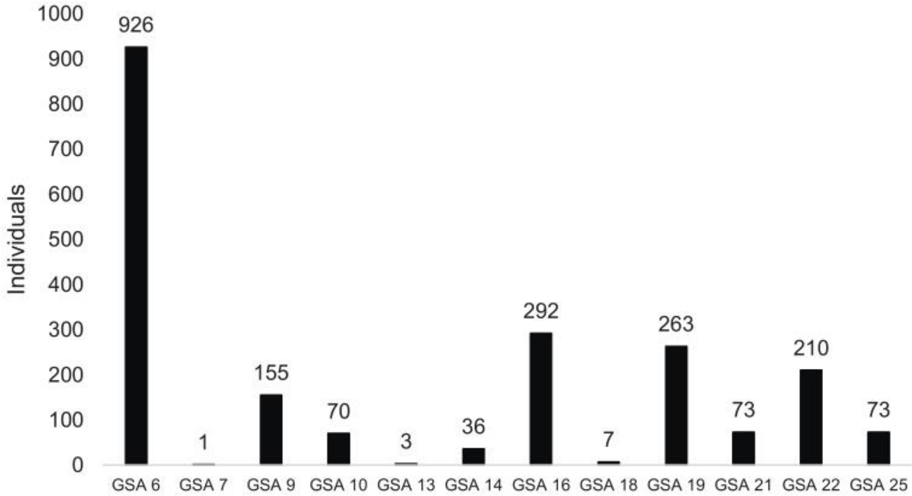
The relationship between the time of the year when there is water stratification and the captures of *H. griseus* was statistically significant (x^2 =53.06; p = 0.00). While no significant difference was found in the seasonal distribution of the fishing effort of bottom trawling (x^2 =1.01; p = 0.32), the seasonal distribution of the fishing effort of bottom longline and trammel and gillnets was significantly different (x^2 =5.77, p = 0.02; x^2 =15.36, p = 0.00).

3.4. At-vessel mortality (AVM)

The results for bottom trawling, bottom longline and drifting longline showed *H. griseus* was usually alive when taken aboard (Fig. 7). In bottom trawling, the most frequent answer amongst interviewed fishermen was that *H. griseus* was always alive at the moment of hauling (60%), followed by sometimes alive (17.50%). The frequencies for those answers that indicated captured individuals were always or most of the time already dead, were low or very low (12.50% and 2.5%, respectively). Bottom and drifting longline shared very similar results. Like in bottom trawling, the most frequent answer in both cases was that individuals were always alive when pulling up the hook (53.85% and 50%), followed by being most of the times alive (30.77% and 30.33%). No fisherman considered that captured individuals were either always or most of the time dead when pulling up the hooks. On the other hand, the highest frequency in trammel and gillnets was found in "sometimes" (40%), being the only gears in which the probability of capturing *H. griseus* alive was as likely as capturing it dead. Capturing individuals always alive had the second-highest frequency (20%), followed by "hardly ever" (16%). Frequencies for capturing *H. griseus* alive, most of the time and never were both the same and also the lowest (12%). Finally, only four answers were obtained from fishermen using other polyvalent vessels and the frequency to which fishermen believed *H. griseus* was always, most of the time, sometimes and never alive had the same value (25%).

3.5. Population trend of Hexanchus griseus

Information was gathered from 7 countries (Albania, Cyprus, Greece, Italy, E Libya, NE Spain and Tunisia) to assess the population trend of *H. griseus* according to the fishermen's perception. A clear majority of the interviewed fishermen from Albania (66.67%) and Tunisia (74.07%) considered that the population of *H. griseus* was decreasing (Fig. 8), whereas respondents from Greece and NE Spain mostly believed the population trend of this shark was stable (56.25% and 38.78%, respectively). The frequency of "increasing" was low in all countries, with Cyprus having the highest frequency for this answer (10.53%). No respondent believed populations of *H. griseus* could be increasing neither in E Libya nor in Italy. The frequency to which respondents considered populations of *H. griseus* to be severely decreasing was really low in



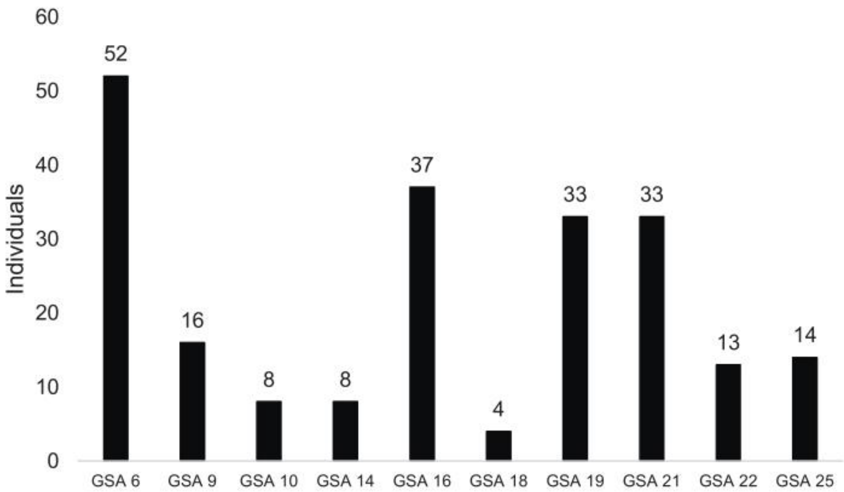


Fig. 4. Number of *H. griseus* captured by interviewed fishermen from 2007 to 2017 (top) and from 2018 to 2019 (bottom) in all GSAs with at least one capture.

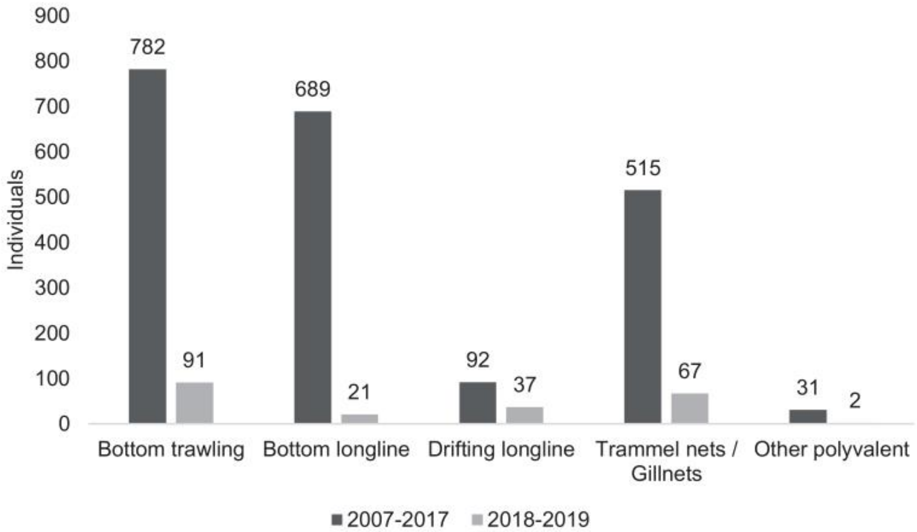


Fig. 5. Recorded captures of *H. griseus* per fishing gear from 2007 to 2017 and from 2018 to 2019 by interviewed fishermen.

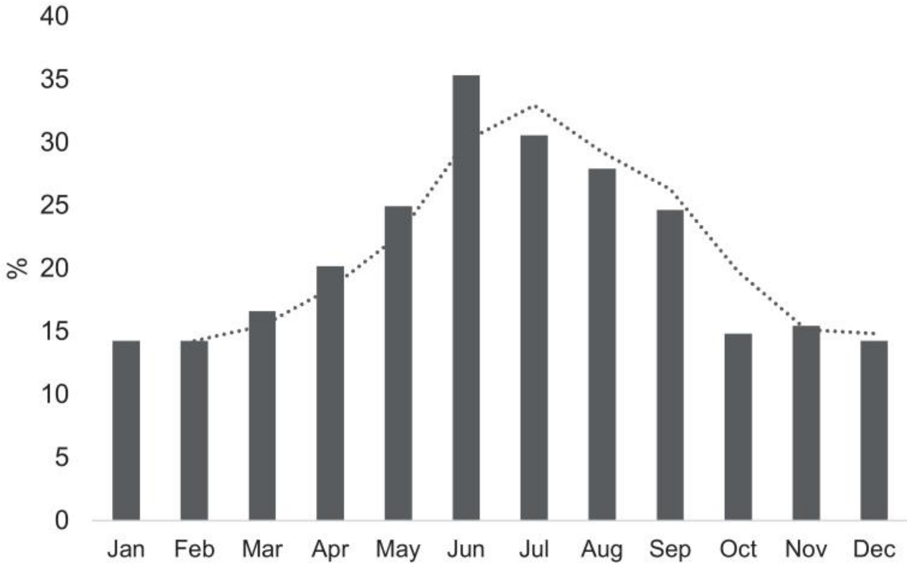


Fig. 6. Percentage (%) of captures of *H. griseus* per month by the interviewed fishermen.

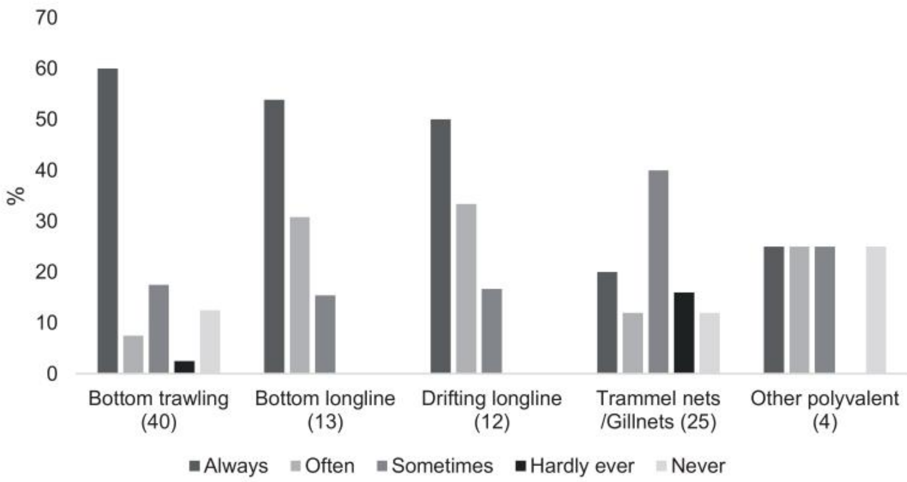


Fig. 7. Frequencies (%) of AVM in *H. griseus* (by interviewed fishermen (n) who had caught at least one *H. griseus* from 2007 to 2019).

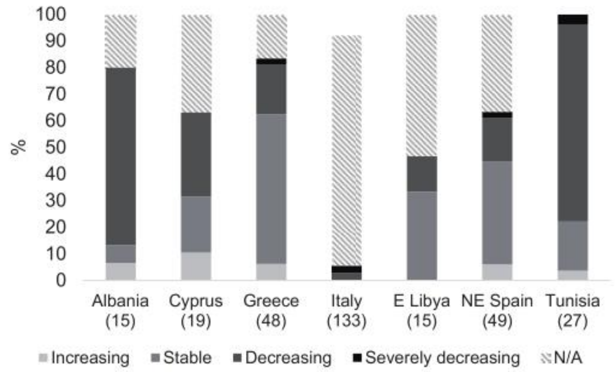


Fig. 8. Population trend of *H. griseus* according to the fishermen's perception.

Greece (2.08%), NE Spain (2.04%), Italy (2.26%) and Tunisia (3.7%), and inexistent in Albania, Cyprus and E Libya. N/A had the highest frequency in Italy (94.74%), followed by E Libya (53.33%), Cyprus (36.84%), NE Spain (36.73%), Albania (20%) and Greece (16.67%).

4. Discussion

4.1. Fleet coverage

Overall, bottom longline had the highest fleet coverage of all fishing gears but a high degree of variability in the fleet coverage was noted when broken down into each country's sampled ports. Bottom trawling, bottom longline and trammel and gillnets had the highest fleet coverage in the ports of Italy, NE Spain, Cyprus and S France. Bottom trawling had a solid fleet coverage in the ports of the first three countries (see Table 2) and was surveyed in ports of all countries except for S France. However, not much information regarding bottom trawling can be extracted from Cyprus, since such a high coverage is a result of a very small trawling fleet in the entire country (one interviewed vessel from a total of two bottom trawlers fishing in territorial waters). A significantly higher number of bottom trawlers were interviewed in the two ports sampled in Albania (n = 14), 6 bottom trawlers from a total of 16 were also interviewed in Montenegro and 11 bottom trawlers were surveyed in Tunisia.

The fleet coverage for bottom trawling in all the sampled ports in E Libya was actually higher than that of Tunisia, yet only one bottom trawler was interviewed in E Libya. We therefore believe results and interpretations concerning bottom trawling in this study were biased towards Italy and Spain, with a total of 107 interviewed bottom trawlers, as they represented the two countries which by far provided the most information about this fishing gear.

While bottom trawling and trammel and gillnets were sampled in almost all countries included in this study (except for S France and Albania, respectively), interviews with bottom and drifting longliners were only carried out in a few countries. The reason why some gears were not surveyed in certain countries had two main explanations: sometimes, researchers in charge of the interviews had to prioritize sampling the most relevant fishing gears for the study. Other times, some fishing gears were not part of the actual fleet of some sampled ports.

The major shortcoming concerning fleet coverage and data collection originated in Libya. This was ascribed to the ongoing period of national instability, which hindered the researcher's fieldwork in the region by not being able to get to the capital and its surroundings due to the constant outbreaks of violence. Libya's situation perfectly exemplifies those fortuitous events that may occur when doing broad-scale multinational studies and can have an impact on the course of it. For safety reasons, this study only used data from E Libya. Only a few vessels, mostly polyvalent, were interviewed in the Libyan ports and no estimation of the fleet coverage could be made for drifting longline due to the lack of an actual reliable fleet volume estimation in those ports. This was another added problem occurring in Libya but also in Tunisia, where coverage values for bottom and drifting longline could not be obtained either.

4.2. Captures

Results of this study indicated that most captures of *H. griseus* tend to occur in the Western and Central Mediterranean Sea. Whereas most captures of *H. griseus* occurred in the Central basin from 2018 to 2019, the Western basin, particularly NE Spain, gathered most of the captures from 2007 to 2017. Occasional captures of *H. griseus* have been reported in the Catalan Sea for decades ([5,61,80]) and this shark has been recently regarded as a frequent bycatch in the Costa Brava [68]. In the Central Mediterranean Sea, the Strait of Sicily has been identified as a biodiversity hotspot [31,90] and hosts a great number of shark species, including the Mediterranean white shark (*Carcharodon carcharias*) [29, 85]. *Hexanchus griseus* is also present in the area [92], with some captures being landed in Tunisian ports (where an unusual capture of a shoal of up to 21 specimens took place recently (see [7]), southern Sicily and also the Maltese fish markets [73,91]. Data coming from the Mediterranean Large Elasmobranchs Monitoring (MEDLEM) also showed that the highest number of reported captures of *H. griseus* concentrated in the Central basin, with a considerable number of these captures occurring in the Tyrrhenian Sea, and the Northern Ionian Sea [59].

The present study did not survey either GSA 12 (northern Tunisia) or GSA 15 (Malta). However, given their proximity to GSA 14 and 16 (between Sicily and Tunisia), where some captures of *H. griseus* were reported, we believe bycatch of this species might also occur in those parts of the Central basin.

In the Eastern basin, records of large sharks in Turkish waters from 1980 to 2015 confirmed *H. griseus* was the predominant species, with the vast majority of specimens being recorded in the Sea of Marmara, followed by the Aegean Sea, the Levantine Sea and a few observations from the Black Sea [57,58]. Capapé et al. [15] also compiled some records of *H. griseus* off Tukey as well as Israel between the 1970 s and the 2000 s, but the number of records of this species coming from the Eastern basin was really inferior to those coming from the Western and Central basins. In their population genetics study, Vella and Vella [92] collected 86 and 34 specimens of *H. griseus* in the Central and Western basins respectively, but only 8 were captured in the Eastern basin. Capapé et al. [15] suggested *H. griseus* could be less abundant in the Eastern basin though other possibilities were considered, like the fact that the waters were less exploited or information was not reported to the same extent as in the other basins. The results of the present study also confirm *H. griseus* was captured in the Eastern Mediterranean Sea, particularly in the Aegean Sea, but the number of captures both from 2007 to 2017 and from 2018 to 2019 was comparatively much lower than those of the Western and Central basins.

Captures of *H. griseus* also take place in the Adriatic Sea [15,27,59], although they tend to be less frequent. The Adriatic Sea has the largest shelf area of the Mediterranean Sea. Although the Southern part (GSA 18) has a much narrower shelf and a steep slope, reaching maximum depths of more than 1200 m, the Northern and Central parts (GSA 17) have a bottom depth of no more than 100 m except in Pomo/Jabuka Pit [41]. Such low depths might not constitute the most suitable habitat for benthonic species and it would be reasonable to assume captures of *H. griseus* are much less likely to occur in the Northern and Central parts of the Adriatic Sea compared to other parts of the Mediterranean Sea. A few captures of this species in the Southern Adriatic Sea and also the southern part of the Central Adriatic Sea, which is represented by Montenegro, were also reported in the present study both from 2007 to 2017 and from 2018 to 2019 indicating that occasional captures of this species continue to occur in the present.

Notwithstanding, the number of sampled GSAs amongst GFCM subregions was not equally proportioned. Whereas ports from up to five GSAs were surveyed in the Central Mediterranean Sea, three GSAs were surveyed in the Western Mediterranean Sea, two in the Eastern Mediterranean Sea and one in the Adriatic Sea. Hence, this data bias must be taken into account when making interpretations.

In all years considered in the study, bottom trawlers were responsible for capturing the highest number of *H. griseus*, although a considerable number of individuals were also captured by bottom longliners. The fact that the bycatch of *H. griseus* mostly happened in these two gears fits in with previous research done in the Mediterranean Sea [6,61]. Both bottom trawling and bottom longline target much deeper depths than the other fishing gears included in this study, consequently having a higher probability of capturing *H. griseus*.

Fewer captures occurred in those fishing gears that are deployed at the surface, though drifting longliners captured a noticeable number of *H. griseus*. The set of biological and ecological features of *H. griseus* makes it difficult to suggest why such a deep-water species can be caught so close to the surface. To the best of the authors' knowledge, the occurrence of this species in the epipelagic region of the water column has never been reported. Instead, gear modifications would be more likely to account for these captures in drifting longlines. In Spanish waters, fishermen attach weights to drifting longlines when going for *Xiphias gladius* [3]. While the mainline remains at the surface, these weights pull the hooks down to much higher depths (400–600 m), very much resembling a bottom longline but without touching the seafloor. Consequently, the chances of capturing *H. griseus* become higher than in a typical drifting longline. In this study, captures by drifting longliners mainly came from Tunisia, E Libya and Cyprus. It is known by the authors of the study that the drifting longliners from these countries can lower the hooks to much deeper waters depending on the target species. However, it remains unknown whether the interviewed drifting longliners made such modifications to the fishing gear. Results also showed there was a substantial number of *H. griseus* captured by trammel and gillnets. Bycatch of this species by nets is not a rare phenomenon [15,56] and although these gears are not as impactful as deep-water gears, the results of this study suggest they can be a significant source of bycatch for this species too.

According to the interviewed fishermen, captures of *H. griseus* were more frequent during warm months, when the water column is stratified. Seasonal shifts in habitat have been reported in *H. griseus* in the northwestern Pacific, where this shark is known to occupy deeper waters in autumn and winter than in spring (Andrews et al., 2009) and the abundance of immature individuals is greater during the summer months than in cold months relative to other months of the year [34]. These seasonal movements are usually associated with feeding, changes in the water temperature or reproduction [79]. The higher frequency of captures of *H. griseus* reported in this study during warm months could have been a result of a change in the species' depth preference and shifting to shallower waters may have increased the likelihood of being captured by more fishing gears, thus explaining why this species was more frequently captured from May to October. Nevertheless, the Chi-square test indicated that the fishing effort of some fishing gears was not equally distributed between warm and cold months. While bottom trawlers generally operate throughout the entire year, bottom longliners and fishermen using trammel and gillnets usually operate during warm months. Therefore, we believe this higher frequency of captures in warm months is more likely to respond to a change in the fishing effort by some of the fishing gears within this study.

At-vessel mortality (AVM) has been reported for a wide number of sharks [37]. However, most of the studies tend to focus on pelagic species [36,60,63], while a few studies addressing AVM of deep-water species exist [14,74]. In this study, AVM of *H. griseus* was rather low considering all gears except for polyvalent vessels, though data from the latter was limited to four vessels and no clear pattern could be inferred. Conversely, results for bottom trawling and the two longlines indicated *H. griseus* tended to be alive at the moment of capturing, agreeing with previous findings [14,83]. This low AVM was especially noticeable in individuals caught by bottom trawling nets, where 6 out of 10 interviewed fishermen believed the species was always alive when taken aboard, compared to just 1 out of 10 fishermen who believed *H. griseus* was always dead when the net was hauled. Several predictors have been suggested to influence AVM of pelagic sharks [12,50,62]. Information regarding AVM of deep-water sharks is still scarce but Brooks et al. [14] and Talwar et al. [83] also found a positive correlation between depth and AVM. In bottom trawling nets, AVM may be influenced by tow duration, catch composition and mass [37], with larger sharks being more easily captured than smaller sharks, since the latter may have a higher chance of escaping through the mesh gaps. *H. griseus* is certainly a large shark and, although it is a common bycatch in bottom trawling, the results of this study suggest it can remain alive in the trawl net before being taken aboard the vessel.

On the other hand, AVM was higher in trammel and gillnets compared to the other three gears. The likelihood of *H. griseus* being alive at the moment of pulling these nets could be close to 50%, represented by "sometimes" in the analysis. Some shark species can exhibit high mortality rates when captured by trammel or gillnets [28,84,95] whereas the mortality rate of other species can be much lower and that could be related to different factors [28,44], which might help explain why the mortality rate of *H. griseus* when caught by trammel and gillnets could be higher than that of bottom trawling, bottom longline and drifting longline. In any case, a deeper knowledge of how bycatch affects *H. griseus* survival could be acquired by monitoring its post-release mortality (PRM), since some individuals that are taken aboard alive may die in short term as a consequence of any physical injury, trauma and physiological stress sustained during capture and handling [65,70]. Deep-water species like *H. griseus* usually live in colder temperatures than pelagic species and the exposure to warmer temperatures may also increase their physiological stress [47,94].

Again, studies evaluating PRM tend to concentrate on pelagic sharks (Musyl and Gilman, 2019; [11]). In one of the few studies assessing PRM in deep-water sharks, a high survival rate after a trawling event was found in *Scyliorhinus canicula* [4], a fact which is totally in contrast with Talwar et al. [83], who found mortality rates ranging from 49.7% to 83% in longline-caught deep-water sharks. However, results from Barragán-Méndez et al. [4] should be interpreted with caution since they may fail to be applicable for *H. griseus*. As opposed to the small *S. canicula*, *H. griseus* is a large species, thus the response to a trawling event might be completely different. Moreover, the trawling events described in that study only lasted for 60 min, which is a much shorter time than that of a commercial trawl event. Further information is therefore needed to better understand how *H. griseus* can cope with post-release stress.

Engaging fishermen in collecting opportunistic data can generate a constant flow of useful information and training them in catch-and-release practices might also help reduce post-release mortality in *H. griseus* if they know how to properly handle and release a captured individual. Specific on-board modifications that could facilitate better handling of the captured individual may also contribute to reducing the stress of the animal, hence minimizing individual mortality. At the same time, finding new ways to reduce the bycatch of *H. griseus* remains crucial for the conservation of the species. Considering Turtle Excluder Devices (TEDs) have proved to be effective at reducing elasmobranch bycatch in trawl nets [46,72], designing and confectioning artisanal Bycatch Reduction Devices (BRDs) for large-sized sharks in such nets might also help avoid captures of *H. griseus*.

4.3. Population trend

The results of this study indicated that fishermen had different perceptions of what the population trend of *H. griseus* was depending on the sampled ports. While fishermen from ports of Greece and NE Spain (the latter by a small margin) mostly believed *H. griseus* was following a stable population trend, those from Albania, Tunisia and Cyprus claimed this species was decreasing in numbers but without doing it at an alarming pace. But perhaps the biggest outcome that could be extracted from these results is the frequency to which respondents were not able to give their interpretations regarding the status of *H. griseus* in their respective countries. That is well portrayed in the cases of E Libya, NE Spain and also Cyprus, with the latter having "n/a" as the most frequent of the answers just above "decreasing". However, the most striking case is that of Italy, where almost 9 out of 10 interviewed fishermen from the different sampled regions did not answer this question because they were totally unaware of the species' status.

The extent to which respondents from Italy and all the other regions wanted to share genuine information cannot be completely known. Nevertheless, practically all interviewed fishermen showed their willingness to collaborate and feel part of this study. Their failure to share their perceptions of the population trend of *H. griseus* might be a result of other constraints we can only speculate about, such as their unawareness of the species, which may depend on the extent to which fishermen of every country have access to information regarding the biology and conservation status of *H. griseus*.

4.4. Conclusions

Despite the data bias, the results of this study are aligned with the different inputs used in the IUCN's 2016 assessment for *H. griseus*, which altogether led to consider it a non-threatened shark species. Even though most of its accidental captures happen in deep-water gears like bottom trawling, *H. griseus* continues to be an occasional bycatch in other fisheries such as longlines, trammel nets and gillnets. Monitoring bycatch in fishing gears that occasionally capture this shark, particularly during warm months when captures are more abundant, would therefore be advisable to help preserve an optimal status of its populations in the Mediterranean Sea, especially in the Western and Central basins. Our findings also seem to indicate a certain degree of AVM in *H. griseus* when it is captured by trammel and gillnets, but AVM tends to be generally low in all the other gears. Although we reckon post-release mortality of *H. griseus* could be low given its apparent resilience when captured, further research on this topic should be done as it would certainly help both the scientific community and managing bodies understand to what extent bycatch can affect the chances of survival of every captured individual. Training fishermen in good handling practices, as well as innovating ways of reducing both on-board mortality and *H. griseus* bycatch is also of great importance for the conservation of the species. Our study highlights the importance of LEK not only for collecting valuable information but also for co-producing knowledge alongside local communities, which in turn incentivises a synergic relationship between fishermen and scientists. Therefore, conservation measures looking after keeping a sustainable relationship between fishermen and marine megafauna should welcome all sorts of insights coming from the experience of the fishing sector.

Finally, two points emerged from our results regarding the population trend of *H. griseus*: On one hand, they did not allow us to suggest any clear population trend for the whole Mediterranean Sea as the fishermen's perception varied quite significantly across sampled regions. On the other hand, they did indicate the species might be showing signs of a potential decreasing trend in certain regions from the Central and Eastern basins. Coupled with the overall elevated proportion of respondents who were not able to guess what the population trend of the species could be, we believe the "stable population trend" assigned by the IUCN in 2016 could be reviewed. In order to obtain a reliable estimation of its population trend in the Mediterranean Sea, future studies should be encouraged to compile regional-specific data on the abundance of *H. griseus*.

CRediT authorship contribution statement

Ignasi Nuez: Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – original draft, Project administration, Funding acquisition. **Ioannis Giovos**: Conceptualization, Investigation, Data curation, Writing – review & editing. **Manel Gazo:** Supervision, Writing – review & editing. **Francesco Tiralongo:** Investigation, Writing – review & editing. **Jaime Penadés-Suay:** Investigation, Writing – review & editing. **Ilija Cetkovic:** Investigation, Writing – review & editing. **Manfredi Di Lorenzo:** Investigation, Writing – review & editing. **Periklis Kleitou:** Investigation, Writing – review & editing. **Rigers Bakiu:** Investigation, Writing – review & editing. **Mohamed Nejmeddine Bradai:** Investigation, Writing – review & editing. **Sara A. A. Almabruk:** Investigation, Writing – review & editing. **Roxani Naasan Aga Spyridopoulou:** Investigation, Writing – review & editing. **Andréa Sabbio:** Investigation, Writing – review & editing.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.marpol.2022.105378.

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DISCUSIÓN

En la actualidad, las poblaciones de muchas especies de tiburones continúan reduciéndose a escala global y la situación en el Mediterráneo es incluso más preocupante. Son los gobiernos y las ORPs, como la Comisión Internacional para la Conservación del Atún Atlántico (ICAAT), los encargados de implementar las medidas de protección y/o gestión apropiadas, y eso sólo puede ser posible si se genera el conocimiento necesario para que pueda ser trasmitido a estas entidades. Este ha sido, en líneas generales, el principal propósito de esta tesis; generar, mejorar y ampliar el conocimiento actual sobre los tiburones de talla media y grande presentes en el Mediterráneo. A continuación, se integrarán y discutirán los principales resultados obtenidos para cada uno de los objetivos definidos. En la última sección de la discusión, se plantearán las principales estrategias destinadas a evitar la captura incidental de tiburones y se cerrará este apartado con una reflexión sobre el enfoque que deberían seguir los futuros estudios de investigación.

Objetivo 1. Estado actual de los tiburones de talla media y grande en la Costa Brava (Mediterráneo Noroccidental).

Tal como se menciona en la introducción de esta tesis, hacer acopio de las experiencias vividas por los pescadores y trasmitidas a lo largo de generaciones es especialmente útil cuando se trabaja con especies de las que no se dispone de suficiente información o que presentan una biomasa y abundancia bajas, como es el caso de los tiburones de talla media y grande que encontramos en el Mediterráneo. Esto tiene su repercusión a la hora de plantear estudios de análisis de su abundancia o tendencia poblacional, ya que diseñar un estudio basado en la observación directa requiere un esfuerzo demasiado costoso en términos de tiempo y financiamiento. El LEK permitió solventar esta limitación. Gracias a la extensa red de contactos que se ha generado a lo largo de estos últimos años, se ha conseguido recopilar información extremadamente valiosa sobre el estado actual de distintas especies de tiburones del Mediterráneo que hubiese resultado muy difícil de obtener si no se hubiera hecho uso del conocimiento de los pescadores. Esta metodología hizo posible la realización de los dos estudios publicados que formaron parte de los **capítulos 1** y **3** de la presente tesis.

Los resultados obtenidos en el **capítulo 1** revelan un escenario preocupante para los tiburones de talla media y grande que podemos encontrar en la Costa Brava (Cataluña, Mediterráneo Noroccidental). Mientras que la captura de tiburones de estas tallas era frecuente en el siglo XIX en la Costa Brava (Cisternas, 1867; Navarrete, 1898), sólo tres de las ocho especies estudiadas (tintorera (*Prionace glauca)*, mielga (*Squalus acanthias*) y cañabota gris (*Hexanchus griseus*)) siguen siendo capturas incidentales frecuentes en la actualidad. La captura de tiburón zorro (*Alopias vulpinus*), tiburón peregrino (*Cetorhinus maximus*), cazón (*Galeorhinus galeus*), marrajo dientuso (*Isurus oxyrinchus*) y el género de las musolas (*Mustelus* spp.) es extremadamente rara. Este hecho es perfectamente atribuible a la continua sobrepesca que han sufrido las poblaciones de estas especies a lo largo de las últimas décadas (Ferretti et al., 2008; Dulvy et al., 2016; Colloca et al., 2017; Walls & Dulvy, 2021), aunque los pescadores que fueron entrevistados en nuestro estudio también sugirieron otros impactos de origen antropogénico, como el aumento de la temperatura del agua y la contaminación, o posibles cambios en la biología de las especies como factores que también podrían explicar el declive de la abundancia de estos tiburones.

Las entrevistas con los pescadores mostraron que el arrastre es el arte de pesca que más diversidad de especies de tiburones captura en la Costa Brava, coincidiendo con resultados similares obtenidos en otras partes del Mediterráneo (Carbonell et al., 2003; Colloca et al., 2003; Yaglioglu et al., 2015), seguido del palangre de fondo y el palangre pelágico. Se encontraron, no obstante, diferencias en cuanto a la contribución de cada arte en la captura de las diferentes especies estudiadas. El marrajo dientuso y el tiburón zorro, dos especies estrictamente pelágicas, fueron capturadas únicamente en los palangres pelágicos, mientras que la tintorera, otra especie pelágica, fue mayoritariamente capturada en el palangre de fondo y en menor medida en palangre pelágico. Las especies bentopelágicas como la mielga o el cazón fueron capturadas tanto por el palangre de fondo como por el arrastre, hecho razonable si tenemos en cuenta que las dos especies habitan en aguas más profundas que las especies pelágicas, pero no a tanta profundidad como especies típicamente demersales, como la cañabota gris. Precisamente, la cañabota gris fue casi exclusivamente capturada por los arrastreros.

A partir de la información recopilada en las entrevistas, se pudo estimar que el total aproximado de capturas de cañabota gris por parte de la flota de la provincia de Girona en los años 2016 y 2017 fue de al menos 89 individuos. Es cierto también que se capturó un número considerable de individuos tanto de tintorera como de mielga, sobre todo en el caso de la primera, pero no se procedió a realizar ninguna estima debido a unos intervalos de confianza demasiado altos. Las capturas de las otras especies durante ese período analizado fueron extremadamente raras y, en el caso de *Mustelus* spp., totalmente inexistentes, cosa que podría estar sugiriendo la desaparición de este género en la Costa Brava. Esta ausencia de capturas de *Mustelus* spp. bien podría estar relacionada con resultados de estudios previos realizados en el Mediterráneo, los cuales documenten el colapso de las poblaciones de estos escualos a lo largo del último siglo debido a la sobrepesca (Colloca et al., 2017).

Coincidiendo con los resultados expuestos en el **capítulo 1** y otros estudios previos (Mate et al., 2000; Ben Amor et al., 2020), los resultados obtenidos en el estudio del **capítulo 3**, realizado en distintas regiones del Mediterráneo, indicaron que los artes de pesca responsables de la mayoría de las capturas de cañabota gris fueron el arrastre y el palangre de fondo. No obstante, el estudio también demostró que una cantidad significativa de las capturas se produjo en trasmallos calados a mucha menor profundidad que los dos artes anteriores y algunas capturas incluso tuvieron lugar en el palangre pelágico. Mientras que las capturas de cañabota gris en trasmallos son conocidas en el Mediterráneo y en otras partes del mundo (Berrow, 1994; Kabasakal 2013), las capturas de esta especie en palangre pelágico resultaron bastante inusuales, teniendo en cuenta que éste es un arte de pesca superficial. Aunque el motivo principal de las capturas en palangre pelágico sea que en ciertos países los pescadores pueden modificar el palangre para alcanzar aguas más profundas (véase por ejemplo “piedrabola” en España) (Barrionuevo, 2008), las capturas de cañabota gris en este arte podrían venir motivadas por algún aspecto comportamental o ecológico de este especie en el Mediterráneo, como por ejemplo la presencia de movimientos de migración vertical que acercaran a los individuos a aguas menos profundas, hecho que ya se ha demostrado en otras partes del mundo (Andrews et al., 2009; Comfort & Weng, 2015).

El estudio también muestra que la mayoría de las capturas de cañabota gris a lo largo de los últimos años ocurren en la parte occidental y central del Mediterráneo. Capturas ocasionales de esta especie han sido reportadas tanto en la parte occidental de la cuenca (Stefanescu et al., 1993; Mate, Barrull & Bueno, 1999; Capapé et al., 2004) como en la parte central (Vella & Vella, 2017; Ben Amor et al., 2019). En el Mediterráneo Central se encuentra precisamente el estrecho de Sicilia, que está considerado como un punto caliente de biodiversidad dentro del Mediterráneo (Di Lorenzo et al., 2018) y varios estudios confirman que la cañabota gris se captura ocasionalmente en esta zona (Ragonese et al., 2013; Ben Amor et al., 2019). Además, los datos obtenidos en el "Monitoreo de Grandes Elasmobranquios del Mediterráneo" (MEDLEM) demuestran que el mayor número de capturas de este tiburón se produce en la parte central del Mediterráneo (Mancusi et al., 2020). Las capturas de cañabota gris también ocurren en la parte oriental de la cuenca (Capapé et al., 2003; Kabasakal, 2009) y en el Mar Adriático (Gugini & De Maddalena, 2003; Mancusi et al., 2020), aunque el registro de capturas de esta especie es claramente inferior. En su estudio de genética poblacional, Vella & Vella (2017) recopilaron 86 y 34 especímenes de cañabota gris de la parte central y occidental, respectivamente, mientras que sólo 8 fueron capturados en la parte oriental del Mediterráneo. La menor frecuencia de capturas de cañabota gris en la parte oriental del Mediterráneo puede ser debida a una limitada cantidad de información disponible sobre abundancia y distribución de grandes tiburones comparado con la parte occidental y central de la cuenca (Damalas & Megalofonou, 2012; Kabasakal et al., 2017), pero también con la oligotrofia general de la cuenca y su mayor temperatura. En el Mar Adriático, las pocas capturas de cañabota gris podrían estar relacionadas con su gran plataforma continental. Mientras que la parte sur del Adriático sí que es más estrecha y de pendiente más acentuada, la parte norte y central tienen una profundidad máxima general de no más de 100 m. Semejantes profundidades no constituirían un hábitat óptimo para una especie demersal como la cañabota gris y, por lo tanto, es de esperar que el número de capturas en el Mar Adriático sea inferior al de las otras partes del Mediterráneo.

La gran novedad del estudio fue el análisis de la mortalidad en la embarcación a partir de la información aportada por los pescadores encuestados. Poco o nada se ha publicado al respecto en el Mediterráneo y los resultados del presente estudio reflejaron que los individuos capturados de cañabota gris suelen encontrarse vivos en el momento de retirar el arte y que la mortalidad en la embarcación era, en general, baja y un poco mayor en los trasmallos. Este hecho es importante de caras a la supervivencia de los individuos capturados una vez se retira el arte, ya que una correcta manipulación del individuo debería garantizar una alta probabilidad de evitar su muerte al ser liberado. Llegados a este punto, surgen dos reflexiones clave; tal como se menciona en el estudio publicado del **capítulo 1**, es recomendable formar a los pescadores para garantizar la mejor y más eficaz manipulación de los individuos posible mientras están siendo liberados. En segundo lugar, se desconoce el grado de mortalidad post-liberación de esta especie, entendida como el grado de mortalidad de los individuos capturados que son devueltos al mar vivos.

Estudios realizados sobre todo en pesquerías oceánicas dirigidas a la captura del atún demuestran que las distintas especies de tiburones pelágicos que son capturas incidentales habituales pueden presentar mortalidades post-liberación totalmente diferentes entre ellos y también en función del arte de pesca utilizado. En el Océano Pacífico, el tiburón sedoso (*Carcharinus falciformis*) puede llegar tener una mortalidad post-liberación superior al 80% en el cerco (Hutchinson et al., 2015), mientras que en palangre pelágico es poco más de un 11%. Este valor es similar al de la tintorera, otra captura incidental común en este arte, reportado en algunos estudios realizados también en el Pacífico (Musyl et al., 2011; Musyl & Gilman, 2018). Sin embargo, en el Atlántico, la mortalidad post-liberación de la tintorera en el palangre pelágico oscilaría entre 10 y 33%, (Campana et al., 2016). Los estudios sobre la mortalidad post-liberación de tiburones demersales son escasos pero los resultados de algunas especies en el Atlántico Nororiental y Noroccidental, a excepción de la pintarroja (*Scyliorhinus canicula*) (Barragán-Méndez et al., 2019), sugieren valores elevados (Rodríguez-Cabello & Sánchez, 2017; Talwar et al., 2017).

En el Mediterráneo se dispone de poca información sobre mortalidad en la embarcación y mortalidad post-liberación de tiburones de talla grande. En su estudio en 2005 sobre las capturas y descartes de tiburones pelágicos en palangres dirigidos a pez espada y atún, Megalofonou et al. (2005) estimaron la mortalidad en la embarcación de algunas de las especies estudiadas en esta tesis; el estado en el que se encontraron los individuos capturados de marrajo dientuso y tiburón zorro era malo o muy malo, mientras que los individuos de tintorera, cazón y cañabota gris se encontraron en bastante o muy buen estado, sobre todo en el caso de la cañabota gris (n = 3).

Aunque los resultados del estudio del **capítulo 3** también indiquen que la mortalidad en la embarcación de la cañabota gris es baja en artes como el arrastre, el palangre de fondo y en menor medida los trasmallos, hay que tener cautela al afirmar que este escualo normalmente sobrevive a la captura si es devuelto al mar vivo. En un estudio realizado en el Pacífico y centrado en analizar las mortalidades en la embarcación y post-liberación de distintas especies pelágicas en las redes de cerco, se encontró que el tiburón martillo común (*Sphyrna lewini*) presentaba una mortalidad en la embarcación del 0% pero, aunque todos los individuos equipados con marcas archivo “pop-up” por satélite (PSATs) parecían estar en muy buena condición, experimentaron una inmediata mortalidad en cuanto fueron liberados (Eddy et al., 2016). En consecuencia, es necesario que futuros estudios evalúen el impacto de la pesca en la cañabota gris centrándose en conocer la respuesta de esta especie al estrés que genera su captura durante y sobre todo después de esta. Las marcas electrónicas pueden ser la herramienta necesaria para cumplir este propósito (Rodríguez-Cabello & Sánchez, 2017).

Finalmente, aunque el LEK recopilado en este estudio no pudo inferir la tendencia poblacional de la cañabota gris a nivel regional, sí que sirvió para detectar un posible declive poblacional de esta especie en ciertas regiones de distintos países del Mediterráneo. Junto con el elevado número de pescadores encuestados que fue incapaz de sugerir qué tendencia poblacional seguía la cañabota gris en el presente según su experiencia, el presente estudio invita a reflexionar sobre si realmente el estado de conservación más reciente de la cañabota gris en el Mediterráneo, otorgado por la UICN en 2016, es el idóneo.

En ese informe, esta especie aparece clasificada como de “Preocupación menor”. La información aportada en nuestro estudio sugiere una revisión de su estado de conservación. Para ello, son imprescindibles nuevos estudios que aporten datos de abundancia específicos para cada región del Mediterráneo.

Objetivo 2. El nicho isotópico de los tiburones de talla media y grande en el Mediterráneo Noroccidental.

La estrecha colaboración con los pescadores durante el transcurso de esta investigación también fue clave para la realización del segundo estudio, que formó parte del **capítulo 2** de la presente tesis. Los tiburones de talla media y grande analizados en el **capítulo 1** fueron también analizados en este estudio a excepción del tiburón peregrino y el género de las musolas.

A pesar del declive poblacional de muchos tiburones documentado en el Mediterráneo, sobre todo de especies de talla grande (Ferretti et al., 2008, 2010; Colloca et al., 2017; Moro et al., 2020) y de la posible pérdida de su relevancia ecológica (Ferretti et al., 2008; Piroddi et al., 2015), el conocimiento sobre el rol de los tiburones en redes tróficas costeras y pelágicas es aún pobre con relación a los peces óseos (Hussey et al., 2011). En el Mediterráneo, gran parte de los estudios sobre la ecología trófica de los tiburones se han focalizado en especies pequeñas (Valls et al., 2011; Navarro et al., 2014; Albo-Puigserver et al., 2015), mientras que solo unos pocos se han centrado en tiburones de talla media y grande (Barría, Coll & Navarro, 2015; Di Lorenzo et al., 2020).

Como puede apreciarse en el estudio del **capítulo 2**, los resultados obtenidos mediante el análisis de isótopos estables (SIA) reflejaron unos valores de $\delta^{13}C$ y $\delta^{15}N$ bastante similares entre todas las especies, excepto en el caso del cazón, cuyo valor promedio de $\delta^{15}N$ fue mucho más elevado que el de las otras especies. Una explicación plausible para tan altos valores de $\delta^{15}N$ podría ser que los individuos de cazón muestreados hubieran entrado recientemente en el Mediterráneo emigrando del Océano Atlántico, un ecosistema distinto con valores basales de $\delta^{15}N$ más elevados. Según MacNeil et al. (2005), el músculo puede tardar hasta 488 días en mostrar un equilibrio isotópico con el nuevo ambiente y, puesto que sólo se muestreó músculo en el presente estudio, los valores extremadamente altos de $\delta^{15}N$ del cazón pueden ser debidos a que el músculo aún no había llegado a su equilibrio isotópico en el momento de la obtención de la muestra y que, por lo tanto, los individuos analizados habrían pasado poco tiempo en el Mediterráneo. Precisamente para evitar una comparativa entre individuos de diferentes ecosistemas, no se incluyó el cazón en los posteriores análisis del estudio.

El descubrimiento de varias hembras de cazón marcadas electrónicamente en el Atlántico Nororiental y posteriormente recapturadas en el Mediterráneo demuestra la existencia de una conectividad entre ambas cuencas (Colloca et al., 2019; Thorburn et al., 2019). No existe aún un claro motivo que explique por qué el cazón realiza estos desplazamientos de tanto recorrido, aunque la presencia de hembras grávidas y juveniles en la costa de Túnez podría indicar que el Mediterráneo podría ser una zona de reproducción de esta especie (Capapé & Mellinger, 1988), hipótesis que podría ser contrastada mediante estudios genéticos (Colloca et al., 2019).

En lo referente al resto de especies analizadas, se aportan dos conclusiones principales: 1) la dieta de los tiburones de talla meda y grande se caracteriza por un alto consumo de cefalópodos y 2) su nicho isotópico es distinto al de otros peces depredadores y los cetáceos odontocetos.

La contribución de los cefalópodos a la dieta de todos los tiburones analizados fue especialmente significativa en el caso del tiburón zorro, el marrajo dientuso y la mielga. Tanto en el Atlántico como en el Pacífico, la importancia de los cefalópodos en la dieta del tiburón zorro y el marrajo dientuso ha sido demostrada en varios estudios sobre todo a través del análisis del contenido estomacal (Stillwell and Kohler, 1982; Preti et al., 2004; MacNeil et al., 2005; Maia et al., 2006). Existe muy poca información sobre la dieta de estas dos especies en el Mediterráneo, pero algunos estudios muestran que la dieta del tiburón zorro estaría caracterizada por un elevado consumo de pequeños peces pelágicos (Finotto et al., 2016), aunque los cefalópodos también podrían ser parte de su dieta (Barría, Coll & Navarro, 2015). En el caso del marrajo dientuso, se han identificado restos de delfínidos en el estómago de dos hembras grandes capturadas en las costas italianas (Storai et al., 2001), mientras que, en Turquía, Tunçer & Kabasakal (2016) encontraron picos de sepia (*Sepia officinalis*) en el estómago de un macho juvenil de 75 cm TL. Por otra parte, estudios realizados en el Mar Negro, el Atlántico y también en el Mediterráneo muestran que la dieta de la mielga consiste principalmente en peces teleósteos, mientras que la contribución de los cefalópodos resulta desde negligible (Avsar, 2001; Demirhan et al., 2007: Gül & Demirel, 2021) hasta importante (Henderson, Dunne & Flannery, 2002; Barría, Coll & Navarro, 2015).

La comparación entre los estudios de dieta realizados en el Atlántico y el Pacífico y los resultados presentados en el estudio del **capítulo 2** de esta tesis muestra una gran diferencia en cuanto a la composición de la dieta del tiburón zorro y el marrajo dientuso. Aunque la importancia de los cefalópodos con respecto a los peces teleósteos era variable en esos estudios anteriormente mencionados, los peces teleósteos fueron parte de la dieta de estos tiburones, mientras que, en el estudio del **capítulo 2**, los peces teleósteos no figuraron como grupo de presas. Los resultados de la dieta del tiburón zorro tampoco se ajustarían a las conclusiones de Finotto et al. (2016), que afirmaron que la presencia de este tiburón en el norte del Mar Adriático está influenciada por la abundancia de la sardina (*Sardina pilchardus*), su presa principal. En cambio, sí que estarían más alineados con los resultados de Barría, Coll & Navarro (2015). Los resultados de la dieta del marrajo dientuso coinciden con los de Tunçer & Kabasakal (2016) en el Mediterráneo, no sólo a en cuanto a la evidencia del consumo de cefalópodos, sino por el hecho de que los individuos muestreados en el estudio también fueron juveniles (97 ± 4,2 cm). No obstante, la escasa información disponible sobre la dieta de esta especie en el Mediterráneo es extremadamente escasa y hacen falta más estudios para conseguir tener una idea suficientemente acurada de los principales grupos de presas de este tiburón.

En cuanto a la mielga, los resultados del presente estudio estarían alineados con los de Henderson, Dunne & Flannery (2002) y Barría, Coll & Navarro (2015), realizados en el Atlántico Nororiental y el Mediterráneo, respectivamente, que también demuestran la contribución significativa de los cefalópodos a la dieta de esta especie. No obstante, cabe resaltar que los peces teleósteos tuvieron una relevancia mucho mayor que los cefalópodos en el estudio de Henderson, Dunne & Flannery (2002) y semejante en el estudio de Barría, Coll & Navarro (2015). En el presente estudio, los peces teleósteos tampoco figuraron en la dieta de la mielga.

En cambio, los peces teleósteos pelágicos tuvieron una notable relevancia en las dietas de la tintorera y la cañabota gris. Como ocurre en el caso del tiburón zorro y el marrajo dientuso, la dieta de la tintorera ha estado descrita en numerosas ocasiones en distintas partes del mundo. La mayoría de los estudios publicados fuera del Mediterráneo muestran que este tiburón se alimenta principalmente de peces teleósteos y también, en menor medida, cefalópodos (Clarke et al., 1996; McCord & Campana, 2003; Lopez et al., 2010), aunque éstos pueden llegar a aportar alrededor del 50% de su dieta (Cortés, 1999). En el Mediterráneo, ciertos estudios confirman la importancia de los cefalópodos en la dieta de la tintorera (Garibalid & Relini, 2000; Barría, Coll & Navarro, 2015). En el caso de Garibaldi & Relini (2000), además, los cefalópodos representaron el grupo de presas más importante. Los resultados obtenidos en el estudio del **capítulo 2** aportan conclusiones sobre la dieta de esta especie similares a las descritas en Cortés (1999) y Barría, Coll & Navarro (2015), pero coincidiendo sobre todo con los resultados de Garibaldi & Relini (2000).

Por el contrario, el grueso de la información referente a los patrones alimenticios de la cañabota gris proviene de unas pocas localizaciones alrededor del mundo (Ebert, 1986,1994; Andrews et al., 2009; Reum et al., 2020). En Sudáfrica, Ebert (1994) realizó el que hasta día de hoy sea, probablemente, el estudio sobre la dieta de la cañabota gris más completo de todos y en él encontró que la cañabota gris se alimenta de cefalópodos y peces teleósteos, pero también de otros elasmobranquios y mamíferos marinos y que la contribución de cada grupo de presas varía en función de la etapa vital del individuo. En el Mediterráneo, algunos estudios han confirmado que los cefalópodos forman parte de la dieta de la cañabota gris, en algunos casos de forma poco significativa (Kabasakal, 2006) pero en otros casos de forma considerable (Celona et al., 2005; Barría, Coll & Navarro, 2015). Los resultados obtenidos en el estudio del **capítulo 2** están alineados con los de Celona et al. (2005) y Barría, Coll & Navarro (2015) y muestran una gran similitud entre la dieta de la cañabota gris y la de la tintorera. Sin embargo, la importancia de los cefalópodos en esos dos estudios era menor que la de los peces teleósteos, mientras que, en el presente estudio, los cefalópodos representaron el grupo de presas principal.

Existen ciertos factores que podrían haber alterado la contribución de cada grupo de presas a la dieta de los tiburones de talla media y grande del **capítulo 2**. Por ejemplo, la dieta descrita de la tintorera, la cañabota gris y el marrajo dientuso podría haber sido influenciada por la gran cantidad de individuos juveniles muestreados. La variación de la dieta debido a cambios ontogenéticos es un fenómeno documentado en varias especies de tiburones (Lucifora et al., 2009; Estupiñán-Montaño et al., 2019; Tamburin et al., 2019; Assemat et al., 2022). En un estudio realizado en California, Preti et al. (2012) mostraron que la dieta del marrajo dientuso sufría, en realidad, una expansión ontogenética (mayor número de taxones consumidos con el aumento del tamaño corporal) y no un cambio en la preferencia por los distintos grupos de presas. A pesar de ello, los peces teleósteos representaron el grupo de presas principal en el caso de los individuos pequeños, difiriendo de los resultados obtenidos en el estudio del **capítulo 2** y del único individuo analizado en el estudio de Tunçer & Kabasakal (2016), si bien la importancia de los cefalópodos aumentaba con el tamaño de los individuos hasta llegar a ser el grupo de presas principal en los individuos grandes.

Esta expansión ontogenética también era aplicable a la tintorera. En esta especie, los individuos pequeños se alimentaban principalmente de crustáceos, mientras que los cefalópodos representaron el grupo de presas más importante para las tintoreras de tamaño medio y grande (Preti et al., 2012), resultados totalmente opuestos a los de McCord & Campana (2003). Por otra parte, Estupiñán-Montaño et al. (2019) demostraron que el cambio ontogenético en la dieta de las tintoreras analizadas estaba asociado a un cambio en el uso del hábitat. Mientras que las tintoreras juveniles de tamaño medio y grande, tamaños muy similares a los de los individuos analizados en el **capítulo 2**, frecuentaron aguas oceánicas, donde se alimentarían mayoritariamente de cefalópodos según Kubodera et al. (2007), los individuos pequeños y adultos mostraron una preferencia por aguas costeras en donde tendrían acceso a otros tipos de presas.

En el caso de la cañabota gris, el estudio de Ebert (1994) sobre la dieta de la cañabota gris afirma que los individuos pequeños (< 120 cm TL) se alimentan principalmente de cefalópodos, mientras que éstos representan un grupo de presas secundario en individuos de entre 120 y 200 cm TL y de poca importancia en individuos mayores de 200 cm TL. En el presente estudio, la longitud total media de los individuos de cañabota gris muestreados fue de 202 ± 60 cm. Eso significa que algunos individuos superaron los 250 cm, mientras que otros medían entre 120 y 250 cm. Sólo un individuo midió menos de 120 cm (90 cm). Por lo tanto, si los cambios ontogenéticos estuvieran modulando la dieta de la cañabota gris en el estudio del **capítulo 2** tal como se muestra en el estudio de Ebert (1994), sería de esperar que la dieta de esta especie reflejara un consumo no tan acentuado de cefalópodos. Sin embargo, esta hipótesis seria únicamente viable en el caso del individuo de 90 cm de longitud total.

En resumen, la variación de la dieta de la tintorera, el marrajo dientuso y la cañabota gris debido a cambios ontogenéticos es un factor que debería contemplarse a la hora de inferir conclusiones sobre sus valores isotópicos, pues cabría la posibilidad de que la presencia de determinados grupos y su contribución a la dieta los tiburones hubiesen sido distinta si la proporción de adultos muestreados hubiera sido más alta. Sin embargo, determinar hasta qué punto es un factor condicionante resulta complejo debido a los pocos estudios publicados sobre la dieta de estas especies en los distintos estados de madurez.

Por otro lado, la elevada proporción de juveniles vs adultos, sobre todo en el caso de la cañabota gris y la tintorera, resalta la absencia de individuos maduros en las capturas incidentales de estos tiburones de talla grande en el Mediterráneo Noroccidental. En el estudio de Megalofonou, Damalas & De Metrio (2009) sobre la biología de la tintorera en el Mediterráneo Oriental, 696 de los 870 individuos medidos (80%) fueron inmaduros de menos de 5 años de edad (< 206,3 cm TL). Años más tarde, también en el Mediterráneo Oriental, las capturas de tintorera analizadas en el estudio de Damalas & Megalofonou (2012) mostraron que los individuos tenían un tamaño promedio superior al del

2009 (225 cm TL) pero también que los individuos eran más pequeños en el Mar Jónico que en la Cuenca Levantina. El tamaño promedio de las tintoreras analizadas en el **capítulo 2** (136 cm TL) muestra una posible diferencia en la distribución de tallas de las capturas de tintorera entre Mediterráneo Noroccidental y Oriental y sugiere porcentajes de juveniles vs adultos similares a los obtenidos por Megalofonou, Damalas & De Metrio (2009). Semejante proporción podría respaldar la hipótesis que considera al Mediterráneo una posible zona de cría para individuos maduros provenientes del Atlántico (Leone et al., 2017; Megalofonou, Damalas & De Metrio, 2009), más la evidencia de una diferenciación genética entre la población del Atlántico y la del Mediterráneo es difusa (Veríssimo et al., 2017; Bailleul et al., 2018). Una baja abundancia de adultos en las capturas podría, a su vez, ser indicativo del alto nivel de presión pesquera al que se enfrentan los tiburones al entrar en el Mediterráneo. La rápida y continua extirpación de individuos maduros imposibilitaría, en consecuencia, la existencia de una población mediterránea de tintorera genéticamente distinta a la del Atlántico Nororiental.

El tamaño promedio de los individuos capturados de cañabota gris en el estudio del **capítulo 2** (203 cm TL) los clasificaría a todos ellos como juveniles, de acuerdo con el tamaño de esta especie en el momento de maduración reportado por Vella & Vella (2010) en el Mediterráneo. Estos resultados difieren de la proporción de juveniles encontrada en algunos estudios realizados en otros sectores del Mediterráneo (Celona et al., 2005; Kabasakal, 2006, 2013), pero resultan similares a los de Mulas et al. (2021) en Cerdeña y muy parecidos a los de Ben Amor et al. (2019) y Barría, Coll & Navarro (2015). Mientras que los resultados del **capítulo 2** y los de Barría, Coll & Navarro (2015) fueron obtenidos en el Mediterráneo Noroccidental, los de Mulas et al. (2021) y Ben Amor et. al. (2019) provienen del Mediterráneo Central. Recientemente, Ouled-Cheikh et al. (2022) demostraron que la presión pesquera sobre las especies pelágicas del Mediterráneo es significativamente más intensa en estos dos sectores, justamente donde existe mayor concentración de barcos de arrastre (Colloca, Scarcella & Liberato, 2017), que es el principal arte en el que se producen las capturas incidentales de cañabota gris. En consecuencia, dicha alta abundancia de individuos inmaduros de cañabota gris en el estudio del **capítulo 2**, junto con la alta proporción de estos encontrada en los estudios anteriormente citados del sector occidental y central del Mediterráneo, muy diferente de la reportada en el sector oriental, podría ser indicativa de una mayor presión pesquera que impediría a los individuos llegar a alcanzar tallas más grandes.

Por otro lado, la alta contribución de los cefalópodos a la dieta de los tiburones de talla media y grande podría estar relacionada con un marcado declive de la abundancia de peces pelágicos pequeños en el Mediterráneo Occidental (Cardona et al., 2015; Ouled-Cheikh et al., 2022). Aunque resulta difícil demostrar esta hipótesis en el presente estudio, la notable reducción poblacional de especies como la sardina (*Sardina pilchardus*) o la anchoa (*Engraulis encrasicolus*) podría implicar cambios estructurales en la red trófica Mediterránea (Ouled-Cheikh et al., 2022) que modificaran las estrategias alimenticias de los tiburones. Como se ha mencionado en la anterior sección, el consumo elevado de cefalópodos en individuos de cañabota gris con talla superior a los 120 cm de longitud contrasta con las afirmaciones de Ebert (1994). No obstante, esto podría verse en explicado si existiera un contexto ambiental lo suficientemente pobre en abundancia de peces pelágicos como para que la principal fuente de materia orgánica de los tiburones fuese, justamente, los cefalópodos. Futuros estudios sobre la tendencia poblacional de las principales especies pelágicas pueden ayudar a discernir si semejante contribución de los cefalópodos a la dieta de los tiburones es resultado de la escasez de peces pelágicos o si, por contra, puede ser producto estrategias alimenticias históricamente consolidadas.

La segunda conclusión principal del estudio hace referencia al nicho isotópico que ocupan los tiburones de talla media y grande en el Mediterráneo Noroccidental. Sus valores de $\delta^{13}C$ y $\delta^{15}N$ indicaron que estos tiburones configuran su propio y único nicho isotópico en la red trófica, apenas solapándose con el de otros peces pelágicos depredadores o el de los cetáceos odontocetos. Los valores de $\delta^{15}N$ fueron ligeramente superiores a los de otros grandes peces depredadores pero inferiores a los de los grandes cetáceos odontocetos, mientras que los valores de $\delta^{13}C$ de los tiburones fueron similares únicamente con los de los grandes cetáceos buceadores. La similitud de valores de $\delta^{13}C$ entre estos dos grupos de organismos depredadores podría ser consecuencia de un consumo similar de cefalópodos, puesto que este grupo de presas también tiene un peso importante en las dietas de cetáceos buceadores como el calderón gris (*Grampus griseus*), el calderón común (*Globicephala melas*) o el zifio (*Ziphius cavirostris*).

Estudios recientes sobre la ecología de los elasmobranquios han complementado el uso de los isótopos de N y C en los modelos tróficos con isótopos estables de otros elementos, como el azufre (Curnick et al., 2019; Raoult et al., 2019). El S permite discriminar organismos que utilizan redes tróficas pelágicas de los que utilizan redes tróficas bentónicas (Hobson, 1999; Curnick et al., 2019), pero únicamente en ambientes costeros.

Los grandes peces depredadores, como los tiburones, están tradicionalmente definidos como consumidores generalistas que ocupan los niveles superiores (4,1 y 4,5; Cortés, 1999) de la red trófica y que se alimentan de especies de menor posición trófica (Hussey et al., 2011). En consecuencia, existe una tendencia generalizada de catalogar a los tiburones de talla grande como depredadores apicales (Andrews et al., 2009; Benavides et al., 2011; Hammerschlag et al., 2015; Pirog et al., 2019). Sin embargo, no todas las especies de grandes dimensiones se encuentran en lo más alto de la red trófica (Frisch et al., 2016; Bond et al., 2018), lo que demuestra que el nivel trófico puede variar también entre especies, uso del hábitat, comportamiento y ontogenia (Heupel, 2014). En el presente estudio, la mayoría de los valores de nivel trófico obtenidos (4,2 a 4,7) guardaron una gran similitud con los que Cortés (1999) obtuvo para estas especies en su análisis de contenido estomacal, mientras que los niveles tróficos de tintorera, marrajo dientuso y tiburón zorro fueron superiores a los obtenidos por Estrada et al. (2003), sobre todo en el caso de la tintorera y los valores de cañabota gris y mielga fueron ligeramente inferiores a los valores obtenidos por Barría, Coll & Navarro (2015) el Mediterráneo Noroccidental. Sin embargo, todos estos autores definen a estos tiburones como depredadores apicales, mientras que los valores isotópicos de los tiburones de talla media y grande del Mediterráneo Noroeste obtenidos en el presente estudio indican que estas especies actúan como mesodepredadores y no tanto como depredadores apicales, una terminología que sí sería ajustada para los grandes cetáceos odontocetos.

Determinar los efectos ecosistémicos de la pérdida de tiburones es una tarea difícil, en parte justamente por el limitado conocimiento de sus roles tróficos (Hussey et al., 2015). Algunos estudios han demostrado que la desaparición de tiburones genera importantes cascadas tróficas a lo largo de la red, degradando el ecosistema en el que habitan (Myers et al., 2007; Heithaus et al., 2008; Barley et al., 2017; Rasher et al., 2017), mientras que en ecosistemas en donde ciertas especies de tiburones son funcionalmente redundantes, las de cascadas tróficas son raras o sutiles (Frisch et al., 2016) y muchos estudios empíricos no consiguen evidenciar la aparición de cascadas tróficas debido a la falta de una relación clara entre los tiburones y los niveles tróficos inferiores (Roff et al., 2016). Haciendo uso de toda la información disponible hasta el momento, es difícil predecir el impacto ecosistémico de la desaparición de los tiburones de talla media y grande en Mediterráneo Noroccidental.

Aportaciones de la presente tesis para reducir la pesca incidental de tiburones en el Mediterráneo.

Según la gran mayoría de los pescadores entrevistados en la Costa Brava en el estudio del **capítulo 1**, la captura incidental de tiburones de talla media y grande se produce debido al solapamiento de la distribución de la especie con el calador donde los pescadores trabajan, coincidiendo con otros estudios (White et al., 2019; Chan et al., 2021; Walls & Dulvy, 2021). La cañabota gris, por ejemplo, se encuentra sobre todo en el límite de la plataforma continental (Stefanescu et al., 1993; d'Onghia et al., 2004) en el Mediterráneo, donde precisamente operan aquellos barcos de arrastre dirigidos a la pesca de las gambas *Aristeus antennatus* y *Aristaeomorpha foliacea*. Las especies objetivo en los artes de arrastre y palangre de fondo se encuentran a mucha más profundidad que las de los artes de superficie y, en consecuencia, tal como pudimos observar en el estudio del **capítulo 3**, las probabilidades de capturar cañabota gris son más elevadas. Por otra parte, la posible preferencia de las especies pelágicas como la tintorera o el marrajo dientuso por zonas oceánicas de elevada productividad y que contienen frentes termales aumentaría las probabilidades de ser capturadas por las flotas de palangre que operan allí debido a la alta densidad de peces pelágicos, como ocurre en el Atlántico Septentrional (Queiroz et al., 2016).

Entonces, ¿cómo evitar la captura de tiburones? Dado que la mayoría de las especies son capturadas incidentalmente y solo unas pocas son especies comerciales en el Mediterráneo (Bradai et al., 2018), la elaboración de medidas efectivas de conservación de estas especies que garanticen la supervivencia de sus poblaciones podría radicar en dos alternativas; 1) minimizar las capturas incidentales y mejorar las técnicas de manipulación de individuos o 2) designar Áreas Marinas Protegidas (AMPs).

La reducción del número de capturas incidentales de tiburones, si no es a través de una reducción del esfuerzo pesquero, se puede conseguir a través de modificaciones tanto en los artes de pesca como en la operativa pesquera. En 2016, Gilman et al. llevaron a cabo una extensa revisión bibliográfica en la que, posteriormente, analizaron el efecto de hasta 19 variables diferentes sobre las capturas incidentales de tiburones en los palangres pelágicos. En resumen, a pesar de una considerable variabilidad en los efectos de los factores de estudio entre especies, el meta-análisis reflejó que el riesgo de captura de todas las especies combinadas (principalmente tintorera) disminuía; 1) al usar anzuelos tipo J en lugar de anzuelos circulares; 2) al usar anzuelos de mayor tamaño, que dificultan la captura de especies con bocas relativamente pequeñas; 3) al usar especies de calamar como cebo en lugar de pescado y; 4) al usar cables de monofilamento en lugar de multifilamento (especies con dientes afilados o serrados pueden romper los cables de monofilamento y escapar, mientras que la probabilidad de escapar es más baja al intentar romper cables de multifilamento). Además, el estudio también menciona el momento del día en el que se cala el arte y el tiempo total que permanece el palangre calado en el agua como factores que inciden en el riesgo de captura de tiburones (Gilman et al., 2016). Estudios posteriores también consideraron que las capturas incidentales de tiburones eran menores durante la noche y cuando el palangre es calado a mayor profundidad (Fowler, 2016; Zainudin et al., 2017), aunque también existe variabilidad de los efectos entre especies. Más recientemente, Doherty et al. (2022) demostraron que las capturas de tiburones pelágicos también pueden disminuir notablemente al usar dispositivos que sobreestimulen los electrorreceptores de los escualos.

Mientras que son varias las estrategias examinadas en los palangres de las grandes pesquerías pelágicas, los ejemplos de mecanismos eficientes de minimización de capturas incidentales de tiburones en otros artes de pesca son menos abundantes. En redes, el acople de dispositivos de exclusión de tortugas marinas (TEDs) ha demostrado ser una forma efectiva de reducir la captura incidental de tiburones, algunos de ellos de talla media y grande (Raborn et al., 2012; Garstin, Oxenford & Maison, 2017). Brčić et al. (2015) diseñaron un dispositivo de exclusión acoplado a la red de arrastre para la pintarroja bocanegra en el Mediterráneo, pero el dispositivo no resultó ser eficiente en la reducción de sus capturas. En el oeste de Escocia, modificaciones en la estructura de la red de arrastre en pesquerías multiespecíficas sí redujeron significativamente la tasa de captura de distintas especies de tiburones de tamaño pequeño y mediano, como la mielga (Kynoch et al., 2015). En trasmallos, el aumento de la selectividad de las redes de trasmallo ha resultado ser un eficiente método de minimización de capturas incidentales de tiburones de talla grande (Thorpe & Frierson, 2009). Es aconsejable que los futuros estudios no solo investiguen nuevos métodos de minimización de las capturas incidentales de tiburones de talla media y grande en los palangres, sino también en otros artes de pesca como los trasmallos y sobre todo el arrastre que, junto con los palangres, es uno de los artes de pesca que captura más cantidad de elasmobranquios en el Mediterráneo (FAO, 2022a).

El desarrollo de estrategias de minimización de capturas incidentales de tiburones debe complementarse con formaciones a los pescadores para que puedan manipular correctamente aquellos individuos que aún están vivos cuando se procede a retirar el arte de peca. Tal como se aborda en el **capítulo 3**, el manejo cuidadoso del individuo capturado puede minimizar la probabilidad de que el animal muera una vez sea liberado o un tiempo después. Este hecho es especialmente importante cuando se trata de especies amenazadas o que presentan una mortalidad en la embarcación elevada, como precisamente es el caso de varios tiburones de talla media y grande (Gilman et al., 2022). Además, mantener una relación sinérgica con los pescadores es una herramienta útil para disponer de un aporte continuo de datos sobre la presencia y abundancia de los tiburones en el Mediterráneo y en cualquier parte del mundo, especialmente en zonas donde el estatus de ciertas especies esté aún lejos de ser conocido y no solo en el caso de especies protegidas, también las comerciales que no estén reguladas a través de un sistema de cuotas.

La designación de AMPs es un enfoque de conservación potente para abordar el problema de la pérdida de biodiversidad (Davidson & Dulvy, 2017). No obstante, la creación de AMPs que garanticen una protección efectiva de los tiburones presenta varias limitaciones. Fundamentalmente, la efectividad de una AMP depende del grado de solapamiento entre los movimientos de la especie y el área de protección espacial (Knip et al., 2012). La mayoría de las AMPs cubren una extensión geográfica pequeña y suelen ser particularmente efectivas en el caso de especies sedentarias (Knip et al., 2012), de tal forma que los beneficios de esta protección disminuyen una vez los individuos se encuentran fuera de sus límites (Bonfil, 1999). Precisamente, los tiburones de talla grande son especies altamente móviles y sus rangos de actividad pueden abarcar muchos km^2 (Heithaus et al., 2007; Stevens, 2008; Stevens et al., 2010; Thorburn et al., 2019). En consecuencia, la mayoría de AMPs fracasan en garantizar una protección efectiva de estos tiburones debido a su limitada cobertura espacial.

Debido a la urgente necesidad de protección del medio marino, muchas AMPs han sido implementadas oportunísticamente sin contar con el suficiente conocimiento previo de cómo funcionarían (Roberts, 2000). Querer garantizar la protección de especies de elevada movilidad, sin contar con suficiente información sobre sus características espaciales puede llevar a la creación de AMPs disfuncionales (Daly et al., 2018; Giménez et al., 2020).

Por otra parte, existen AMPs que abarcan una gran extensión de océano y que han demostrado ser beneficiosas para los tiburones de talla grande (Albano et al., 2012; Knip et al., 2012; Speed et al., 2018; White et al., 2017). El caso más conocido es el de los famosos “santuarios de tiburones”, que pueden tener superficies mucho mayores que otras AMPs (4,771,088 km^2 en la Polinesia Francesa) debido a que la prohibición de captura, retención y venta de tiburones se aplica a toda la Zona Económica Exclusiva de un país (Ward-Paige, 2017). No obstante, en la actualidad existen pocos santuarios y tanto estos como la mayoría de AMPs grandes se encuentran en zonas relativamente remotas en las que el volumen de embarcaciones de pesca es menor. Además, según la base mundial de áreas protegidas, gestionada por el Centro Mundial de Vigilancia de la Conservación (UNEP-WCMC), menos del 3% del total de 8.2% de superficie marina protegida en 2023 está cubierta por AMPs que prohíben cualquier tipo de actividad pesquera. Este bajo nivel de protección absoluta es debido en gran parte a los conflictos con el sector pesquero y con sectores que realizan otras actividades extractivas.

Asimismo, la falta de recursos humanos y financieros de muchas AMPs en la actualidad limita su capacidad para garantizar una gestión eficiente, lo que puede acabar convirtiendo cualquier medida de legislación en redundante y con ningún impacto en la biodiversidad de tiburones como ocurrió en Myanmar, un país que decretó totalmente prohibida la pesca de tiburones a nivel nacional pero que nunca tuvo definido un objetivo ni se pudo llevar a cabo ninguna forma de gestión (Mizrahi et al., 2019).

Por lo tanto, la creación y gestión de las AMPs plantea retos importantes a nivel logístico, social e informativo. Mientras que AMPs relativamente pequeñas pueden ofrecer cierta protección a algunos tiburones de movilidad más reducida (Da Silva et al., 2013; Speed et al., 2016; Heldsinger et al., 2023), la protección efectiva de los tiburones de talla grande mediante la designación de AMPs de gran extensión que prohíban la extracción de cualquier tipo de recurso es una opción poco realista en zonas de alta actividad y tradición pesquera. Este es precisamente el caso del Mediterráneo, donde, además, la gestión de semejantes AMPs podría llegar a ser compleja debido al elevado número de países involucrados en la pesca. Finalmente, el alto nivel de degradación que ha sufrido el Mediterráneo en el último siglo disminuye la probabilidad de que la designación de AMPs a escala local garantice la recuperación de la misma diversidad de tiburones altamente móviles y de nivel trófico alto que la que existía cuando la intensidad pesquera era menor, ya que muchas de estas especies son escasas a nivel regional (Cardona et al. 2022). En consecuencia, el desarrollo de métodos efectivos de minimización de capturas incidentales, en combinación con la formación a los pescadores en las correctas técnicas de manejo y liberación de los individuos capturados, emerge como principal estrategia de conservación de tiburones a corto y medio plazo.

Futuras direcciones en la conservación de los tiburones de talla media y grande en el Mediterráneo.

En líneas generales, los estudios realizados en esta tesis indican que los tiburones de talla media y grande del Mediterráneo Noroccidental ocupan una posición única en el ecosistema. Como depredadores situados en los niveles medio-altos de la red trófica, la función de control que ejercen sobre organismos de niveles inferiores es vital para mantener el ecosistema marino equilibrado y sano. Sin embargo, los resultados obtenidos en la Costa Brava, alineados con otros estudios realizados en el Mediterráneo a lo largo de las últimas décadas, constatan el continuo declive de estos tiburones debido, principalmente, a la sobrepesca. La protección de sus poblaciones no solo debe recaer en un firme compromiso de las entidades gubernamentales o en el cumplimiento de las normativas por parte de la comunidad pesquera, sino que también exige a los biólogos que se siga generando y mejorando el conocimiento de esas especies que más lo necesitan. Tal como se ha discutido anteriormente, el conocimiento sobre la abundancia, la ecología o el impacto de la pesca sobre varias especies es aún prematuro, como ocurre en el caso de la cañabota gris.

En el Mediterráneo, los primeros estudios sobre esta especie se realizaron a principios del siglo XXI (Capapé et al., 2004; Celona et al., 2005; Kabasakal 2006) recopilando información sobre individuos que eran capturados incidentalmente y aportaron los primeros datos sobre su dieta, reproducción y distribución. Años más tarde llegarían los primeros estudios sobre la genética de esta especie en el Mediterráneo (Vella & Vella, 2010, 2017). Ahora, los resultados de esta tesis sobre el estado actual de la cañabota gris en el Mediterráneo plantean nuevas cuestiones a las que futuros estudios podrían intentar dar respuesta. Estas incluyen i) determinar si el mayor número de capturas en meses cálidos es debido a un mayor esfuerzo pesquero o si, en realidad, existe un verdadero patrón estacional, ii) investigar si las capturas incidentales en artes de superficie podrían estar relacionadas con movimientos de migración vertical que acercaran a los individuos a profundidades menores de las que se han documentado, aumentando así la probabilidad de captura, iii) examinar si el declive poblacional detectado en ciertos países puede ser sintomático de un declive generalizado en el Mediterráneo y, en especial, iv) conocer la respuesta de esta especie al estrés que genera su captura y su mortalidad post-liberación mediante el uso de marcas electrónicas.

Paralelamente, urge la aplicación de medidas que minimicen o eliminen la mortalidad por pesca de los tiburones de talla media y grande en el Mediterráneo, sobre todo en el caso de las especies amenazadas. La sinergia con el sector pesquero es clave para permitir a los investigadores diseñar y comprobar la efectividad de nuevos métodos de reducción de capturas específicos para determinadas especies.

Los avances significativos en el conocimiento sobre los tiburones en el Mediterráneo son la clave para poder darle a las entidades gubernamentales algo en lo que respaldar su voluntad de proteger sus poblaciones y conseguir aprobar medidas de conservación que consigan lo que todos en el fondo queremos: tener un mar sano (y lleno de tiburones).

CONCLUSIONES

- Los tiburones de talla media y grande que habitan en la Costa Brava (Mediterráneo Noroccidental) han sufrido un declive drástico en abundancia debido en gran parte a impactos antropogénicos, sobre todo por culpa de la sobrepesca.
- La tintorera (*Prionace glauca*) y la cañabota gris (*Hexanchus griseus*) son los únicos tiburones de talla grande que aún se pescan frecuentemente de forma incidental en el Mar Catalán.
- El arrastre y el palangre de fondo son los artes de pesca que capturan una mayor diversidad de estas especies de tiburones, especialmente en el caso de la cañabota gris.
- En el Mediterráneo, la cañabota gris es habitualmente capturada por los artes de pesca de profundidad, pero las capturas también tienen lugar en tos trasmallos e incluso en palangres pelágicos.
- La mayoría de capturas ocurren en el Mediterráneo Occidental y Central, especialmente durante los meses cálidos.
- La mortalidad de la cañabota gris en la embarcación es generalmente baja en todos los artes de pesca, aunque no tanto en los trasmallos. Se necesita más investigación para entender como los individuos responden a la captura después de ser liberados vivos.
- El declive percibido en ciertas regiones de algunos países del Mediterráneo debería incentivar a la UICN a que hiciera una nueva valoración del estado de la cañabota gris en el Mediterráneo.
- Los valores de $\delta^{15}N$ y $\delta^{13}C$ revelan un nicho isotópico único de los tiburones de talla meda y grande en el Mediterráneo Noroccidental,

diferente a los de otros peces depredadores grandes y los cetáceos odontocetos.

- En la red trófica del Mediterráneo Noroccidental, los tiburones de talla media y grande ocupan niveles altos, pero no apicales. En consecuencia, deberían ser considerados como mesodepredadores.
- Los modelos de mezcla identificaron a los cefalópodos como el grupo de presas dominante en la dieta de estos tiburones.
- La baja contribución de los peces pelágicos a la dieta de estos tiburones puede ser consecuencia de un cambio ontogenético en la dieta, pero también puede indicar una escasez de peces pelágicos.
- El LEK es una herramienta especialmente útil en estudios sobre especies raras o poco abundantes. La sinergia con el sector pesquero nos facilitó el acopio de información valiosa sobre el estado de diferentes poblaciones de tiburones, tanto a escala local como regional, que de otro modo habría resultado difícil de obtener.
- La protección de los tiburones de talla media y grande en el Mediterráneo, sobre todo en el caso de estos últimos, es poco probable que se consiga mediante la designación de AMPs. En su lugar, el desarrollo de métodos de prevención y minimización de las capturas incidentales, complementados con técnicas de manipulación eficaces, representan la mejor estrategia de protección de estas especies en la actualidad.

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