Universitat de les
Illes Balears

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INSTITUTO ESPAÑOL DE OCEANOGRAFÍA 1914

DOCTORAL THESIS

2015

MULTISCALE ENVIRONMENTAL - ICHTHYOPLANKTON ASSEMBLAGES RELATIONSHIPS IN THE BALEARIC SEA

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Doctor by the Universitat de les Illes Balears

LIST OF MANUSCRIPTS

Published

Álvarez I, Catalán IA, Jordi A, Palmer M, Sabatés A, Basterretxea G (2012) Drivers of larval fish assemblage shift during the spring-summer transition in the coastal Mediterranean. *Estuarine, Coastal and Shelf Science* 97: 127-135

Basterretxea G, Catalán IA, Jordi A, **Álvarez I**, Palmer M, Sabatés A (2013) Dynamic regulation of larval fish self-recruitment in a marine protected area. *Fisheries Oceanography* 22: 477-495

Rodríguez JM, **Álvarez I**, Lopez-Jurado JL, Garcia A, Balbin R, Álvarez-Berastegui D, Torres AP, Alemany F (2013) Environmental forcing and the larval fish community associated to the Atlantic bluefin tuna spawning habitat of the Balearic region (Western Mediterranean), in early summer 2005. *Deep-Sea Research Part I: Oceanographic Research Papers* 77: 11-22

Under revision

Álvarez I, Catalán IA, Jordi A, Alemany F, Basterretxea G. Interaction between spawning habitat and coastally steered circulation regulate larval fish retention in a temperate Bay. *Under second review in Estuarine Coastal and Shelf Science*

Álvarez I, Rodríguez JM, Catalán IA, Balbín R, Álvarez-Berastegui D, Aparicio-González A, Hidalgo M, Alemany F. Larval fish assemblage structure in the surface layer of the NW Mediterranean under contrasting oceanographic scenarios. *Under second review in Journal of Plankton Research*

The PhD candidate has also contributed in two scientific publications that although not considered as a part of the present thesis have been used to support the General Discussion

Hidalgo M, Reglero P, Álvarez-Berastegui D, Torres AP, **Álvarez I**, Rodríguez JM, Carbonell A, Balbín R, Alemany F (2015) Hidden persistence of salinity and productivity gradients shaping pelagic diversity in highly dynamic marine ecosystems. *Marine Environmental Research* 104:47-50

Hidalgo M, Reglero P, Álvarez-Berastegui D, Torres AP, **Álvarez I**, Rodríguez JM, Carbonell A, Zaragoza N, Tor A, Goñi R, Mallol S, Balbín R, Alemany F (2014) Hydrographic and biological components of the seascape structure the meroplankton community in a frontal system. *Marine Ecology Progress Series* 505:65-80

A mis padres,
que además de enseñarme a andar, me enseñaron a escoger mi camino.

TABLE OF CONTENTS

SUMMARY

Understanding the early life stages of fishes and the processes influencing their survival has been at the heart of the fisheries oceanography since the beginning of the 20th century. By focusing on spatial and temporal patterns in the ichthyoplankton (those early stages whose horizontal location is largely determined by currents), it is possible to gain some understanding of interrelationships among environmental conditions, fish spawning phase and dispersal/survival dynamics of the planktonic stages of fish.

The different physical and/or biological processes controlling Larval Fish Assemblages (LFAs) variability (abundances, composition and distribution) act at very different space and time scales. Sampling the sea at the appropriate frequency and at adequate time and space scales is required to evaluate those mechanisms. These studies are insufficiently developed in the Balearic Archipelago, a hotspot for biodiversity located in an extremely dynamic area of the Mediterranean. With this premise in mind, the main objective of the thesis was to deepen in the knowledge of LFA dynamics in the Balearic Sea (NW Mediterranean) at different spatio-temporal scales. Four different approaches were addressed.

At a sub-seasonal temporal scale, the influence of coastal environmental conditions during the shift from winter-spring to summer on fish larvae assemblages in a temperate area was evaluated. Larval fish assemblages were sampled fortnightly at three stations located in coastal waters off southern Mallorca from March to August 2007, covering the main spawning period for the resident coastal fish in this region. The larval fish assemblage showed clear seasonality with higher specific abundance but lower diversity in the spring, probably linked to a spatial (at the vertical scale) shift in the energy flow, which may trigger the summer spawning of many bottom-dwelling species.

At the submesoscale domain, the factors that may regulate the previously suggested high levels of larval self-recruitment were explored in Cabrera National Park (CNP), an insular Marine Protected Area (MPA) located off southern Mallorca. Our study attributes the regulation of larval arrival to the MPA to a combination of retention by topographically generated circulation patterns around the island and shelf break frontal dynamics.

Also at scales smaller than the mesoscale, we examined fish larval distribution drivers in Palma Bay, a large (~20 Km) wind-driven microtidal bay in the southern coast of Mallorca. Distributions and abundances of fish larvae in the Bay were analyzed and interpreted in the context of the observed circulation patterns, adult habitat distribution and spawning traits. Acoustic Doppler Current Profiler (ADCP) observations showed the presence of retentive flow patterns in the middle of the Bay enhancing local larval accumulation and self-recruitment. A multivariate approach based on Redundancy Analysis (RDA) revealed differences between the larval fish assemblages in the Bay, constituted by small pelagic and benthopelagic families (Gobiidae, *Chromis chromis* and *Serranus hepatus*) and offshore larvae, mostly from meso and large pelagic fish. These larval fish assemblages were structured according to depth variations and zooplankton abundance, and remained relatively unmixed because of the circulation patterns in the mouth of the Bay that uncouple its dynamics from alongshelf circulation.

At mesoscale level, we investigated the effect of two hydrographic scenarios, representing well-known contrasting examples of the early summer mesoscale dynamics in the archipelago, on the summer larval fish assemblages during two cruises in 2004 and 2005. While depth was the most important variable in explaining the assemblage structure and diversity observed under both scenarios, indicators of mesoscale activity (dynamic height, geostrophic velocity) contributed significantly to understanding the dynamics of the larval fish community. The larval assemblage dynamics are discussed in terms of species-specific and extrinsic factors, including future consequences of potential changes in these environmental scenarios.

The main results of this thesis are put together in context in a general discussion section and shortcomings and future directions are explored.

RESUMEN

Desde principios del siglo veinte, el estudio de los estadios tempranos de los peces y de los procesos que influyen en su supervivencia forma parte de la oceanografía pesquera. La investigación de los patrones temporales y espaciales del ictiopláncton hace posible entender las relaciones entre las condiciones del ambiente, la fase reproductiva de los adultos y la dinámica de supervivencia y retención de los estadios planctónicos de los peces.

Los diferentes procesos físicos y/o biológicos que controlan la variabilidad (abundancia, composición y distribución) en las comunidades de larvas de peces (a partir de aquí LFA, del inglés Larval Fish Assemblage) actúan a escalas espaciales y temporales muy diferentes. Se hace necesario por tanto muestrear en el mar con la frecuencia apropiada y a la escala espacio-temporal adecuada para evaluar esos mecanismos. Este tipo de estudios son escasos en el archipiélago Balear, punto de interés de la biodiversidad y situado en un área del Mediterráneo extremadamente dinámica. Teniendo todo lo anterior en cuenta, el principal objetivo de la tesis fue profundizar en el conocimiento de la dinámica de las LFA en el Mar Balear, a diferentes escalas espacio-temporales. Se realizaron cuatro aproximaciones diferentes.

A escala temporal, se evaluó la influencia de las condiciones ambientales costeras durante la transición primavera temprana-verano sobre las LFAs. Se realizaron muestreos quincenales entre marzo y agosto (cubriendo el pico de puesta de la mayoría de las especies de la zona) en tres estaciones de la zona costera del sur de Mallorca. Las LFAs reflejaron claramente la estacionalidad de la zona con una alta abundancia de especies pero bajas densidades de larvas en primavera, probablemente relacionada con la transición espacial (en el plano vertical) del flujo de energía que seguramente desencadena la puesta estival de muchas de las especies cercanas al fondo.

A una escala menor que mesoescala, se estudiaron los factores que regulan los altos niveles de auto reclutamiento previamente sugeridos para el Parque Nacional de Cabrera. Nuestro estudio atribuye la regulación de la llegada de larvas al área a una combinación de retención por los patrones de circulación generados por la topografía alrededor de Mallorca y la dinámica asociada a un frente de plataforma.

También a escala inferior a la mesoescala, examinamos los agentes responsables de la distribución de LFAs en la bahía de Palma en la costa sur de Mallorca. Se analizaron

e interpretaron la abundancia y distribución horizontal de las larvas de peces en la bahía en el contexto de los patrones de circulación observados, el hábitat de los adultos y las estrategias de puesta. Mediante observaciones de un perfilador de corrientes mediante Doppler, se describió la presencia de patrones retentivos de circulación en el medio de la bahía que favorecen la acumulación de larvas locales y el auto reclutamiento. Una aproximación multivariante basada en el análisis de redundancia (RDA) reveló diferencias entre la comunidad de la bahía formada por familias bentopelágicas y de pequeños pelágicos y una LFA de especies más lejanas a la costa, principalmente mesopelágicos y grandes pelágicos. Esas comunidades estaban estructuradas según variaciones en profundidad de abundancia de zooplancton y permanecían relativamente separadas debido a que los patrones de circulación a la entrada de la bahía separan su dinámica interna de la circulación en la plataforma.

A nivel de mesoescala investigamos mediante dos campañas en años consecutivos el efecto que ejercen dos escenarios hidrográficos (que representan ejemplos de escenarios muy contrastados entre sí característicos de la dinámica de mesosescala en verano en el archipiélago) sobre las LFAs estivales en la zona. Bajo ambos escenarios, la profundidad resultó ser la variable que mejor explicaba la estructura de la comunidad y su diversidad. Aun así, los indicadores de actividad mesoescalar (altura dinámica, velocidad geostrófica) contribuyeron de manera significativa a entender la dinámica de las LFAs.

Los principales resultados de esta tesis se tratan como conjunto en una discusión general final donde también se comentan las limitaciones y se exploran las posibilidades de futuro.

RESUM

Des de principis del segle vint, l'estudi dels estadis primerencs dels peixos i dels processos que influeixen en la seva supervivència forma part de l'oceanografia pesquera. La recerca dels patrons temporals i espacials del ictioplàncton fa possible entendre les relacions entre les condicions de l'ambient, la fase reproductiva dels adults i la dinàmica de supervivència i retenció dels estadis planctònics dels peixos.

Els diferents processos físics i biològics que controlen la variabilitat (abundància, composició i distribució) en les comunitats de larves de peixos (d'aquí endavant LFA, de l'anglès larval Fish Assemblage) actuen a escales espacials i temporals molt diferents. Es fa necessari per tant mostrejar la mar amb la freqüència adient i a la escala espai-temporal adequada per avaluar aquests mecanismes. Aquest tipus d'estudi son escassos a les Illes Balears, punt d'interès de la biodiversitat i situades a un àrea de la Mediterrània extremadament dinàmica. Amb tot lo anterior en ment, l'objectiu principal d'aquesta tesi va ser augmentar el coneixement de la dinàmica de les LFA a la Mar Balear, a diferents escales espai-temporals. Es varen realitzar quatre aproximacions diferents.

A l'escala temporal, es va avaluar la influencia de les condicions ambientals costaneres durant la transició primavera-estiu sobre les LFAs. Es varen realitzar mostreigs quinzenals de març a agost (pic de posta de la majoria de les especies de la zona) a tres estacions costaneres del sud de Mallorca. Les LFAs varen reflectir clarament la estacionalitat de la zona amb una alta abundància d'espècies però amb baixes densitats de larves a la primavera amb molta probabilitat relacionada amb la transició espacial (dins del pla vertical) del flux d'energia que segurament desencadena la posta estival de moltes especies properes al fons.

A una escala menor que la mesoescala, es varen estudiar els factors que regulen els alts nivells de auto reclutament prèviament suggerits per el Parc Nacional de Cabrera. El nostre estudi atribueix la regulació de l'arribada de larves al àrea a una combinació de retenció pels patrons de circulació generats per la topografia al voltant de Mallorca i la dinàmica associada a un front de plataforma.

També a escala inferior a mesoescala, vàrem examinar els agents responsables de la distribució del LFA a la badia de Palma a la costa sud de Mallorca. Es varen analitzar i interpretar la abundància i distribució horitzontal de les larves de peixos a la badia en el context dels patrons de circulació observats, l'habitat dels adults i les estratègies de

posta. Mitjançant observacions amb un perfilador de corrents Doppler es va descriure la presencia de patrons retentius de circulació al mig de la badia que afavoreixen la acumulació de larves locals i el auto reclutament. Una aproximació multivariant basada en l'anàlisi de redundàncies (RDA) va revelar diferencies entre la comunitat de la badia formada per famílies bentopelàgiques i de petits pelàgics i una LFA d'espècies mes allunyades de costa, principalment mesopelàgics i grans pelàgics. Aquestes comunitats estaven estructurades segons variacions en profunditat de abundància de zooplàncton i romanien relativament separades degut a que els patrons de circulació a l'entrada de la badia separen la seva dinàmica interna de la circulació a la plataforma.

A nivell de mesoescala vàrem investigar mitjançant dues campanyes a anys consecutius l'efecte que exerceixen dos escenaris hidrogràfics (que representen exemples d'escenaris molt contrastats l'un de l'altre característics de la dinàmica de mesoscale a l'estiu a l'arxipèlag) sobre les LFAs estiuenques a la zona. Sota ambdós escenaris, la fondària va resultar ésser la variable que millor explicava l'estructura de la comunitat i la seva diversitat. Tot i això, els indicadors d'activitat mesoscalar (alçada dinàmica i velocitat geostrofica) varen contribuir se manera significativa a entendre la dinàmica de les LFAs.

Els principals resultat d'aquesta tesi es tracten com a conjunt a una discussió general final on també es comenten les limitacions i s'exploren les possibilitats de futur.

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Me gusta pensar en esta tesis como el resultado de una carrera de fondo, con sus subidas y bajadas de ritmo. Han sido un poco más de diez años, y el inicio de este proyecto está entremezclado con el inicio de mi carrera profesional. Durante estos años he pasado por 4 institutos de investigación en 3 ciudades diferentes, he superado 2 oposiciones, comprado un piso, ganado amigos, perdido alguno también… En fin, lo que viene siendo parte de una vida. Durante todo el recorrido me he sentido extremadamente acompañada y quiero aprovechar este espacio para agradecer a todas las personas que ya sea durante un tramo o durante todo el trayecto han contribuido a que pueda hoy estar escribiendo este apartado de mi tesis doctoral. Quiero nombrar a todos así que me disculpo de antemano si me olvido de alguien y también por la longitud que este texto pueda alcanzar.

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En siguiente lugar, agradecer a todos los coautores de los trabajos que forman esta tesis por sus aportaciones y a todo el personal que ha participado en las 5 campañas que han sido necesarias para recolectar todo el material incluido en este trabajo, ha sido un placer participar en cada una de ellas. La Dra. Ana Sabatès paso muchas horas solucionando mis dudas en la identificación de las larvas de Cabrera. Mil gracias también.

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I

GENERAL INTRODUCTION AND OBJECTIVES

"The problem of relating phenomena across scales is the central problem in biology and in all of science"

(Levin 1992)

I.1. The beginning of fish larvae studies: Recruitment variability in fish

Understanding the early life stages of fishes and the processes influencing their survival has been at the heart of the fisheries oceanography since the beginning of the 20th century, after the seminal works by Johan Hjort (1914, 1926). Many advances have taken place since then but many questions remain the same, although appear in different forms (Llopiz et al., 2014). Understanding the population dynamics of fish is still an elusive topic when it comes to clarify (and predict) the enormous interannual variability attributed to the biomass of the new fish incorporating to the fish stocks (Cushing, 1995). The lack of predictable relationships between spawning stock biomass (at moderate to high stock levels) and recruitment is the main concern in fisheries stock assessment (Hare, 2014; Punt et al., 2014; Rice et al., 2014), and is the entrance gate to the “fisheries oceanography”, a subfield of fishery science that tries to understand the causes of this variability (Govoni, 2005). Thus, the effort in understanding the relationship between reproductive outputs and recruitment of fishes is vital if they are to be managed properly and has driven the fisheries research in the last century (Houde, 2008).

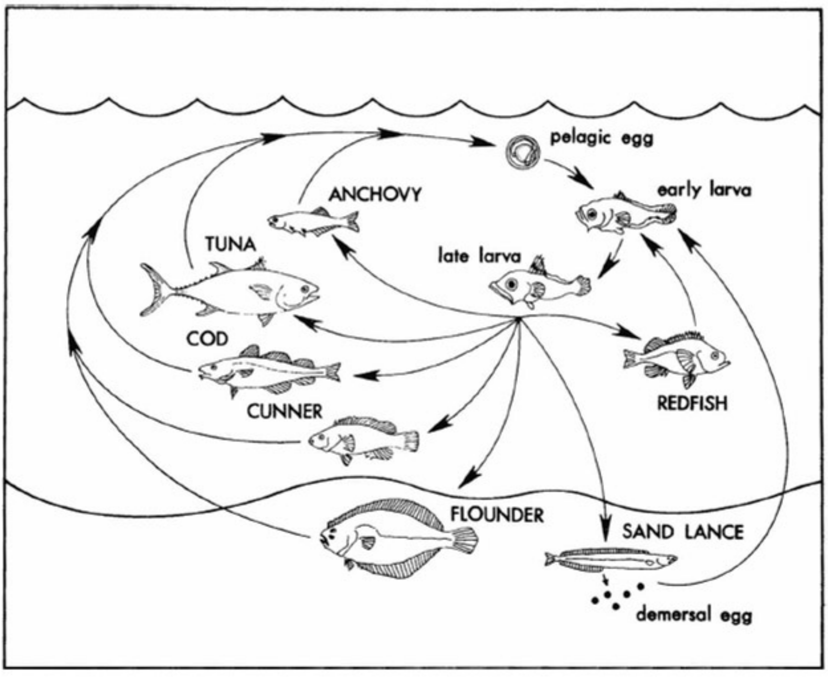

Figure I.1. Diagram representing some of the variety of reproductive patterns of marine fishes (not scaled). From Miller and Kendall (2009)

Within evolutionary postulates, live beings adapt to maximize the probability of fitness (understood as the probability of producing surviving offspring that manages to transfer the parent's gene pool, Miller and Kendall, 2009).

To these respect, fishes, the eldest vertebrates in earth, have evolved to develop a diversity of reproductive patterns that by far surpasses that seen in other group of vertebrates (Miller and Kendall, 2009). Fish usually have floating eggs (showing positive buoyancy) which are released directly into the sea. Eggs then pass directly to a free swimming yolk-sac stage, which turns into plankton-feeding larval stage that ends up transforming in a juvenile stage, with almost all external characteristics of adult fish. However, among many species there are distinct juvenile forms and in some there are distinct transformation stages which are quite unlike either larval or juvenile stages (Fig.I.1). Meso- and bathypelagic fishes (inhabiting between 200-1000m and 1000-4000m depth in the water column, respectively Fig. I.2) follow a similar pattern as regards to their eggs and larvae found in the surface layers where there is abundance of food. Exceptions include the beloniforms and the atheriniforms, which produce eggs with filaments to attach to floating algal mats or flotsam. Other small pelagics, as *Clupea harengus,* release eggs that sink to the bottom. On the other hand, demersal fishes living and feed on or near the bottom, from coastal areas on the continental shelf to deeper slope or abyssal planes, exhibit an even wider variety of reproductive strategies (Fig. I.2). Some produce their eggs in large gelatinous masses (most monkfish, some scorpaeniforms) which float to the surface while development proceeds to yolk-sac or first feeding stage at hatching. Shorefishes usually release pelagic eggs, which are swept out to the pelagic realm where development proceeds. Other shorefishes have demersal eggs, which are either attached to a surface or held, in guarded nests. However, upon hatching, often in a first feeding stage, the larvae are pelagic and are carried out to sea depending on current patterns. Early stages of shorefish must eventually return to the shore and timing of spawning, timing of development duration, and mode of development all enter in to completing the cycle. Mortality is extremely high from the egg to the end of the larval period, with average mortality surpassing 99 % (Houde, 1989, McGurk 1986), which makes quite true the phrase "an average fish larva is a dead larva". However, there are also viviparous fishes, such as syngnathiforms and some scorpaeniforms, whose development is completed within the parent and viable larvae or juveniles are released directly into the sea.

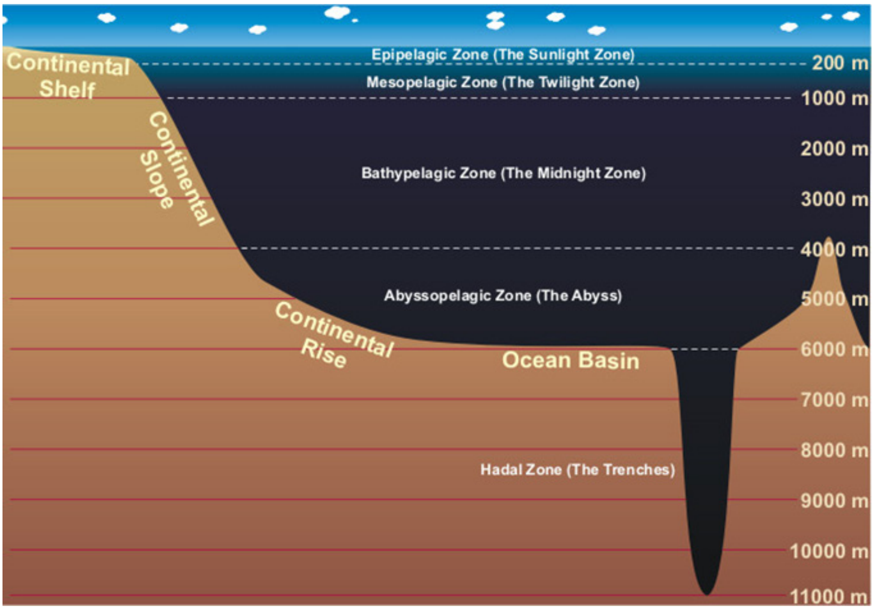

Figure I.2. Diagram representing the layers of the ocean. NOAA National Weather Service

The different developmental stages have unique habitat requirements. The link between recruitment and abundance/survival during pre-juvenile life stages of marine fishes is sufficiently well documented to justify a continued interest in factors regulating survival and abundance in the egg and larval stages. Factors affecting reproduction success and survival of early life stages of fish have been examined since the mentioned pioneering works by the Norwegian Johan Hjort. It should be noted, however, that interacting processes operating during the post-larval stages can significantly moderate, or under some circumstances even regulate, recruitment in fishes (see Bailey, 1994; Houde, 1989; Anderson 1988).

Within larval fish ecology, several hypotheses have been developed in an attempt to explain recruitment variability. The first hypotheses were focused mainly on trophodynamics. Hjort's "Critical period" (1914) one proposed that larval survival pivots on whether or not a larval fish successfully feeds during the "critical period", considered by Hjort to be the transition from relying on its yolk sac to exogenous food sources. Cushing (1974) with his "Match-mismatch" hypothesis tested that success of larval recruitment is linked to a temporal alignment of fish reproduction, larvae hatching, and plankton (prey) blooming (generally associated with spring). Hjort did not explicitly specify predation as a mechanism controlling recruitment. In commenting on the relative importance of predation versus food-mediated processes to larval fish dynamics, Bailey & Houde (1989) concluded that the question of whether starvation or predation is more important as a cause of early life mortality remains unresolved, and there may be no unequivocal answer because the situation may vary with species, area, and year (see also Legget and Deblois, 1994). Actually, recent investigations using laboratory experiments suggest that first feeding may be an intrinsically critical period due to purely physical mechanisms linked to the extremely inefficient feeding mode at the viscous scale of a fish larva (China and Holzman, 2014).

The inclusion of the growth and condition of fish larvae in the hypotheses followed. The ‹stage duration› hypothesis, also known as the ‹single process› (Cushing, 1975), predicts that larvae which experience favorable feeding conditions, and therefore grow quickly, will achieve metamorphosis at earlier ages and experience lower cumulative mortality due to predation during the larval stage when mortality rates are known to be high. The “bigger is better” concept (Houde, 1987) holds that larger larvae are less susceptible to predation. Hence, the prediction is that larvae which hatch at larger sizes, or grow at faster rates, thereby achieving larger body size at a given age, should be less vulnerable to predation (Anderson 1988-concealing several hypotheses into the “growth-mortality” hypothesis-, Hare and Cowen, 1997).

Hjort (1926) offered a second hypothesis to explain variability in year-class success, the “Aberrant Drift” hypothesis. He proposed that larval recruitment is affected by winds and ocean currents which cause dispersal of eggs and larvae, removing them from essential larval and juvenile habitat. This idea was less tested than the Critical Period hypothesis until late in the 20th century, when a series of hypotheses taking into account hydrodynamics were performed to explain variability in recruitment. Lasker (1978) developed for upwelling systems the “Stable Ocean” hypothesis. He stated that when tranquil ocean conditions occur in upwelling systems, the water column becomes stratified in layers that concentrate larvae and plankton, which increases successful larval feeding, which in turn increases larval recruitment and contributes to year class strength. Also for upwelling systems, Cury and Roy (1989), and Roy and Cury (1992), constructed the “Optimal Environmental Window” hypothesis. For these systems, the larval recruitment is increased depending on the presence/absence optimal ranges of turbulence caused by wind, storms and other energetic events. Iles and Sinclair (1982), with their “Stable Retention” hypothesis progressed forward on Hjort’s aberrant drift hypothesis. They stated that prey availability is not as critical to recruitment as the physical retention of the larvae, so spawning events must coincide with suitable wind and current conditions.

Houde (2008) revised all hypotheses concerning recruitment variability and concluded that recruitment variability can result from numerous processes operating on different time and space scales, and represents integrated process acting throughout pre-recruit life. There is no single process, mechanism or factor responsible for recruitment by itself, but many processes may act together over the entire egg to pre-recruit juvenile period. He proposed five mechanisms that dominate recruitment in fish: prey, predators, growth, temperature and physical processes and features. After over one century after Hjort's papers, recruitment variability is only understood for particular cases, and the processes behind are far from being incorporated into population dynamics models. New methodologies, computer power and insights into behavioral and physiological aspects enable the integration of physical and physiological processes in a more holistic way (Hinrinchsen et al., 2011; Peck and Hufnagl., 2012), and testing for multiple hypotheses at a time has been advocated for, instead of trying to employ the typical experimentally-derived single-hypothesis testing (Hare et al., 2014). In the following decades, it is foreseen that complex mechanisms at several spatial/temporal scales will be incorporated into predictive models.

I.2. Evolution of Fish Larvae studies (1996-2014)

Although Scopus (a widespread online engine to assess the impact of scientific disciplines, journals, works and authors) has launched its *Cited References Expansion Program* to include cited references in its database going back to 1970, for the moment only the 1996-present period can be analyzed. With the increasing numbers of scientific journals, and the increase of the world population (and to some extent the scientific population), the number of fish larvae studies published is growing fast, revealing that it is a growing and active topic in science. In the last 18 years, the number of published peer-reviewed literature including the word *fish larv** has been more than doubled (from 569 in 1996 to its maximum of 1370 in 2013 and 1277 in 2014).

With the objective of exploring how the fish larvae science topics evolve with time, a small exercise has been performed on the 16507 SCI papers including the word *fish larv** in the 1996-2014 period. The most interesting results have been represented in Figure I.3. Some terms have been left apart in order to have a clear graphic. That doesn't mean they are not important, but only the topics with an important number of papers or with interesting evolution have been included.

From the evolution graphic (Figure I.3) and the summary in Table I.1, it is possible to infer two kind of evolutions for the topics. A group of topics have evolved in parallel with the evolution of the Fish larvae studies; they represent more or less the same percentage of the total of larval studies at the beginning and at the end of the period. These topics are the most “classical”: Recruitment, Growth, Trophic, Taxonomy and Assemblages/Communities/ Associations. The percentage represented by the papers of the rest of the topics from the total Fish Larv* papers has increased (the limit we selected was “in more than 2%”) in the last 18 years. These topics can be related with “modernity”, in terms of technology (Genetics and Aquaculture) or in terms of the rising concern with the environment (Diversity, Climate/Global Change/Warming, and Connectivity).

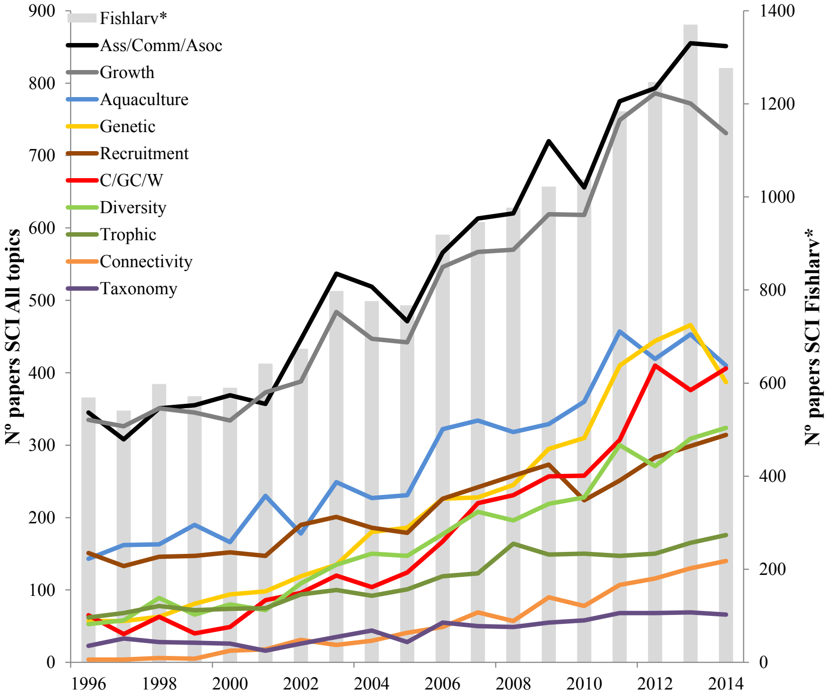

Figure I.3. Evolution of fish larvae peer reviewed SCI papers (1996-2014). Ass/Comun/Asoc: assemblages, comminities and associations. C/GC/W: climate, global change and warming

Although in Figure I.3 and Table I.1 the different topics or branches in fish larvae science have been addressed separatedly, they are not necessarily mutually exclusive. For example, in all studies regarding any topic of fish larvae collected in the wild, knowledge of taxonomy is required to identify fish larvae species. Most of studies on diversity and on global change and climate include assemblage identification.

	Ass/Comm/Asoc	Growth	Aquaculture	Genetic	Recruitment	C/GC/W	Diversity	Trophic	Connectivity	Taxonomy
1996	60.6	58.9	25.1	10.0	26.5	11.4	9.3	10.9	0.7	4.0
2000	62.5	56.6	28.1	15.9	25.8	8.3	13.6	12.5	2.7	4.4
2005	61.4	57.6	30.1	24.3	23.3	16.2	19.2	13.2	5.3	3.7
2010	63.2	59.5	34.7	29.9	21.6	24.9	22.0	14.5	7.5	5.6
2014	66.6	57.2	32.1	30.3	24.6	31.8	25.4	13.8	11.0	5.2

Table I.1. Percentage that each of the selected topics represent from the total of Fish Larv* papers in the corresponding year. Ass/Comun/Asoc: assemblages, comminities and associations. C/GC/W: climate, global change and warming.

I.3. Larval Fish Assemblages

When a novel system or area has to be examined, it is usual to deal with more than one of the above mentioned topics. Three consecutive phases were previously suggested by Juniper and Tunnicliffe (1997) as a useful approach to understand the dynamics of a system, and successfully followed by, for example, Torres (2015) for analyzing the Decapod larval community in the Balearic Islands. The consecutive phases involve 1) determining the composition of the system (taxonomy), 2) determining its structure (assemblages identification in our case) and 3) using that basic data, together with covariates, to infer the dynamics of the system.

As expected, one classical way of analyzing ecosystem properties is through the multivariate analysis of it components, and how they vary through time and space. Understanding the ecology of fish and the system they inhabit is classically linked to the analysis of the fish communities during their life cycle. The eggs and larvae from most fish are typically found within the upper 200 m of the water column (e.g. Olivar and Sabatés 1997). That position in the water column makes them more susceptible to collection than are adult fishes that can avoid mid-water trawls or seek protection from bottom trawls in benthic substrates, or just live too deep to be collected routinely. Due to the complex 3D configuration of adult fish habitats (occupying all layers in Fig. I.2), focusing on their early stages is an invaluable tool to compile large amounts of information on the adult fish communities producing the observed eggs and larvae (Ahlstrom 1965), which tend to concentrate in surface layers amenable to sampling.

The operational term Larval Fish Assemblage (LFA) is used for all those early stages of fish that occur together in a single place, such that they have at least a reasonable opportunity for daily contact with each other. Throughout this work, we will indistinctly refer to these associations as Larval Fish Assemblages, Larval Fish Communities, Ichthyoplankton Assemblages and Ichthyoplankton Communities. The immediate consequence analyzing planktonic larval assemblages is that they often reveal more diversity in the fish fauna than do surveys of juvenile and adults (e.g. Shakell and Frank, 2000; Norberg, 2004). Nevertheless, estimates of the absolute abundance of fish eggs and larvae are difficult to obtain, given the patchy distribution of ichthyoplankton, which owes in part to advective aggregation and diffusion, as well as the location of spawning.

Co-occurrence of individual species in an ichthyoplankton assemblage suggests that they share common requirements during their early life. Frank and Leggett (1983) proposed that LFAs are adaptive and are the result of similar responses among species to the pelagic environment. An alteration in the ecosystem that negatively affects one species will likely affect all species in the assemblage negatively. The characterization of a functional linkage between key physical features and fish habitats was recognized as a first and important step towards understanding the variability of spatial patterns and population dynamics (e.g. Leis and Miller, 1976). Some first approaches to investigate ichthyoplankton spatial patterns have been to identify larval fish assemblages and relate their occurrence and variability to the biology of the component fish species and to the pelagic ecosystem in which they dwell (e.g. Frank and Leggett, 1983; Young et al., 1986).

The spatial organization of larval fish assemblages is expected to play a key role in population dynamics and its response to environmental forcing (Sinclair, 1988). By focusing on spatial patterns in the ichthyoplankton, it is possible to gain some understanding of interrelationships among fish species during their early life histories, as well as at the adult spawning phase. Examining these patterns in relation to oceanographic conditions provides insight into the adaptation of spawning strategies to the prevailing physical and biological processes. Information concerning optimal environmental conditions for larval fish survival may also be gained. Such knowledge is important to understand resource utilization and niche occupation among fish species in marine ecosystems (Doyle et al., 1993). Modification of local assemblages including changes in biomass, species composition, and ratios of species of feeding groups, species diversity and recruitment success can be used as biotic indicators of habitat degradation (Jones et al., 2005; McCormik et al., 2010) and changes in the overall ecosystem productivity

(Cushing, 1990; Beaugrand et al., 2005).

The broad scale changes in productivity and/or hydrography that global change might bring about will impact the entire assemblage and not just individual species. The impact on the assemblage may not be to reduce the abundance of all or any of the species of which it is composed, but rather, the impact may be to shift the geographic location or seasonal timing of the appearance of the assemblage (Miller, 2002; Bakun, 2014).

I.4. Oceanographic processes: a matter of scale

The different proposed mechanisms (physical and/or biological) controlling recruitment variability (and thus assemblages composition) act at very different space and time scales. Sampling the sea at the appropriate frequency and at adequate time and space scales is required to evaluate those mechanisms. Also, in attempting to identify environmental determinants of assemblage structure across geographic domains, assemblages and environmental factors should be viewed at comparable scales (O' Neill et al., 1988; Wiens, 1989; Levin, 1992).

In approaching the subject of study it is useful to have a feeling of the size scale for the organisms and phenomena to be discussed (Fig. I.4). Ocean basins are typically 10000 km wide and confine the largest biological communities. The average depth of the ocean is 3800 m but the depths of the euphotic layer (100~200 m) and the mixed layer (~100 m) are more often critical to open-ocean biological processes. Mann and Lazier

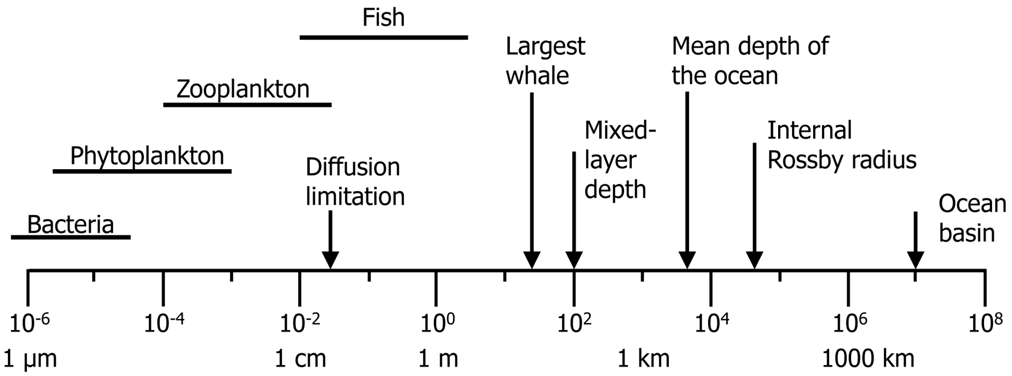

Figure I.4. The size scale from 1 µm to 100000 km, showing some characteristic size ranges of organisms and physical lenght scales. Adapted from Mann and Lazier (1991)

(1991) described this issue in a prominent way, which is here condensed as it is core to the motivation of the thesis.

The Coriolis and gravitational forces give rise to the Rossby internal deformation radius, a frequently encountered length scale in physical/biological oceanography. It arises in flows of stratified water when a balance between the two forces is established. This scale, which varies strongly with latitude, is the typical width of ocean currents such as the Gulf Stream, the width of the coastal upwelling regions, or the radius of the eddies in the ocean (Mann and Lazier ,1991).

The viscous or Kolmogoroff length is the scale where viscous drag begins to become important, that is, where viscosity starts to smooth out turbulent fluctuations in the water. The scale represents the size of the turbulent eddies where the viscous forces are roughly equal to the inertial forces of the turbulent eddies. This scale also induces important changes in the methods of locomotion and feeding. Thus, organisms larger than ~10mm are not seriously affected by viscous drag, while for the smallest organisms (including eggs, a large fraction of fish larval life and its food) swimming is akin to a human swimming in honey (Mann and lazier, 1991). Because of the change in the turbulent motions, the smallest organisms must depend on molecular diffusion for the transfer of nutrients and waste products. For the larger animals nutrients and wastes are moved rapidly by turbulent diffusion, which is not affected by viscosity.

As a first approximation, as regards hydrographic features, time scales change in direct proportion to length scales. On the global scale, the thermohaline circulation may take 1000 years to complete a circuit. On the ocean-basin scale, the major gyres may require several years to complete a circuit. Eddies and gyres spun off from the major currents have lifetimes of weeks to months, and as energy cascades through smaller and smaller scales of turbulence, the characteristic time for rotation decreases to seconds at the smallest scale.

While physical features determine the spatial scales of ecological processes, the organisms determine the time scales. While the life span of a large marine mammal may be close to 100 years, those of fish are more like 1-10 years, and zooplankton may complete a generation in a few days or weeks. Phytoplankton has doubling times on the order of days, and bacteria on hours. It follows that small organisms are likely to undergo more rapid fluctuations in numbers than large ones. Since, in general, each type of organism tends to feed on organisms smaller than itself, the process of trophic transfer has the effect

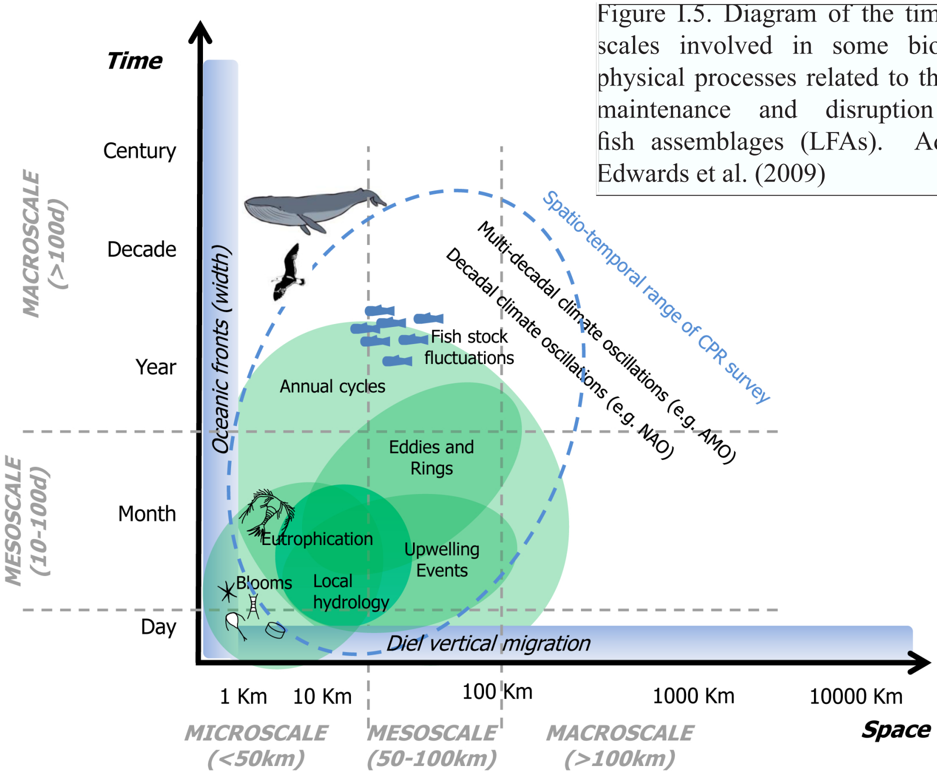

Figure I.5. Diagram of the time and space scales involved in some biological and physical processes related to the formation, maintenance and disruption of larval fish assemblages (LFAs). Adapted from Edwards et al. (2009)

of smoothing out the rapid fluctuations. Conversely, predators may impose on their prey longer term fluctuations that correspond with fluctuations in predator numbers (Mann and Lazier, 1991).

The dominant external force on marine ecosystems depends on the scale of study (Fig. I.5, Edwards et al., 2010). For example, in small-scale studies (e.g. weeks and km), biological patterns could be driven by biological forcing (e.g. predation), whereas in large-scale studies patterns could be predominantly forced trough hydro-climatic variability. Since accurately describing the strength and significance of species-environment relationships is central to understanding the functioning of ecosystems, conserving biodiversity and managing ecosystems, explicitly considering scaling issues should be part of the formal framework within which proper estimation and inference are carried out (de Knegt et al., 2010).

Prior to the surveys design, a brief overview of the space and time scales of the biological and physical processes to study will increase the probabilities of properly describing the phenomena. Time-scale diagrams, such as Figure I.5, are very useful for that purpose. It is not infrequent, however, to find out that the problem that wants to be resolved cannot be tackled within the sampling scheme of the analyzed survey.

The sampling scheme must 1) resolve the main physical features that govern the spatial resolution of organisms of interest and 2) be carried out in a timely manner so as to avoid significant changes in distribution over the course of the survey (Helbig and Pepin, 1998a, Pepin and Helbig 2012).

I.5. Scales and Factors affecting Larval Fish Assemblages

Integrating the information above, it is derived that the composition, abundance and distribution of larval fish assemblages in any area depend on i) biological factors such as the structure of adult fish communities, which in turn is conditioned by the characteristics of the habitat and especially on the species reproductive habits that are related to the location and time of spawning, resulting from an evolutionary process aiming at maximizing the survival of the offspring, and ii) the hydrodynamics of the area that constitute a preponderant factor for the planktonic stages, eggs and larvae. The spatial larval distribution will condition the environmental scenarios encountered by the larvae along the development, both considering biotic and abiotic factors, and hence their survival, which ultimately determine the structure of larval assemblages. Thus, the observed larval assemblages are the result of the initial distribution of the offspring and the hydrographic scenarios determining larval drift and survival.

Within the general processes previously mentioned, efforts to describe and understand ichthyoplankton assemblages must address the processes that affect the formation, maintenance, and disruption of the assemblage. Assemblage dynamics respond to evolutionary, biotic, and environmental forcing at different scales (Miller, 2002).

Miller (2002) detailed space and time scales related to the factors affecting the different stages of a larval fish assemblage: from its formation to its disruption. Table I.2 presents a synthesis of those processes and was the scheme followed in the present section to explain them.

I.5.1. Formation of LFAs

Both physical and biological processes regulate the formation of LFAs (Table I.2). Usually, the distinct LFAs identified through multivariate statistical techniques identify ichthyoplankton assemblages that exhibit little spatial overlap at the scales of tens of kilometers. This separation can be mostly explained by differences in the physical characteristics of the environment, partly linked to the adult spawning habitat.

An input of energy is necessary to mix water masses of different densities. This energy can be provided for example by wind or tides. In the absence of this input of energy the mixing of water masses will not occur. Thus, within any large body of water, different water masses can become isolated and distinct. Whereas in freshwater density differences are driven only by temperature, in the marine and estuarine realms density differences result from both temperature and salinity. In marine systems, it is usual that density driven currents reinforce the separation of the water masses. In general, different ichthyoplankton assemblages are often associated with different water masses (e.g. Carassou et al., 2012a), and it is not uncommon to find interactions between adult habitat and water masses (e.g. Alemany et al., 2010).

Physical processes may concentrate eggs and larvae, which promotes assemblage formation. In marine systems, interfaces between different water masses, known as fronts, have effects on both the distribution and survival of plankton. Convergent fronts, in which water from the two different water masses is brought together, are a concentrating mechanism, perhaps leading to assemblage formation (e.g. Govoni, 1993). The role of fronts may not simply be one of concentrating larvae; they may also aid favorable transport to juvenile habitats (Bakun, 2006).

The ultimate cause of ichthyoplankton assemblage formation must be the spawning behavior of adults. As a response to the diversity of existing environments, fish have developed a wide range of life-history strategies. For a lot of fish species, early life stages are separated spatially from later stages (Miller and Kendall 2009). That implies that the closing of the life cycle is essential in the evolution of their life-strategies. Any offspring must be produced at a time and a in a place from which the resulting larvae can grow, develop, and mature to join the spawning population. The range of times and locations that meet these requirement of closing the life cycle may be limited (Cury and Roy, 1989). Species that are similarly restricted become members of the same LFA.

Table I.2. Processes and scales of time (*t*) and space (*s*) important to the formation, maintenance, and disruption of larval fish assemblages. Modified from Miller (2002).

	Type of process	**Macroscale** ($s>10^5$ m; $t>$ 1 month)	**Mesoscale** (10^5 m$>s>5*10^4$ m; month$>t>$days)	**Microscale** ($s<10^2$ m; $t<$ days)
FORMATION	Physical	Currents and circulation patterns (separation of water masses)	Convergent fronts (concentrating available larvae)	
	Biological	Spawning behavior (seasonal) Retention areas	Spawning time (daily or lunar rhythms)	
MAINTENANCE	Physical	Currents and circulation patterns (maintenance of water mass distinctions)	Convergent fronts (increased local production)	Lasker events (prey patch formation in stable environm.)
		Upwelling (maintenance of water mass distinctions)	Gyres and eddies (limited advection and diffusion)	Small scale turbulence (increases in feeding rates)
			Upwelling (uniform advection patterns)	
	Biological	1º and 2º production (provision of suitable prey field)	Larval growth and survival (condition-dependent distributions)	Foraging behavior (area restricted searching)
			Primary and secondary production (distribution of prey field)	
			Swimming behaviour (light,temperature,salinity preference)	
DISRUPTION	Physical	Current meanders (breaking down water mass distinctions)	Divergent fronts, diffusion and advection (disruption of patches)	Small scale turbulence (disruption of patches)
	Biological	Growth, development to metamorphosis (change to adult habitats)	Competition (reduction in prey availability)	
		Seasonal declines in production (declines in prey availability)	Predation (mortality)	

Fishes must spawn in the right place to ensure that their progeny hatch into a favorable environment. But equally, fishes must also spawn at the right time to maximize survival. Considerable effort has been expended in defining both the spawning and larval periods for a wide variety of fishes. Ichthyoplankton assemblages tend to be more distinct seasonally at higher latitudes than comparable assemblages in lower latitudes (Miller, 2002). By themselves, patterns in seasonal occurrence are not sufficient to define ichthyoplankton assemblages. Abundance must be considered as well as species richness. While larvae of an individual species may be present over a number of months, only a few species may be common in only a few months. Distinctly different ichthyoplankton communities during the course of the year (seasonal) have been reported often (e.g. Barletta et al., 2003) and are likely to be typical of LFAs generally (e.g. spring and summer assemblages). It was the relationship between spring zooplankton production and the abundance of larval cod that was at the heart of Cushing's Match/Mismatch Hypothesis mentioned in subsection I.1, which suggests that the timing of larval production is tied directly to the timing of secondary production that is necessary to support larval growth and survival. Cushing also suggested that in systems in which secondary production is pulsed, the timing of larval release would be pulsed to match production cycles, whereas in systems in which secondary production is continuous, larval production would be more continuous. The Match/Mismatch Hypothesis remains the most influential concept relating the seasonality of larval production to assemblage formation (e.g. Siddon et al., 2013, Peck et al., 2012).

The role of spawning behaviour in assemblage formation is not restricted to seasonal time scales (Table I.2). In many fish species, spawning behaviour is synchronous and results in the formation of large patches of larvae. Spawning synchrony in coral reef fishes, for example, may be related to the onset of favorable environmental conditions or by the need to swamp locally abundant predators (Claydon, 2004).

In summary, patterns in spawning behaviour of adults are in first term responsible of the formation of LFAs and have probably evolved to maximize the coincidence of the timing of offspring release with the reasonable abundance of the larva's principal food resources. Moreover, the location of release likely reflects locations of favorable hydrography from which the survival of larvae is sufficient to ensure adequate numbers survive to replace the spawning stock.

I.5.2. Maintenance of LFAs

Physical and biological agents are also responsible for the LFAs maintenance (Table I.2). Processes affecting maintenance of assemblages are mainly those that operate at the mesoscale or the microscale. The principal physical forces responsible for the maintenance of LFAs relate to mesoscale circulation patterns and density differences that retain larvae within particular water masses and microscale physical processes that promote growth and survival. The principal biological processes that help maintain LFAs relate to factors that promote growth and survival. It would be wrong, however, to draw sharp distinctions between the two categories, as they interact strongly. Once developed, assemblages will only be maintained if they overcome the forces causing their disruption. These forces are principally diffusion, advection and dispersal.

From a “macroscale point of view”, all these features that maintain water mass distinctions (currents, circulation patterns and upwelling systems, Table I.2) also cooperate in the maintenance of the assemblages.

At smaller scales than macroscale, those features that concentrate particles such as fronts and eddies are in many cases responsible of the maintenance of the LFAs (Bakun, 2006). Frontal regions act to maintain assemblages as they actually concentrate larvae and overcome both diffusion and advection. Convergent fronts may concentrate larvae, thereby overcoming diffusive and advective flows. Fronts may act to maintain assemblages by promoting growth and survival (Bakun, 2006). Riverine plumes, the frontal region between marine and estuarine water masses, are locally very important to the maintenance of ichthyoplankton assemblages because they promote retention, growth, and survival of fish larvae (Whitfield, 1999). Also, tidal–stream transport has been reported to be used by LFAs both for movement into the estuary and for maintenance within the estuary (Boehlert and Mundy 1988). At a broader scale, gyres and eddies limit outward diffusion. Gyre-like structures may be important to maintaining ichthyoplankton assemblages on coastal banks, isolated islands and sea mounts, and on coastal shelf slopes (Werner et al., 1993; Bakun, 2006).

Although involving advection, upwelling areas are also responsible for the maintenance of LFAs. Provided that the advection is sufficiently consistent and prolonged, the assemblage will move along with the water. Thus, the strong directional advection simply swamps physical processes that would lead to diffusive losses and so the assemblages maintain its integrity. The many upwelling-related ichthyoplankton assemblages are examples of such a system (e.g. Moyano et al., 2014). The LFA are not necessarily stablished in the horizontal plane. In the vertical plane, the existence of different LFAs at different depths is possible. In stratified periods, different LFAs above and below the thermocline can coexist, separated by very few meters but never interacting because of the physical barrier.

In coastal areas, the shape of the coast or interactions with the topography have been shown to be key physical elements for retention and dispersion of LFAs (Basterretxea et al., 2012). Thus, in these areas maintenance or disruption of LFAs are promoted by retention and/or dispersion.

Two physical processes acting at microscales have been proposed as encouraging maintenance of assemblages through their presumed impact on growth and survival (Table I.2). Following intensive study of the growth and survival of the northern anchovy (*Engraulis mordax*), Lasker (1975, 1978) concluded that the establishment of a local concentration of their dinoflagellate prey, resulting from a “period of calm” (which later became known as a Lasker event), was crucial to the survival of newly hatched northern anchovy larvae. Conditions that disrupted these local concentrations of dinoflagellates produced lower survival and recruitment. Small-scale turbulence is the final physical force that may promote maintenance of assemblages. Small scale turbulence, within certain limits, increases the ingestion rates of larval fish suggesting that growth and survival may be higher in more turbulent regions (Mackenzie and Leggett, 1991). But to date no one has addressed the costs of growth in such environments, and so the overall impact of small-scale turbulence on survival is uncertain. Moreover, the net effects of small-scale turbulence are equivocal as it also disrupts local patches of prey (Davis et al., 1991), and this reduction in prey availability may offset the increases in potential feeding rates.

Regarding the biological processes involved in the sustenance of the LFAs, it is essential that the individual larvae that comprise the assemblage survive and grow for considering that an assemblage has been maintained. Thus, the main biological processes supporting maintenance of assemblages are those that promote growth and survival and thus analyzing the distribution of the suitable prey tends to become of key importance to understand assemblage dynamics (e.g. Olivar et al., 2014).

Fish larvae are not passive particles and also larvae are not often distributed randomly. Besides the well-known ability of larval fish to perform diel migrations, higher horizontal swimming ability of larval fish than previously believed was proved to exist, mainly in reef species (Stobutzki and Bellwood 1997; Fisher et al., 2000; Leis 2006). This has led to speculation that larvae may have considerable ability to control their position both horizontally and vertically in the water column and thus influence their spatial fate (Leis et al., 1996). Fish larvae have been shown to respond to physical structures (Bakun, 2006) and chemical/sound cues (Kingsford et al., 2002), and these responses may affect the assemblage composition through time. Further, the maintenance of assemblages will thus also be affected by behaviour such as schooling of larger individuals (Sponaugle et al., 2002). Foraging (including diel vertical migrations etc.) is a key factor shaping assemblages at small scales (Stergiou and Karpouzi, 2002). For example, different assemblages can be obtained depending on the time of the day for a given depth (Neilson and Perry, 1990), which must be considered in sampling designs and in the interpretation of results.

I.5.3. Disruption of LFAs

Again, both physical and biological processes, over a range of scales, can lead to the disruption of larval assemblages. Many of the processes that lead to disruption do so only because of the magnitude, timing or location of their impact. For example, at large scale, the same currents and circulation that help form larval assemblages can also be responsible of their disruption when they form meanders. Similarly, when an individual reaches metamorphosis and adopts the adult habitat and life style (which is often different and separate from that of the larvae) it leaves the LFA and the responsible are factors affecting growth and survival, that were before related to the LFA maintenance. Accordingly, behavioral patterns leading to morphological formation can also induce disruption.

Entrainment of the assemblage in hydrographic features that move them away from favorable environments will lead to dissolution. Divergent fronts and areas, involving diffusion and advection mechanisms are examples of these features. On the northeast coast of North America, these processes, specifically the formation of warm-core rings, have been hypothesized to be so frequent as to affect recruitment patterns (Flierl and Wroblewski 1985). At smaller scale, turbulent mixing in general leads to the disruption of patches in aquatic systems (Mann and Lazier 1991). However, the detection of these processes will depend, again, on the survey design.

Three principal biological processes; metamorphosis, competition and predation, may lead to disruption of larval assemblages. The production patterns of the area and the seasonality will drive the duration of the assemblages whose disruption depends on the metamorphosis of its individuals (which either abandon the habitat or escape the sampling nets, producing a false change in the assemblage). More transient ichthyoplankton assemblages will be a result of environments that support faster growth (shorter times to metamorphosis) and long duration assemblages will develop in environments of lower productivity (longer times to reach metamorphosis).

The evidence for the importance of predation in the disruption of LFAs is unequivocal. Potential predators of ichthyoplankton assemblages are not limited to juvenile and adult fishes. Medusae, chaetognats, ctenophores, and even other fish larvae have all been shown to be significant predators of fish larvae. In fact, larvae may face a gauntlet of predators as they grow and develop. In summary, predation losses are probably the single largest cause of mortality in larval fish assemblages (Bailey and Houde, 1989; Leggett and Deblois, 1994). In some cases, other factors, such as poor condition or disease may have increased the susceptibility of larvae to predation (but see Elliott and Leggett 1998), but predation remains the ultimate cause of death. Clearly, differential mortality among the species that comprise an assemblage will lead to variation in the composition of the assemblage. Finally, competition among larvae within the assemblage may represent another mechanism leading to the dispersal/change of larval assemblages (Hixon and Beets, 1993).

I.6. LFAs in the Balearic Sea: State of the Art

In an extensive literature analysis performed for invertebrate and most vertebrate species, Coll et al. (2010) showed that the Mediterranean is a hot spot showing a decreasing gradient of species richness from northwest to the southeast. The sea around Sicily, followed by areas in northwestern coastal and shelf areas, had the highest species richness. Although data from the Balearic Islands were not used for the description, the archipelago is situated between these two species-rich areas and appears as a very species-rich area in the estimates. This geographic position makes the archipelago an ideal place to focus studies on marine ecosystem structure and function and stablish a baseline to evaluate the possible changes and threats that future scenarios can provoke.

The archipelago delimits the Balearic sub-basin (BsB) in the north from the Algerian sub basin (AsB) in the south. These sub-basins are characterized by different oceanographic conditions (Balbín et al., 2014), and are connected by a series of channels with depths between 100 and 800m, which play an important role in the regional circulation, as passages for the exchange of water masses between them. The BsB is more influenced by atmospheric forcing and Mediterranean waters, which are colder and more saline, whereas the AsB is affected basically by density gradients and receives warmer and less saline Atlantic waters (Pinot et al., 2002; Balbín et al., 2014). Probably the confluence of these water masses, together with the isolation of the Balearic Islands, can account for the diversity of species found in these areas (e.g. for decapod crustacean larvae, Simao et al., 2014; Torres et al., 2014)

The circulation in the Mediterranean Sea follows a cyclonic path along the continental slope (e.g. Millot, 1985). The inflow of Atlantic Waters (AW) through the Gibraltar strait extends across the Alboran Sea and follows the North African coast, configuring the Algerian Current (AC). In the northwestern Mediterranean, at the Ligurian subbasin, the AW flowing from the Algerian sub-basin joins that coming from the Tyrrhenian Sea (Astraldi and Gasparini, 1992) forming the Northern Current (NC), which flows along the continental slope (Fig. I.6 a and b). The regional circulation in the Balearic archipelago is dominated by this Northern Current (NC), which carries down waters from the Gulf of Lions along the continental slope of the Iberian Peninsula into the BsB (Font et al., 1998). This current bifurcates when reaching the Ibiza Channel; one significant part crosses the channel transporting waters from the BsB into the AsB, while the other part cyclonically returns to the northeast forming the Balearic Current (BC), along the northern coast of the Balearic Islands. This latter current is also increased by flows of new AW passing northwards through Ibiza and Mallorca channels (Fig. I.6 a). This pattern, which is the one expected for late spring and early summer after a mild winter in the north-western Mediterranean, changes considerably after a cold winter (García Lafuente et al., 1995; Pinot et al., 2002; Balbín et al., 2014). If significant amount of Western Intermediate Water (WIW) is generated in the Gulf of Lions during cold winter, these waters, reaching the Balearic channels in the late spring, usually deflect downwards the more saline resident AW, which normally occupies these levels when WIW is absent. The NC may then be blocked when reaching the Ibiza Channel and mostly re-circulates cyclonically joining the BC, without significant transport of waters through this channel (Fig. I.6 b). This fact produces a clear inter-annual variability of the regional circulation around the Balearic Islands, which is strongly related to the properties and the amount of WIW reaching the channels in late spring (Millot, 1999; Pinot et al., 2002; Balbín et al., 2014) and consequently to the winter climatic conditions in the Gulf of Lions (Monserrat et al., 2008; Balbín et al., 2014).

The values of water temperature in the area characterize clear seasonal cycles. During the colder months (October-May), there is a mixing period followed by a stratification period from June to October (Fernandez de Puelles et al., 2007). The salinity values are less driven by the local ocean-atmosphere interaction than temperature, and for that reason, they are good indicators of the water mass origin. The main differences in water masses in the area are then well characterized by density gradients.

Chlorophyll-a values and zooplankton biomass also follow the seasonal pattern closely related to the development of the thermocline that acts as a barrier to the supply of nutrient to the upper levels. The first semester of the year is characterized by higher mean zooplankton biomass (maximum in April) while the second semester presents lower values (minimum in August) (Fernandez de Puelles et al., 2007). Within the general oligotrophic environment of the Mediterranean, the waters around the Balearic Islands show more pronounced oligotrophy than the adjacent waters off the Iberian coast and the Gulf of

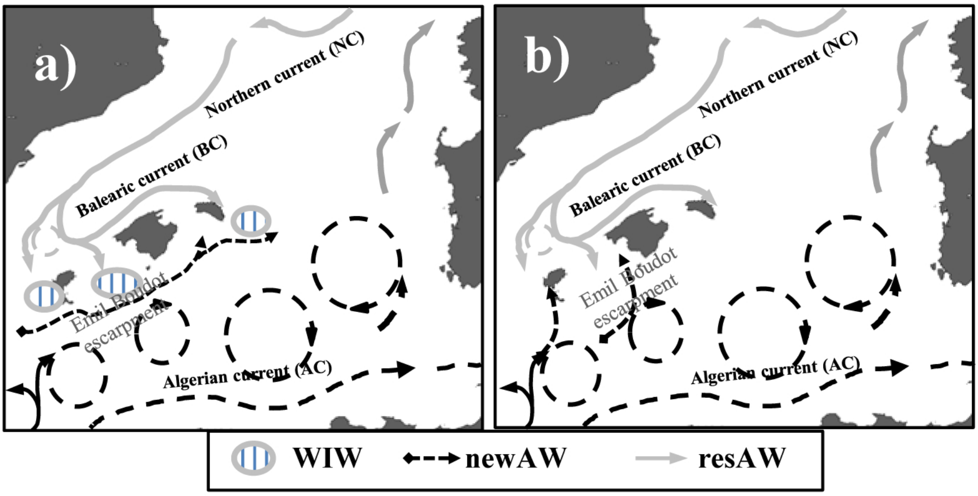

Figure I.6. Averaged regional ocean circulation in the western Mediterranean corresponding to late spring–summer after a relatively cold winter (a) and after a relatively mild winter (b). Major currents in the region, the Northern Current (NC) and the Balearic Current (BC) are indicated. AW: AtlanticWater; WIW:Western Mediterranean Intermediate Water; Adapted from Monserrat et al. (2008).

Lions due to the lack of supply of nutrients from land runoff (Bosc et al., 2004; Estrada, 1996). Frontal meso-scale events between Mediterranean and Atlantic waters (Pinot et al., 1995) and input of cold northern water into the channels (Fernández de Puelles et al., 2004), can act as external fertilization mechanisms that enhance productivity off the Balearic Islands. Trophic web structures show differences between the BsB and AsB: they are supported more by plankton biomass than by benthic productivity in the AsB, while supra-benthos plays a more important role in the BsB (Cartes et al., 2001; Maynou and Cartes, 2000).

The ichthyoplankton of the Balearic Sea was extensively described by Alemany (1997), through the analysis of mesozooplancton samples taken with a variety of plankton nets at different depth ranges all around de Balearic Archipelago and in different periods of the year. This allowed to describe, including original drawings, the developmental series of 166 fish species inhabiting the Balearic Sea. Thus, such descriptions represents a complete guide of most of larval forms of fish species that can be found in the area, and because of that, besides other relevant bibliography about fish larvae taxonomy (e.g. Riedl, 1986), represents an useful reference to carry out the basic taxonomic identification tasks in the Mediterranean. This document constitutes also a first approximation to the fish larvae spatial distribution in the Balearic Sea, both in the horizontal and vertical planes, and to the spawning periods of adults. Seasonality has also been reported for the presence of some fish larvae in mesozooplankton samples in the Balearic archipelago. Fernandez de Puelles et al. (2007) described the average monthly abundances of the 9 most abundant species of a four-year high resolution time series concentrated only on one station. The peaks of abundance were then used to describe the spawning period of these species. The sampling methods were primarily designed for the smaller fractions of zooplankton; the sampler net was a Bongo-20 and the stations were relatively offshore. Thus, the number of larvae caught was very low and mainly from mesopelagic and small pelagic species. The definition of summer or winter LFAs, the spawning season for coastal resident species and the comparison of biodiversity with other areas or between seasons was not possible.

The primary process affecting the formation of summer LFAs in the Balearic Islands is (as elsewhere) the spawning behaviour of adults. The time and areas of spawning determine to which of the LFA a larvae will belong (should it survive). In the west waters of Mallorca Island, Alemany et al. (2006) were able to distinguish between a more coastal summer LFA, with most of its fish larvae belonging to neritic species and a more oceanic summer LFA, being mesopelagic species the dominant. If significant physical processes are involved at the time and area sampled, and representative variables that characterize them are included in the analysis, it is possible to distinguish between LFAs related to them. Alemany et al. (2006) also found, in other area (the southeastern waters of Mallorca Island), two distinct summer LFAs, related to differences in salinity that successively impacted the narrow sampling area.

Covering a wider area (following the continental slope, from western Mallorca Island to eastern Menorca Island), and sampling bigger individuals thanks to the use of a Bongo-90 net fitted with 500 microns meshes (Alemany et al. (2006) used Bongo-40 and Fernandez de Puelles et al. (2007) Bongo-20 nets fitted with 250 microns meshes), Torres et al. (2011) identified also two summer LFAs: a "neritic" and an "oceanic" one. That scenario was interpreted by the authors as a result to the distances of the stations to coast during one of the surveys (summer 2006), and to mesoscale hydrographic activity for the second season surveyed (summer 2008). The quantitative contribution of spawning behavior (station depth) and hydrology (geostrophic velocities, dynamic height, salinity etc.) was not explored.

Three vertical mesopelagic LFAs have been reported for western Mallorca (~Sóller) and southern Mallorca (Cabrera) in few shelf and slope stations in two seasons (Olivar et al., 2014): a surface assemblage during daytime but with wider night distributions, a mid-water assemblage, and a deep one. Small seasonal differences in the vertical position of these LFAs have been hypothesized to derive from the differences in the distribution of fluorescence and zooplankton between seasons in the area: an homogenous distribution in the surface layer (~60m) in autumn and a summer surface stratification of the first ~50m that restricts the highest fluorescence and zooplankton values below the thermocline. These studies, however, could not be related to wider spatial scales or to the influence of different water masses.

Contrarily to the aforementioned LFAs, coastal LFAs are frequently affected by processes responding to smaller scales linked to wind effects interacting with topography etc. In the Balearic Islands, and in the NW Mediterranean in general, these processes have received relatively less attention, probably because many ichthyoplankton surveys are directed to commercial species dwelling large shelf areas or to large pelagics inhabiting offshore waters (e.g. Alemany and Massutí, 1998; Olivar et al., 2001; Sabatés et al., 2007; Alemany et al., 2010; Reglero et al., 2012; Laíz-Carrión et al., 2013). The highly dynamic oceanographic environment that characterizes coastal areas in the Balearic archipelago was suggested to be the main obstacle to detect numerical effects of dispersal and retention of four neritic species around Cabrera Marine Protected Area (MPA) (Crechirou et al., 2010). Nevertheless, the authors could confirm Cabrera as a spawning area for these species and discussed the potential export of fish eggs to nearby areas. When facing the potential connectivity through numerical modelling in the southern coast of Mallorca, weak and variable flow dynamics, together with topographically driven differences in the response of currents to wind changes, were the main determinants of high retention rates (Basterretxea et al., 2012). The authors also emphasize the importance of small spatial structures (20-30 km) as hotspots for larval retention and lack of short-scale connectivity (e.g. Palma Bay), which has been linked, together with the effect of coastal fishing to phenotypic differences in adult fish (Alós et al., 2014).

Given the high biodiversity expected for the Balearic archipelago and the importance of the mesoscale activity processes around it, a big amount of information on LFAs in the area is missing, when compared with other highly biodiverse areas (e.g. the nearby Catalan Sea (from Sabatés et al., 1990 a,b to Lopez-Sanz et al., 2011 and Sabatés et al., 2013).

Following a decreasing spatial scale of events, the complete “picture” of all the LFAs around the archipelago is still unknown. The patchiness of the ichthyoplankton distribution added to the spatial “patchiness” of the existing works in the area doesn’t seem enough to draw it. Information on the seasonal and interannual variations of these LFAs across spatial scales would be the next basic piece of knowledge to be gathered.

The relevance of providing a more complete picture of LFAs across scales is key to understand several aspects on the marine functioning, and to set a solid base for prospecting changes due to impinging issues such as invasive species, habitat degradation, climate change etc. The high diversity of coastal habitats also requires the exploration of processes acting at scales smaller than the mesoscale. The knowledge of the local processes that act in bays and other coastal features, and that promote self-recruitment in the area, and/or export to adjacent habitats, will improve the existing theoretical models of dispersion, and will help understanding the functioning of protected/exploited areas as source/links of individuals. Often, resource management in large portions of coastal areas escapes National laws and depends on regional/local managing bodies (as is the case in the Balearic Islands). Therefore, information relevant to ecological processes in littoral areas (often disconnected to other shelf areas), is invaluable (Alós et al., 2014).

Further work on processes affecting the vertical dynamics of LFA is also needed. Although sparse data exist as commented above, high resolution information on the processes driving LFA dynamics at the vertical scale are needed, particularly at coastal areas where interactions with bottom topography, breeze regimes, odor cues and coastal fishing may exist and have only been seldom explored (Bradbury et al., 2003; Leis et al., 2007).

A large effort is also needed at the microscale level to elucidate the meaning of LFA changes. Most processes at the microscale level are biological processes (see Table I.2), including feeding behaviour, the development of the natation capabilities, the small turbulence events, predation and competition for resources etc. Many of these processes are difficult to investigate in the natural environment. However, only by obtaining reliable information within all these scales will it be possible to get closer to a mechanistic understanding of observed patterns. It is foreseen that in the next years, complex individual-based models for single species (e.g. Rose et al., 2015) will be better parametrized through better field and experimental studies, which will enable the scientific community to slowly abandon purely correlational analyses and combine observed data with mechanistic models. However, the rich information obtained from LFAs will probably not be amenable to such models in the short term, and a large degree of (lately in decline) taxonomic expertise, together with a multidisciplinary approach, will continue to be needed to understand the ecology of marine fish communities.

I.7. Objectives

As a primary motivation, the present thesis was designed to increase the knowledge of the factors affecting LFAs in the Balearic Sea trying to fill some of the existing gaps mentioned above (see subsection I.6). Indirectly, filling those gaps was expected to open questions concerning the usefulness of the information yielded by LFAs. In particular, we aimed at revealing what are some of the forcing factors explaining mesoscale dynamics around the Archipelago, and to understand processes driving larval fish assemblages at smaller scales, particularly in coastal areas.

The specific objectives are:

1. The description of the summer LFAs around the whole archipelago, from a mesoscale point of view.
2. To explore the inter-annual dynamics of these LFAs.
3. The evaluation of the environmental factors responsible both for the formation of the different LFAs and also responsible of their dynamics at the mesoscale level.
4. The description of coastal summer assemblages, at scales smaller than mesoscale in contrasting coastal habitats: around a small archipelago and in a bay.
5. The evaluation of the environmental factors responsible both for the formation of the different LFAs and also responsible for their dynamics at scales smaller than mesoscale in different coastal habitats.
6. The description and understanding of the seasonal coastal LFAs, through high frequency temporal surveys.

I.8. Structure of the Thesis

The present work has been structured in five main Sections (I to V), the first being this introduction and followed by a second one that highlights the common methodological aspects of the thesis. The results from exploring the specific goals (Section III) have been detailed in 5 different chapters (chapter 1 to chapter 5). Time and space scales covered by each of the chapters are represented in Figure I.7. The processes expected to be of key importance at each of the scales are underlined.

The specific goals that each of the chapters address are as follows:

Chapter 1: sub-seasonal temporal scale. This chapter covers the goal of describing the seasonal coastal LFAs through high frequency (fortnightly) sampling of three coastal stations: prior, during, and after the production peak in the area. The causes of the coupling between demersal and pelagic biological compartments are insufficiently studied in these coastal areas, despite some interaction between surface and bottom production must exist due to their closeness. This chapter lacks spatial resolution and is centered on temporal changes.

Chapter 2: Scales smaller than mesoscale. This chapter also addresses coastal LFAs, but from a spatial perspective at a scale smaller than the usual mesoscale surveys. The analysis elucidates the local environmental factors better explaining the LFAs around Cabrera Archipelago National Park.

Chapter 3: Scales smaller than mesoscale. In this chapter we tackle an even higher grid resolution, centered in the Palma Bay, to shed some light into Bay dynamics and how this dynamics affect LFAs.

Chapter 4: Mesoscale. We jump one scale to provide the first mesoscale analysis of the LFAs around the Balearic Islands, using a grid of 200 stations. We analyze the variables that best explain the LFA structure, including key variables such as dynamic height, to interpret basic structure of the community.

Chapter 5: Mesoscale. We make a step further to contribute to the understanding of summer mesoscale LFA dynamics in the Archipelago by comparing two contrasting hydrographic scenarios and their potential effects on LFAs.

Although each chapter includes a discussion of the results obtained facing each specific goal, Section IV develops a General Discussion of all the results that merge from the thesis. The information that can be extracted from the knowledge of LFAs in the area, the influence of the scale of sampling in the results obtained and the future needs to improve knowledge in the subject are discussed. The conclusions extracted from this thesis are summarized in Section V.

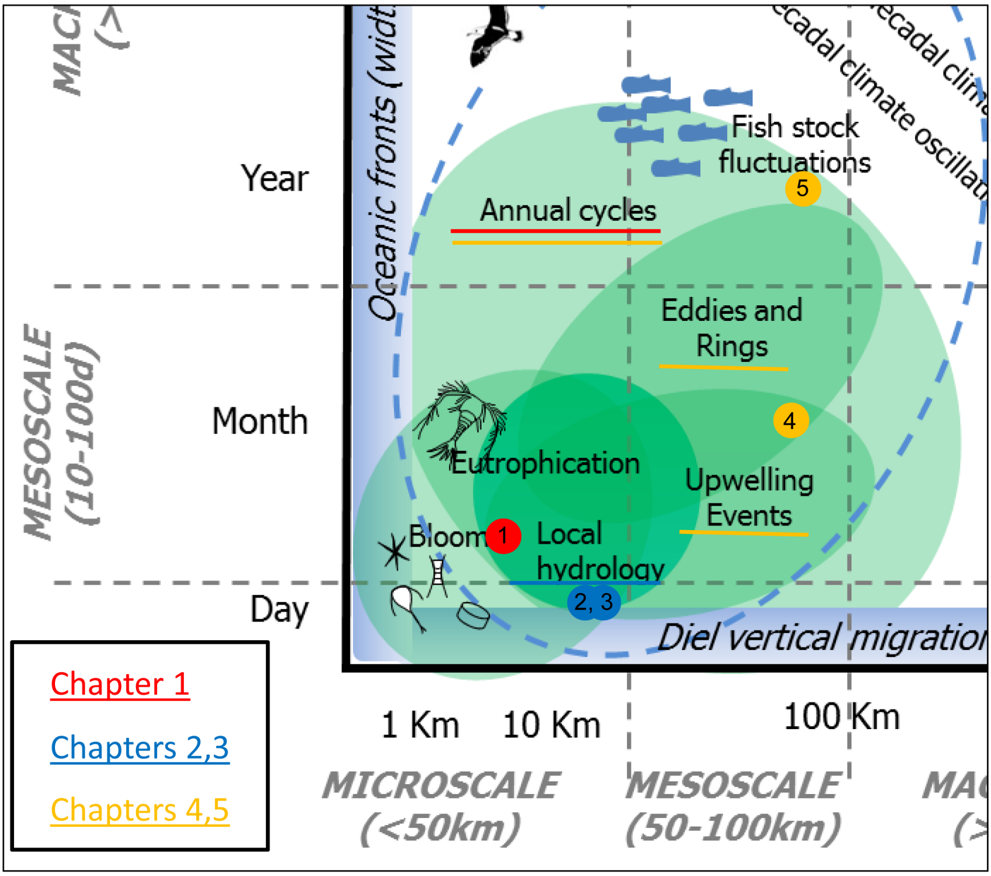

Figure I.7. Time and space scales covered by each of the chapters. The processes expected to be of key importance at each of the scales are underlined.

II

GENERAL METHODS

In this chapter the common methods used for all the chapters will be described. The high specificity of some of the data analysis performed at each chapter prevents from trying to describe them all here, so only commonalities and the main methodological differences between chapters will be commented here. The detailed description is given in each chapter from Section III. Table II.1 has been developed to summarize all the methods used at each chapter and to quickly compare them.

II.1. Sampling design

The exploration of the relationship between environmental variables and ichthyoplankton assemblages at different scales required different survey designs. The scale of the process or processes object of study determined the sampling methodology for each of the chapters. Consequently, the different designed sampling grid required different vessels to cover them. In some cases the type of vessel constrained the operational limits for the samplings, mainly the size of the zooplankton sampling nets. The different grids, vessels and nets chosen to cover the specific objectives were:

Temporal high frequency series (Chapter 1): Three stations, with depths ranging from 50 to 80m in an area between Archipelago de Cabrera National Park and the south-eastern coast of Mallorca (Fig. II.1). The ichthyoplankton sampling was performed fortnightly, during the daytime (between 8:00 and 11:00), between March and August 2007 (prior, during and after the production peak in the area). The Imedea vessel (IMEDEA-

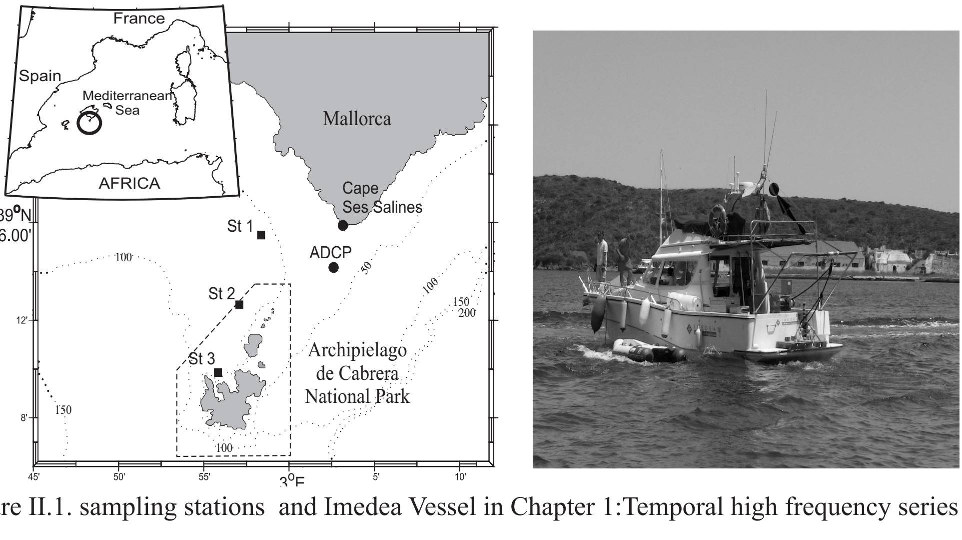

Figure II.1. sampling stations and Imedea Vessel in Chapter 1:Temporal high frequency series .

Table II.1. Summary of the general methods employed. CH: Chapter; Nº St.: Number of stations covered by the survey; St. Distances: Mean distances between the grid stations. SYN: Grade of synopticity expected from the survey design, H (high), M (Medium) and L (Low). RV: Research Vessel used for the survey(s); RV. L: length of the research vessel employed; Circul. Pattern: method employed to characterize circulation patterns; Water mass identif.: method employed to characterize water masses; Chl-a: Method employed for the Chlorophyll-a sampling; Microzoo.: Structure and mesh nets employed for the microzooplankton sampling; Ichthyop.: Structure and mesh nets employed for the ichthyoplankton sampling; LFA Ident.: Statistics used to identify distinct Larval Fish Assemblages (LFA); ENV-LFA.: Kind of multivariate analysis performed to explore environment-LFAs relationships

CH	OBJECTIVE	PERIOD	Nº St	St. Distance	SYN.	RV	RV L (m)	Circul. pattern	Water mass identif.	Chl-a	Microzp	Ichthyo	LFA Ident.	ENV -LFA
1	Temporal high frequency series	Fortnightly March - August	3	~2 nm	-	Imedea	12	ADCPMoored	CTD T-S Flu All St.	Niskin bottles	WP2-60 cm 53 µm	B-40 335 µm	CLUSTER PCA	RDA
2	Smaller than mesoscale: Small archipelago	5 days 9- 13 Jul. 2007	63	2-3 nm	M	Regina Maris	34	ADCPMoored	CTD T-S Flu All St.	Niskin bottles	WP2-40 cm 53 µm	B-60 335 µm	CLUSTER PCA	-
3	Smaller than mesoscale: Small Bay	2 days 22-23 Jul. 2010	34	1- 3 nm	H	Imedea	12	ADCP Towed	CTD T-S Transect	-	-	B-40 335 µm	CLUSTER PCA	RDA
4	Mesoscale:	~1 month Jul. 2005	183	10 nm	L	Cornide de Saavedra	66.7	Geostr. vel	CTD T-S Flu All St.	Niskin bottles	Calvet-net 55 µm	B-60 335 µm	CLUSTER MDS	CCA
5	Mesoscale and interannual	~1 month Jul. 2004 Jul. 2005	145 (*2)	10 nm	L	Cornide de Saavedra	66.7	Geostr. vel	CTD T-S Flu All St.	Niskin bottles	Calvet-net 55 µm	B-60 335 µm	CLUSTER PCA	RDA

CSIC) was selected (Fig. II.1). It is a 12 m length boat and the main operational limitation was the weight that the boat is able to drag. The bongo-40 nets were chosen to ensure the achievement of the surveys.

Scales smaller than mesoscale (Chapter 2): spatial sampling around Archipelago de Cabrera National Park. A grid of 63 stations consisting of seven transects perpendicular to the coast and placed at intervals ~4 km around Cabrera and 6 km elsewhere (Fig. II.2). The ichthyoplankton sampling was conducted during 5 days (from 9 to 13 July 2007) only during daytime. The RV Regina Maris (Junta de Andalucia) was selected (Fig. II.2). The vessel was 34 m length and allowed a week survey. The Bongo-60 nets were used in this case.

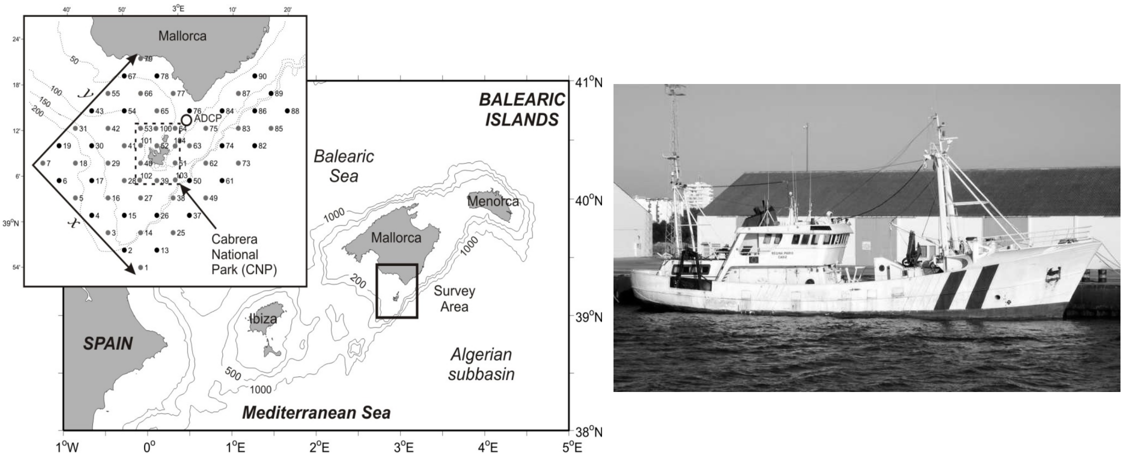

Figure II.2. Sampling grid and RV Regina Maris used in Chapter 2: Scales smaller than mesoscale: spatial sampling around Archipelago de Cabrera National Park.

Scales smaller than mesoscale (Chapter 3): Palma Bay (approx. 20 km wide). A 34 stations grid was designed to enable sampling in a quasi-synoptic fashion, with a slightly increased spatial resolution at the inner part of the bay (distance between stations varying 1 to 3 nm) (Fig. II.3). The ichthyoplankton sampling was conducted during 2 days (22 and 23th July, 2010). The Imedea vessel and the Bongo-40 net were again selected.

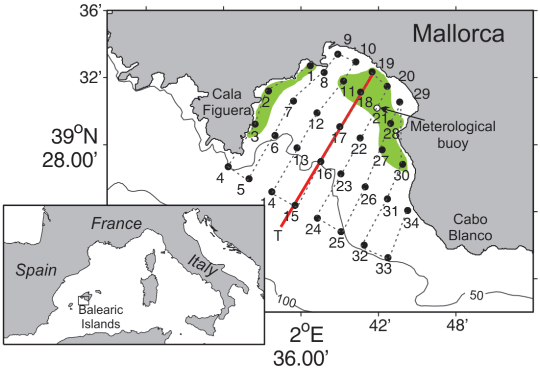

Figure II.3. Sampling grid used in Chapter 3: Scales smaller than mesoscale: spatial sampling in a small bay (Palma Bay). Speciphic details on Chapter3

Scales smaller than mesoscale (Chapter 3): Palma Bay (approx. 20 km wide). A 34 stations grid was designed to enable sampling in a quasi-synoptic fashion, with a slightly increased spatial resolution at the inner part of the bay (distance between stations varying 1 to 3 nm) (Fig. II.3). The ichthyoplankton sampling was conducted during 2 days (22 and 23th July, 2010). The Imedea vessel and the Bongo-40 net were again selected.

Mesoscale (Chapters 4 & 5): Balearic Sea. A regular sampling grid of 10x10 nm around the Balearic archipelago was sampled covering 165 stations in 2004 and 183 during the 2005 survey. Chapter 4 includes the results of all the 2005 stations (183) whilst only the 145 common for both years were included in Chapter 5 to compare LFA

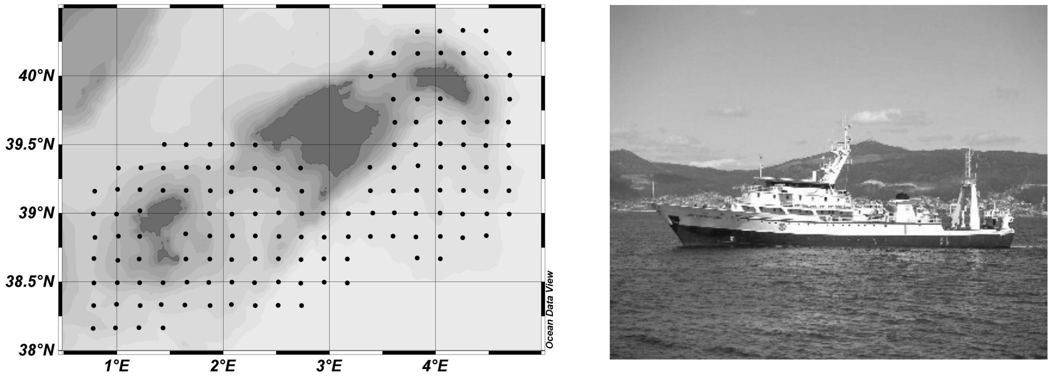

Figure II.4. Sampling grid and RV Cornide de Saavedra used in Chapters 4 & 5. Mesoscale: Balearic Sea distribution between years (Fig. II.4). Both surveys took place in summer, mostly on July and taking around a month of duration. For the coverage of all the Balearic Sea during nearly a month, a bigger RV was used: the Cornide de Saavedra (Instituto Español de Oceanografía, IEO) (Fig. II.4). The vessel is 66.70 m length and allows a 31 people scientific team on board. For these surveys the Bongo-60 net were also employed.

II.2. Data collection

Characterization of circulation patterns:

A bottom mounted ADCP (1MHz Nortek Aquadopp) was deployed at 25 m depth to characterize flow variations for chapters 1 and 2 (Cabrera National Park, Figures II.1 and II.2). The measures of wind speed and direction (10-min intervals) at Palma Airport were provided by the Spanish Metereological Service (AEMET)

In the case of Chapter 3 (Palma Bay), temperature (surface), currents and backscattering values were recorded with a 1200 kHz RDI Workhorse sentinel ADCP mounted on an Endeco/YSI 703 V-Fin towed along the stern of the vessel, which followed the transect in figure II.3. No ADCP data were employed for chapters 4 and 5. The circulation patterns were determined from geostrophic velocities, from CTD casts.

Characterization of water masses:

Vertical profiles of temperature, conductivity and fluorescence (except for Chaper 3) were obtained with a conductivity-temperature-depth (CTD) probe in all stations except for the Palma Bay survey (Chapter 3), where only a central transect was conducted (Figure II.3).

The different data derived from CTD casts are specified at each chapter (stratification, geostrophic velocities…).

Chllorophyll-a sampling:

Water samples at different depths (depending on the chapter) for Chllorophyl-a determination were obtained at all stations with Niskin bottles. In chapter 3 only the central transect (Fig. II.3) was sampled and unfortunately lost.

Microzooplankton sampling:

With the exception of chapter 3 (Palma Bay), microzooplankton samples were collected in all stations by means of vertical hauls, with maximum depths depending on the survey. The sampling nets were: WP2-60 cm ring-net, with a 53 µm mesh net for the temporal high frequency series (Chapter 1). A WP2-40 cm ring-net, with a 53 µm mesh net in the spatial sampling around Archipelago de Cabrera National Park (Chapter 2). For chapters 4 and 5, a Calvet-net was used, equipped with a 55 µm mesh net. In some cases the samples were used to determine dry weight and in others for taxonomic purposes. (see at each chapter for methods detail)

Ichthyoplankton sampling: (Smith and Richardson, 1968)

As commented above, the selection of the research vessel, determined in some cases the utilization of small nets (Bongo-40). In all cases the mesh net selected for sampling ichthyoplankton was 335µm and flowmeters were installed in the mouth of each net to measure the volume of water filtered. Double oblique hauls (with maximum depths depending on the survey) were performed in all stations except for the very shallow stations in Palma Bay (Chapter 3, Fig. II.3) where a series of up and down tows until a 5 min fixed period were performed in order to filter a similar water volume. Once onboard samples were immediately fixed in 4% buffered formalin for preservation.

II.3. Fish larvae identification and LFA characterization

All the fish larvae and eggs were sorted from the samples under a stereomicroscope. Individuals were counted and identified to the lowest taxonomic level possible. We used drawings and descriptions from several identification guides and works including Alemany (1997), Sabatés (1989), Olivar and Fortuño (1991), Richards (2006), and Blaxter (1974). The larvae of Chapter 4 (representing also half of the chapter 5 data) were sorted by Dr. JM Rodríguez at the IEO laboratory in Gijón. The rest of the larvae were identified by the author of the present thesis with the supervision of Dr. Alemany and Dr. Sabatés when needed.

For each station, the larval fish catches were standardized to number of larvae per 10 m^{-2} abundance except for stations in chapter 4, that were standardized to number of larvae per 1000 m^{-3}. The same data were again standardized to number of larvae per 10 m^{-2} in chapter 5 for comparative purposes.

The characterization of the multivariate structure of the LFAs was conducted in different ways. The larval fish assemblages were characterized by hierarchical cluster analysis (CLUSTER) and also ordination techniques: Non Metric Multidimensional scaling (MDS) for chapter 4 and Principal Component Analysis (PCA) for all the rest.

CLUSTER and MDS start explicitly from a triangular matrix of similarity coefficients computed between every pair of samples. The coefficient is usually an algebraic measure of how close the abundance levels are for each species, averaged over all species and defined such that 100% represents total similarity and 0% complete dissimilarity. There is a range of properties that such a coefficient should possess but still some flexibility in its choice: it is important to realize that the definition of what constitutes similarity of two communities may vary, depending on the biological question

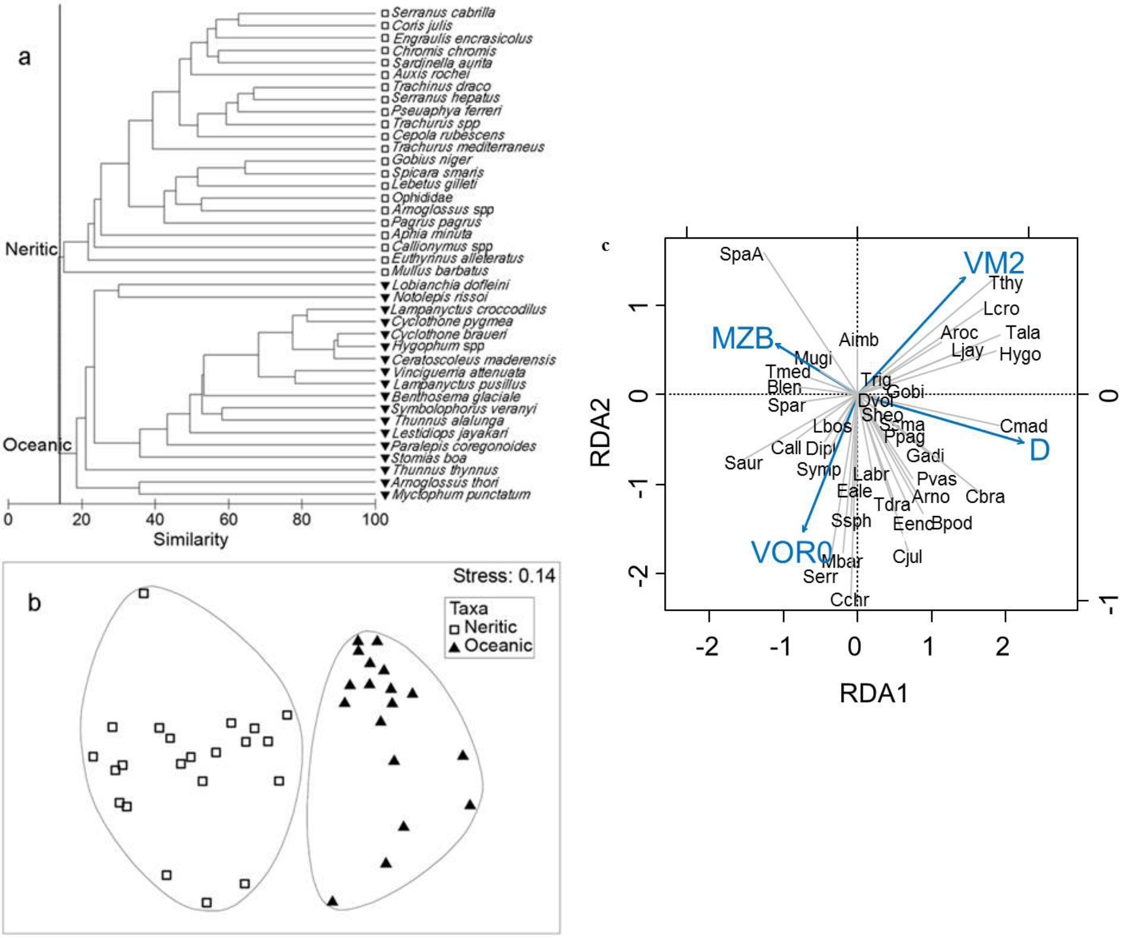

Figure II.5. Examples of some of the statistical methods employed; a) Dendrogram; b) MDS ; c) RDA under consideration. This multivariate analysis attempts to reduce the complexity of high-dimensional community data by taking a particular (low-dimensional) “view” of the structure it exhibits. A view in which most of the emphasis is on the pattern of occurrence of rare species may be very different than one in which the emphasis is wholly on the handful of species that numerically dominate most of the samples. Therefore, these considerations must be accounted for prior to the analysis. One convenient way of providing this spectrum of choice, to match the biological imperatives whilst retaining desirable theoretical properties, is to restrict attention to a single similarity coefficient but allow a choice of prior transformation of the data. A useful transformation continuum ranges through no transform, square root, fourth root, logarithmic and finally reduction of the sample information to the recording only of presence or absence for each species: at the former end of the spectrum all attention will be focused on the dominant counts, at the latter end on the rarer species (Clarke and Warwick, 1994).

For the clustering technique, representation of the communities for each sample is by a dendrogram (e.g. Fig. II.5a), linking the samples in hierarchical groups on the basis of some definition of similarity between each cluster. This is a particularly appropriate representation in cases where the samples are expected to divide into well-defined groups, perhaps structured by some clear-cut environmental distinctions. Where, on the other hand, the community pattern is responding to abiotic gradients which are more continuous, then representation by an ordination is usually more appropriate. Several types of ordination techniques exist and vary typically depending on the type of data and how these data is going to be treated in later analyses (e.g. modelling potential divers of multivariate composition etc). The method of non-metric MDS makes no assumption about the data properties and attempts to place the samples on a “map”, usually in two dimensions (e.g. Fig. II.5b), in such a way that the rank order of the distance between samples on the map exactly agrees with the rank order of the matching (dis)similarities, taken from the triangular similarity matrix. If successful (and success is measured by a “stress coefficient” which reflects the extent to which the two sets of ranks do not agree), the ordination gives a simple and compelling visual representation of “closeness” of the species composition for any two samples (Clarke and Warwick, 1994). However this method tends to be less amenable than others to quantitative analysis of driving forces.

The Principal Component Analysis (PCA) technique takes a different starting position, and makes rather different assumptions about the definition of (dis)similarity of two samples, but again ends up with an ordination plot, usually in two or three dimensions, which approximates the continuum of relationships between samples (Clarke and Warwick, 1994). PCA carries out a rotation of the original system of axes defined by the variables, such that the successive new axes (called principal components) are orthogonal to one another, and correspond to the successive dimensions of maximum variance of the scatter points. The principal components give the positions of the objects in the new system of coordinates. It is exclusively devoted to the analysis of quantitative variables (not absence/presence data). The distance preserved is the Euclidean distance and the relationships detected are linear. Although traditionally it was not considered appropriate to the analysis of raw species abundance data, with new distance measures (e.g. Hellinger's distance) it is possible to construct similarity matrices that perform similarly to Bray-Curtis similarity matrix (Legendre and Gallagher, 2001).Therefore, the old division between the use of PCAs for environmental variables and other ordination techniques for biotic variables is no longer supported in many instances (Borcard et al., 2011)

II.4. Exploration of the environment-LFA relationships

In field studies, the explanations of biological patterns are correlational, and any attempt to derive causality is only to be understood in the frame of plausible hypothesis attending to the available knowledge. However, in oceanography many hypotheses are usually probable (Hare, 2014). When the process or pattern to be understood is multivariate in nature (such as the LFAs), the variance that one is expected to explain decreases sharply. Several techniques exist to describe the multivariate variability according to potential explanatory variables, alone or in combination. In this thesis, we have adopted different approaches depending on the chapter:

One of the most used method, together with Canonical Correlational Analysis (CCA, see further) has been the Redundancy Analysis (RDA; Chapters 1, 3 and 5, Fig. II.5c). RDA is a method combining regression and principal component analysis (PCA). It is a direct extension of regression analysis to model multivariate response data. RDA is an extremely powerful tool in the hands of ecologists. Conceptually, RDA is a multivariate (meaning multiresponse) multiple linear regression followed by a PCA of the table of fitted values. This method seeks, in successive order, a series of linear combinations of the explanatory variables that best explain the variation of the response matrix. The axes defined in the space of the explanatory variables are orthogonal to one another. RDA is therefore a constrained ordination procedure. In RDA one can truly say that the axes explain or model (in the statistical sense) the variation of the dependent matrix. Furthermore, a hypothesis (H_0) of absence of linear relationship between response data and explanatory variables can be tested in RDA; this is not the case in PCA (Borcard et al, 2011).

In chapter 4, the environment-LFA relationships where analyzed trough Canonical Correspondence Analysis (CCA). CCA shares many characteristics with RDA. It preserves the X^2 distance among sites, and species are represented as points in the triplots. One particularly attractive feature of a CCA triplot is that species are ordered along the canonical axes following their ecological optimal. This allows a relative easy ecological interpretation of species assemblages. Also, species scores can be used as synthetic descriptors in a clustering procedure to produce a typology of the species in assemblages (Borcard et al., 2011).

Finally, a small exercise based on the philosophy of the Individual-Based Models (IBMs; Grimm and Railsback, 2005; Peck and Hufnagl 2012) is included in one of the chapters (2). The IBMs simulate individual particles (that can be virtual organisms) that interact with the environment and with other organisms at several degrees (e.g. being transported by currents, growing according to encountered prey and temperature fields etc), thus producing emerging patterns not predictable using conventional population models. In our case, the effect of directional swimming vs passive larvae was tested with respect to the produced patterns of retention around a small island (Chapter 2).

III

RESULTS

CHAPTER 1

Drivers of larval fish assemblage shift during the spring-summer transition in the coastal Mediterranean.

Abstract

The influence of coastal environmental conditions during the shift from winter-spring to summer on fish larvae assemblages in a temperate area is evaluated. Larval fish assemblages were sampled fortnightly at three stations located in coastal waters off southern Mallorca (Western Mediterranean) from March to August 2007, covering the main spawning period for the resident coastal fish in this region. The larval fish assemblage showed clear seasonality with higher specific abundance but lower diversity in the spring. Two main assemblages were identified: a spring assemblage, occurring at surface seawater temperatures < 20ºC and dominated by species with relatively larger home ranges, such as *Boops boops, Sardina pilchardus, Trachurus trachurus,* and *Spicara smaris*, and a summer assemblage characterised by the presence of the benthopelagic *Coris julis, Serranus hepatus*, *Serranus cabrilla and Mullus spp.*, among others. The shift between these ichthyoplankton communities occurred in early June, coinciding with the onset of summer hydrographical conditions and the local benthic productivity peak. We propose that the seasonal shift in coastal environmental conditions produces ecosystem-level variation through which trophic pathways shift from the pelagic to the benthic system. This variation may be related to marked effects in the reproductive strategies in the fishes inhabiting the area and indirectly affect ichthyoplankton assemblages.

1.1. INTRODUCTION

The coastal realm is thought to provide more suitable conditions for fish eggs and larval survival than open sea areas because of higher water mass stability and higher food availability (Myers and Cadigan, 1993). Larval fish assemblages in coastal waters undergo notable temporal changes in abundance and composition, particularly on a seasonal basis. Factors such as the availability of suitable food, decreased predation pressure, behavioural change and transport towards nursery grounds are relevant for timing of spawning, but their taxon-specific relevance and overall importance are not clear. For example, the availability of a suitable quantity and quality of food influences mortality (e.g., Lasker, 1975, 1978; Houde, 1987) and, for many commercially important species, the spawning season is thought to be closely coupled with seasonal plankton blooms (Cushing, 1975; Chambers and Trippel, 1997). However, this conceptual model is based on competition for resource and may not be completely valid for most oligotrophic regions, including many Mediterranean coastal areas in which other factors may be dominant, at least during some periods.

Despite the increase in phytoplankton productivity during late winter (e.g., Estrada et al., 1993), in the Mediterranean Sea, energy is funnelled through intricate interactions with other components of the trophic web. Indeed, many coastal fish species spawn during summer when oligotrophic conditions prevail and putative food sources for fish and their larvae could be lower. However, during this season, alternative food sources may become important in most shallow waters where coupling between pelagic and benthic systems is narrower. For example, coastal fish species in the Mediterranean may display euryphagous behaviour, with a mixed diet, mainly, but not strictly, based on benthos and plankton prey (Macpherson and Roel, 1987; Cartes, 2002). Further evidence shows that many littoral fish in the Mediterranean feed on seagrass and associated invertebrate communities (Stergiou et al., 2002) following a seasonal pattern that depends on local production dynamics (Mees and Hamerlynck, 1992; Rodríguez-Ruiz et al., 2001; Fanelli et al., 2009; Deudero et al., 2011). Unlike the pelagic cycle, sublittoral benthic production peaks in spring–summer (Ballesteros, 1991, 1992). Therefore, it is plausible that a combination of pelagic and benthic-derived food sources modulates the reproductive characteristics of coastal fish.

The ichthyoplankton assemblages in the coastal waters of the Mediterranean Sea are complex in terms of species composition and distribution patterns, both of which change continually with environmental fluctuations and overlapping reproductive strategies (Sabatés et al., 2007). Traditionally, ichthyoplankton studies conducted in the Western Mediterranean have focused on mesoscale surveys over the continental shelf and slope (e.g., García and Palomera, 1996; García-Lafuente et al., 1998; Masó et al., 1998), and with some exceptions (e.g., Sabatés et al., 2003; Sabatés et al., 2007), studies on the taxon-specific temporal variability in the coastal realm are scarce. Although some focus has been placed on the relationship between the energy of the system and the reproduction response in pelagic fish (e.g. Somarakis et al., 2000), these relationships have been scarcely explored in mixed assemblages, where sources of energy of composing species may come from both benthic and pelagic realms.

Many abundant littoral species in the Mediterranean are permanent residents with limited displacement ranges during their adult phase (Alós et al., 2010; March et al., 2010; Palmer et al., 2011). This strong territorialism of some of the species together with the coastal habitat heterogeneity of the Mediterranean coasts, where seagrass meadows alternate with rocky and sandy bottoms (e.g., Bussotti and Guidetti, 2009), affect the variability and diversity of the coastal assemblages. These assemblages are characterised by small pelagic fishes, such as clupeiforms, and benthic species, including the families Gobiidae, Sparidae and Serranidae. (Sabatés et al., 2003; Alemany et al., 2006). The most

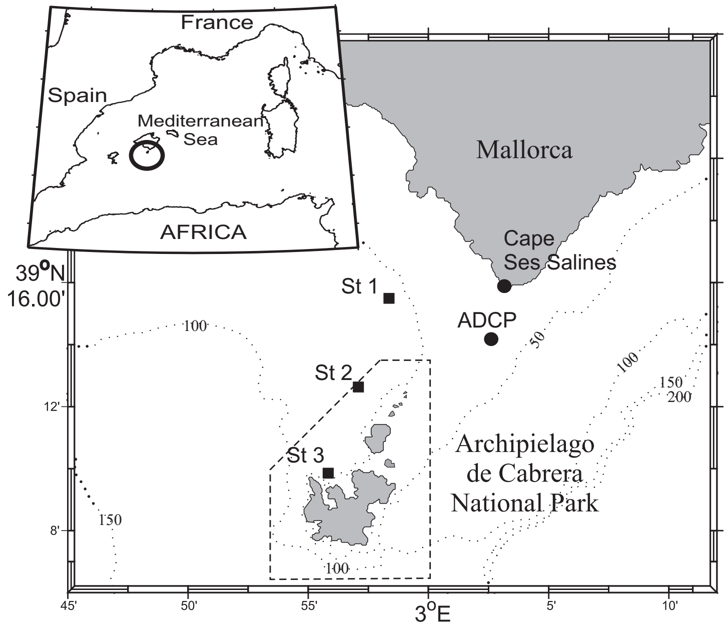

Figure 1.1. Location and bathymetry of the study area and adjacent shelf. St 1-3 indicates the position of the sampling stations, and ADCP marks the location of the moored current meter.

usual explanation for interannual and regional differences in the relative abundance of larval species in the Mediterranean obeys to the different spawning strategies and to the bathymetric distributions of adults (Somarakis et al., 2000, 2002).

The aim of this work is to provide an ecosystem perspective on the species structure and intra-annual temporal stability of the ichthyoplankton assemblages in coastal waters off Mallorca (Western Mediterranean). In particular, we intend to determine how external factors, such as coastal dynamics and food availability, shape the spring-summer transition of coastal larval fish assemblages in a context in which hydrographical conditions are a part of the seasonal dynamics and where wind conditions drive the vernal water column stratification, causing a marked seasonal shift between spring-summer conditions (Salat and Font, 1987; Lopez-García et al., 1994).

1.2. METHODS

Field sampling was conducted in an area between Archipelago de Cabrera National Park and the south-eastern coast of Mallorca (Balearic Islands, NW Mediterranean), between March and August 2007. During this time, a bottom mounted ADCP (1 MHz Nortek Aquadopp) was deployed at 25 m depth to characterise flow variations in the sampling area (Fig. 1.1). Vertical profiles of current velocities were measured every 30 minutes at 4 m depth intervals, with the first depth level 3 m above the bottom. The Spanish Meteorological Service (AEMET) provided measures of wind speed and direction at 10-min intervals at Palma airport. We have performed a spectral analysis (Fourier transformation) of wind and current records in order to provide information on the energy levels of the atmospheric and oceanographic conditions during each season herein considered. For the purpose of this paper we refer to spring as the period from March to May, and summer from June to August.

Three stations, with depths ranging from 50 to 80 meters, were sampled fortnightly during the daytime (Fig. 1.1). All samples were collected between 08:00 and 11:00 a.m. to minimise diurnal variations in zooplankton and ichthyoplankton abundance. At each station, temperature and conductivity were obtained with a SBE-25 CTD probe.

Stratification defined by the Brunt-Väisälä frequency N^2 was derived from CTD measurements:

$$N^2 = \left(g \Big/ \rho \right) \left(\partial\rho \Big/ \partial z \right)$$

where g is the gravitational acceleration, ρ is the water density (derived from salinity) and z is the depth.

To derive the stratification of the water column for each station, we used Simpson's stability index (Simpson, 1981) and the pycnocline depth was calculated at each station from the density profile.

Water samples for chlorophyll-a determination were collected with a 2.5 l Niskin bottle and filtered through GFF filters. Chlorophyll samples were immediately frozen, and subsequent analysis of the acetone (90%) extracts were conducted with a Turner Designs bench fluorometer.

Microzooplankton was sampled in vertical hauls, from 1 m above sea floor to the surface, with a 60 cm diameter WP2 net fitted with a 53-µm nylon mesh. Samples were preserved immediately after collection in 2% seawater borax-buffered formalin. In the laboratory, the samples were filtered in GFF filters, and the microzooplankton dry weight (mg) was derived from the differences in filter weight before the filtration, and after 24-hour of dessecation in a 60ºC oven. Values were expressed in g m^{-2}.

Ichthyoplankton samples were obtained with a Bongo-40 equipped with 335 µm mesh nets. Each sampling consisted of a double-oblique tow down to 2 m above the seafloor. The volume of water filtered was measured/estimated by two GO 230 flowmeters mounted in the mouth of each net. Samples were preserved in 2% seawater borax-buffered formalin until they were sorted and identified to the lowest possible taxon using a stereoscopic microscope. Larval abundance values were standardised to the number of individuals per square meter (Ind m^{-2}). The different taxa identified were also grouped considering the habitat of their adult stage (spawners) in epipelagic, mesopelagic and benthopelagic species, following Isari et al., 2008. Once larvae were sorted, the remaining sample was filtered through 335-µm mesh and dried for 24 hours in the oven to estimate mesozooplankton biomass, which was standardised to g m^{-2}. Although the samples come from a 335-µm sampling instead of the typical 200-µm sampling, hereafter we will use the term mesozooplankton for our estimated biomass values. However, it must be made clear that mesozooplankton values may include here macrozooplanktonic organisms, as a 2 mm sieve was not used before processing.

A cluster analysis was performed using the log (x+1) transformed abundance (Ind m-2) of the taxa after pooling by dates. Only those taxa that represented >0.2% of the total were included to explore the temporal distribution of larval fish assemblages. The unpaired weight group average was used as the aggregation algorithm on the matrix of pairwise Bray-Curtis similarity. In order to explore relationships among the environmental variables, a descriptive principal component analysis (PCA) was completed on the correlation matrix of the normalised values. The environmental variables used for this analysis were surface temperature and salinity, surface chlorophyll-a, microzooplankton biomass, pycnocline depth and Simpson's water column stability index. The relationships between the larval assemblage (response matrix) and the environmental variables (putative explanatory matrix; statistical units were stations/dates, i.e., 3*12 rows) were

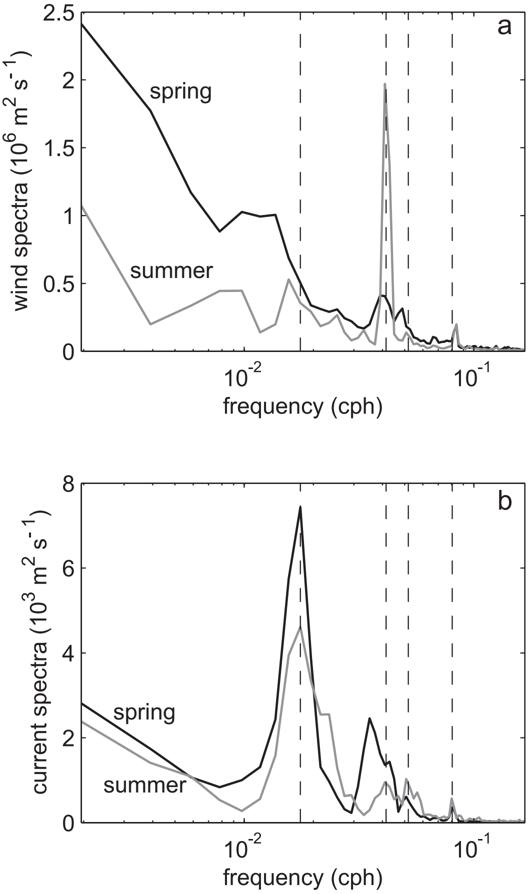

Figure 1.2. Mean power spectra of a) currents and b) wind at the study site for winter (black) and summer (grey) conditions.

evaluated using a redundancy analysis (Boccard et al., 2011). Raw data (Ind m^{-2}) were pre-transformed (Hellinger transformation; Boccard et al., 2011). Forward variable selection combining the environmental variables mentioned above was completed looking for the most parsimonious model. The models were evaluated using the permutation capabilities of CANOCO (i.e., samples were only permuted within blocks [=stations]; then the within-block time series were permuted via cyclic wrapping with common pattern between stations). A complementary PCA on the pre-transformed species abundance data were completed and a descriptive biplot (species and sites; Boccard et al., 2011) were produced.

1.3. RESULTS

1.3.1. Environmental components

The power spectrum of wind data collected from Palma Airport during the study period illustrates the seasonal variations in wind energy in the study area (Fig. 1.2a). For most frequencies, the energy contained in the spring spectra was higher revealing the intensification of wind forcing in this season. Currents were also more energetic in spring in response to the more intense wind forcing (Fig. 1.2b). The exception is the 24 h period, which reflects the dominance of sea breeze during the summer (thermally induced sea-land circulation with diurnal frequency). Breeze circulation is a characteristic feature of the meteorology in Mallorca between late spring and early summer when temperatures are warmer and when prevailing winds weaken. A more detailed analysis of current variability during the survey can be found in Jordi et al., (2009b).

The seawater temperature evolution (Fig. 1.3a) shows typical conditions in the western Mediterranean with minimum temperatures (~14 ºC) and a well mixed water column during late winter and maximum temperatures in late August. Lower salinity waters (<37.6) occurred most of the time (related to the presence of recently Modified Atlantic Water), but eventual intrusions of higher salinity water were observed in some samplings. In particular, this was evidenced during March and early June (Fig. 1.3b). The evolution of water column stability showed a notable change after March. Thereafter, water column stability was increasingly driven by thermal stratification, yet changes in surface salinity (i.e., in late April, Fig. 1.3b) provoked remarkable stabilisation of the water column. For most of the study period, current shear was not sufficient to offset stratification, and a surface layer (i.e., at depths <40m) remained relatively isolated from the subsurface. Because of the absence of river discharges, changes in surface water salinity are largely attributable to the influence of different surface water masses that affect Mallorca.

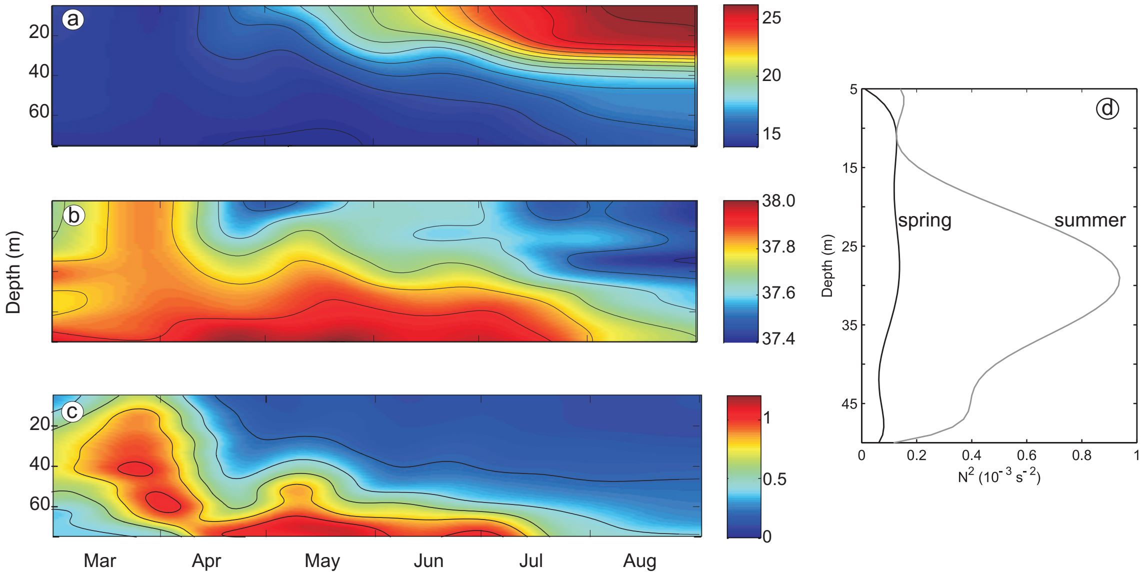

Figure 1.3. Time series of (a) temperature (ºC), (b) salinity and c) chlorophyll (mg m^{-3}) during the survey period. (d) Mean water column stability (Brunt-Väisälä frequency) for spring and summer conditions.

1.3.2. Biological variables

The evolution of chlorophyll-a was consistent with the seasonal cycle described for this region. In late winter, high chlorophyll-a concentrations (approximately 1 mg m^{-3}) were found all along the water column (Fig. 1.3c). The subsequent thermocline development prevented vertical mixing, and by the end of spring, deep chlorophyll maximum (DCM) was well developed below the thermocline. The temporal evolution of the different components of the planktonic trophic web is presented in Figure 1.4. Microzooplankton biomass was highly variable during spring and showed lower average values as summer progressed (Fig. 1.4d). Mesozooplankton biomass showed the highest values (3.87 g m^{-2}) a little later, from April to the beginning of May, when chlorophyll-a values were still high (Fig. 1.4c, d). Minimum seasonal values (0.72 g m^{-2}) were observed at the end of August when the water column was strongly stratified.

The PCA on all environmental variables explained 58% of the system variability in its PC1, where surface temperature and salinity were main drivers; the variation of surface chlorophyll-a was the main driver of the PC2, which explained 23% of the variation.

1.3.3. Larval fish assemblages, abundance and diversity

A total of 3,583 fish larvae were collected, from which 88% were identified into 8 epipelagic, 15 mesopelagic, and 35 benthopelagic taxa. The remaining 12% was not identified because of their small size or damaged state. Ichthyoplankton abundance followed a quasi-dome-shaped distribution, with very low abundances recorded at the beginning of the season (<50 ind m^{-2}) and at the end of July as well as sustained abundance values exceeding 100 ind m^{-2} for most of the remaining period (Fig. 1.4a). Maximum abundances of >150 ind m^{-2} were recorded in late April (Fig. 1.4a); however, the number of species increased throughout the study period, with the highest values recorded from June to August.

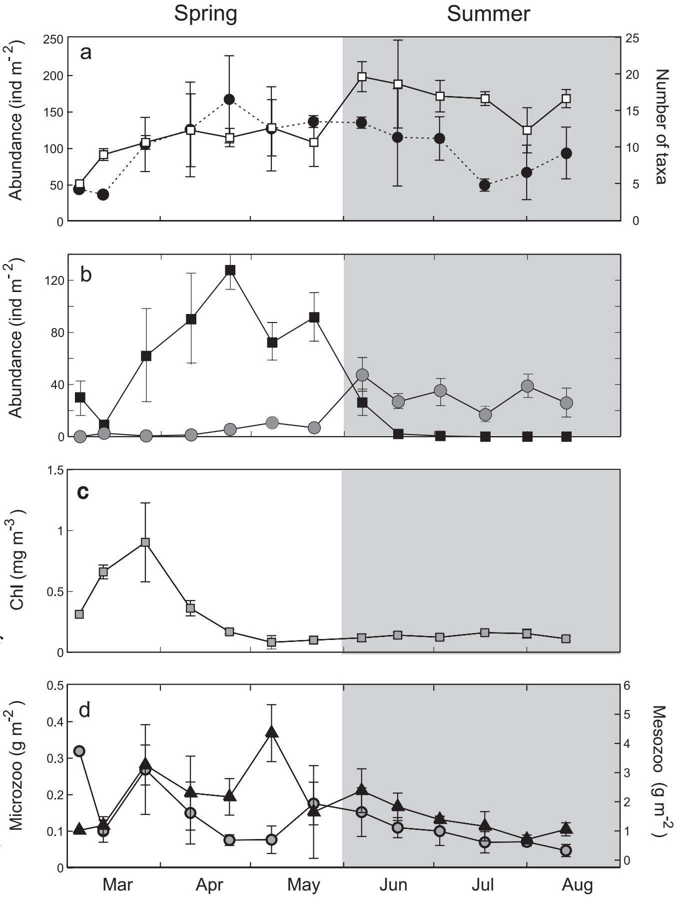

Figure 1.4. Seasonal variation of (a) larval fish abundance (●) number of taxa (•); b) larval fish abundance for the spring (■) and summer (●) assemblages as defined in the cluster analysis; (c) surface (5 m) chlorophyll-a; (d) micro- (●) and mesozooplankton (▲) biomass (g m^{-2}). Error bars represent standard deviation.

Figure 1.5 shows the seasonal evolution of the identified taxa. In early March, when seawater temperature reached the seasonal minimum (<14ºC), few coastal species are captured, of which some were winter-spawning species (*Sardina pilchardus*, *Gymnammodytes cicerelus* and *Trachurus trachurus*).

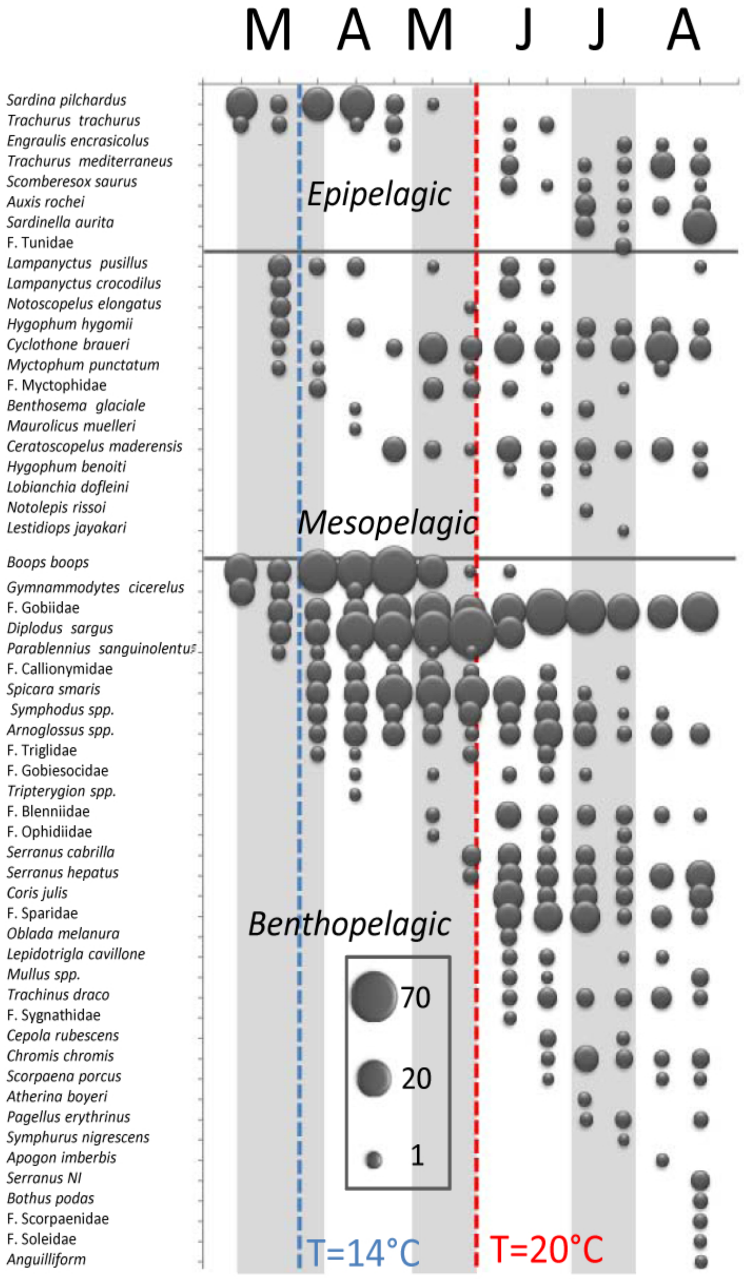

Figure 1.5. The presence and abundance of fish larvae taxa during the sampling period. Bubble size is proportional to the abundances (ind m^{-2}) fourth root transformed. NI means Not Identifyed species.

Larvae became more abundant (>100 Ind m^{-2}) by late March, with assemblages dominated by the parids *Boops boops* and *Diplodus sargus*. This situation extended to early June, when a number of benthopelagic fish species (*Coris julis* and *Serranus hepatus*, *Serranus cabrilla*, *Spicara smaris*) appeared in the water column almost simultaneously. One family (Gobiidae) and two genera (*Arnoglossus* and *Symphodus*) were present throughout the sampling period. While most of the species in those families spawn in spring-summer, certain other spawn during the winter. Mesopelagic species did not show marked seasonality, although some species, such as *Ceratoscopelus maderensis* and *Hygophum hygomii,* were particularly abundant during the summer.

Cluster analysis identified two assemblages (Fig. 1.6a). The first cluster included samplings conducted from the end of March to the end of May, with similarities above 35%. The second cluster comprised the rest of the samples, from early June to late August, also with similarities above 55%. The variation of larval assemblages throughout the study period was evaluated using PCA analysis (Fig. 1.6b). Temporal and spatial dynamics of assemblage structures displayed a remarkable influence of seasonality (sampling date), as evidenced by the counter-clockwise rotation in the order of samples. The above mentioned spring and summer assemblages showed different signs along the first PCA axis. The second axis of variability was also related to seasonality.

A complementary PCA on the pre-transformed species abundance data was completed. The corresponding descriptive biplot (Fig. 1.6b, species and sites; Boccard et al., 2011) was produced. The dynamics of the assemblage structures displayed a remarkable influence of seasonality (sampling date), as evidenced by the counter-clockwise rotation in the order of samples. The above mentioned spring and summer assemblages were clearly discriminated, illustrating the spring-summer succession in the species assemblage (species displaying similar temporal patterns of occurrence). This succession began with a few winter-spawning taxa (e.g., *S. pilchardus*, *G. cicerelus*), followed by early spring spawners (*B. boops*, *D. sargus* and *S. smaris*), with larvae being particularly abundant between April and May. The most abundant group of species were typically summer spawners such as *Sardinella aurita*, *C. julis*, *S. cabrilla* or *Mullus* spp., which were present from late June to August.

The relationships between species assemblage and environmental variables were formally tested using a redundancy analysis. The results of the redundancy analysis indicated that the simplest combination of environmental variables describing the species variation was build up by surface seawater temperature only. This model explained 34% of the variability of the species assemblage matrix (F-ratio= 17.4; P-value = 0.03; Note that this P-value is reliable because the permutation scheme used was very conservative at took into account the spatio-temporal sampling structure).

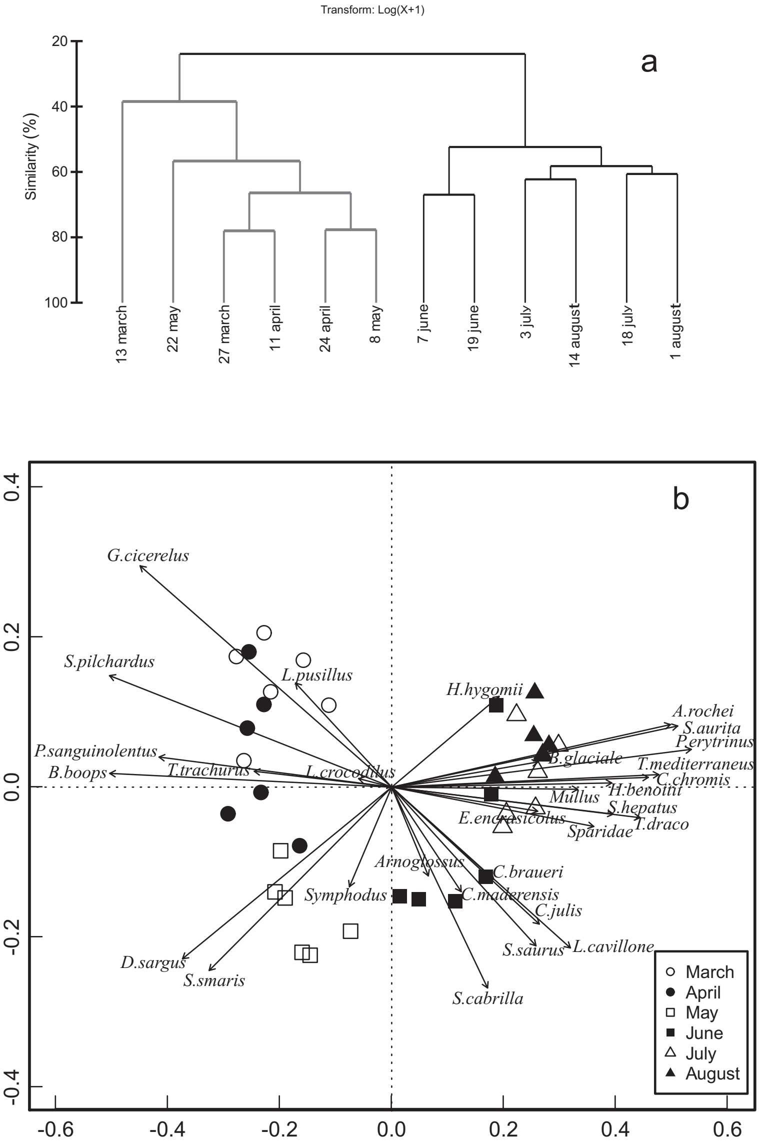

Figure 1.6. (a) Clustering and ordination representation of the species composition at each sampling. Two groups were identified: Spring (before the June sampling, in grey) and Summer (black lines). Similarity within each group is at least 40%. (b) Principal component analysis (PCA) ordination for all sampled months, displaying the vectors for the different species and the spots for the sample assemblages. At each spot, the number indicates the sampling order (from 1 (St1, 13 march 2007) to 36 (St3, 14 August 2007)). Spot shape indicates the sampling month.

1.4. DISCUSSION

Our study shows substantial seasonal variability in the species composition and abundance of fish larvae in the coastal waters of southern Mallorca. The fortnightly sampling resolution has allowed a detailed description of physical-biological covariates in the change in larval fish assemblages, which we discuss in a frame of fish adaptation to both differing energy sources and changes in physical structure of the system. According to conceptual models of seasonal variation, we expected a progressive species succession along the seasonal environmental gradient. As shown by the larval species PCA (Fig. 1.6b), a progressive change in assemblage composition is detected throughout spring, but a sharp change, mainly owing to the increase of benthopelagic species (Fig. 1.5), occurs in early summer. The winter-spring assemblage is characterised by only a few species with relatively high abundance. This assemblage, occurring at surface seawater temperatures below 20ºC, is dominated by epipelagic species whose adults display relatively large horizontal movement ranges. Species such as *S. pilchardus* and *T. trachurus* dwell over the continental shelf searching for enriched, productive surface waters (Agostini and Bakun, 2002). The benthopelagic species such as *S. smaris* or *B. boops* also conform an important part of the winter-spring assemblage, and their adult phases can also perform large horizontal movements in comparison with other benthopelagic species reproducing in later months.

In contrast, a significantly higher number of taxa coexist in the summer ichthyoplanktonic assemblage. This assemblage is characterised by larvae of benthopelagic species, such as *C. julis, S. hepatus, S. cabrilla* and *Mullus* spp., among others. Indeed, the spawning of most benthopelagic fish species in the Mediterranean (e.g., Sparidae, Labridae, Blenniidae, Mullidae, and Serranidae) takes place during the summer (Sabatés et al., 2007; López-Sanz et al., 2009). Furthermore, spawning of some large migratory epipelagic species, for example, *Thunnus thynnus*, *Coryphaena hippurus*, small tuna such as *Auxis rochei*, or other large Scombroids such as *Xiphias gladius,* also takes place during the summer around the Balearic Islands (Alemany et al., 2006). This observation implies that during spring-summer the ichthyoplankton diversity is the highest in the region. This seasonal variability in both abundance and specific composition of the larval fish assemblage has been reported previously for the NW Mediterranean (Palomera and

Olivar, 1996; Sabatés et al., 2003; de Puelles et al., 2007).

Some mesopelagic species spawn almost year-round (Fig. 1.5) and do not show any clear peak of spawning (e.g. *Benthosema glaciale, Myctophum punctatum* or *Lampanyctus pusillus*). Contrarily, other mesopelagic species display marked seasonal variations in their abundances, peaking in winter and at the beginning of spring (e.g. *Notoscopelus elongatus*) or between the end of spring and the beginning of autumn *(*e.g. *Cyclothone braueri, Cyclothone pygmaea, Lampanyctus crocodilus, Hygophum benoiti and Ceratoscopelus maderensis*) (Sabatés and Masó, 1990). This species might have arrived to our study area with an Atlantic Water intrusion, and probably will leave it as soon as the larvae capabilities allow them to swim to oceanic areas.

The causal analysis of multispecies co-occurrence in the ichthyoplankton has received relatively little attention (Frank and Leggett, 1983; Somarakis et al., 2000). Larval mortality is extremely high in most fish species (Houde, 1989; Legget and Deblois, 1994), and adaptive traits may have evolved in different species that share time and space as larvae but that display widely different reproductive strategies and life-cycles.

The spring-summer ichthyoplanktonic transition in temperate waters is highly marked, and is characterised by the change of species that, as adults, exploit different habitats.

We propose that this remarkable change is the result of a shift in environmental conditions (mainly variability in hydrography and food availability) that triggers variation in the ecosystem structure, which affects the reproductive strategy of coastal fishes. In the present study, underlying variations in larval abundance and species composition, a clear change in the different components of the pelagic trophic web was observed between spring and summer conditions (Fig. 1.4b, c, and d).

The basic hypothesis is that in winter-spring, the food web in coastal areas is linked to plankton production processes that enhance pelagic food-webs exploited by certain type of species, which have adapted their reproductive behaviour to maximise fitness in relatively unpredictable environments. In spring-summer, the thermocline setting completely changes the energy flows, and, coupled to the temperature increment, enhances benthic-associated production processes to which benthopelagic species have matched their reproductive activity. We will frame this hypothesis within the entropy theory as a plausible mechanistic background to support the discussion.

We are aware that seasonal changes in the composition of ichthyoplankton assemblages are not exclusively attributable to the outcome of ecological succession but rather to the alternations between autogenic, equilibrium dynamics and non-equilibrium reactions of the community to allogenic, environmental variability (e.g., Sommer et al., 1986; Ludovisi et al., 2005). Ecosystem development is a very complex process whose description requires the measurement of different system properties, which may "orient" ecosystem evolution or else represent indicators whose variations are more apparent, but in different moments of ecosystem development (Fath et al., 2004). Yet, the concept of entropy-producing and entropy-reducing processes can aid in the understanding of some integral features of the coastal system and the way they explain the observed differences in ichthyoplankton assemblages

When open systems are subject to a sufficiently large thermodynamic gradient (such as a temperature, velocity or concentration difference), self-organised structures can spontaneously emerge. Conceptually, the differences between spring and summer conditions can be considered as structures containing different entropy. Entropy is driven by the randomness of a signal: high randomness implies high entropy. In the analysis of natural systems, two types of entropy can be distinguished, abiotic and biotic (Fig. 1.7). In this work, both types of entropy are understood as levels of ecosystem complexity, the most complex systems being the more entropic (Ludovisi et al., 2005). Both entropy types are related because biological systems are typical self-organising dissipative structures that tend to maintain themselves far from equilibrium by pumping out entropy.

Abiotic entropy is high early in the spring season when the environment is subjected to strong atmospheric forcing, unpredictable energy fluxes, enhanced mixing and nutrient availability for phytoplankton growth. Therefore, hydrodynamic forcing plays a major role in shaping the dynamics of planktonic organisms in this season. Aside from dispersal, species spawning in this season prioritise pelagic food availability. Spring reproduction favours high growth rates in a food rich environment with high turnover rates.

We can assume that feeding opportunities for larvae in the water column are higher during spring, just after the phytoplankton bloom, and consequently, mortality by starvation-associated processes would be reduced. Most of the species reproducing during this period are epi and mesopelagic, and would fit the reproductive strategy of "income breeders", who can fine-tune their reproductive output to the immediate energy availability (Stearns, 1992; Somarakis et al., 2000). As shown in figures 1.4c and 1.4d, zooplankton abundance, particularly mesozooplankton, is higher in the months following the late winter phytoplankton bloom, which represents an advantage for planktonic feeders. Reproduction in a period with high abiotic entropy (winter-spring) maximises dispersal probability. This wider dispersal capability weakens the relevance of competitive equilibrium and niche separation. The occurrence of a longer spawning period with multiple age groups and/or multiple spawning can be a safety measure to ensure the continuity of the species in the face of enhanced abiotic variability, therefore increasing the resilience of these spring spawners.

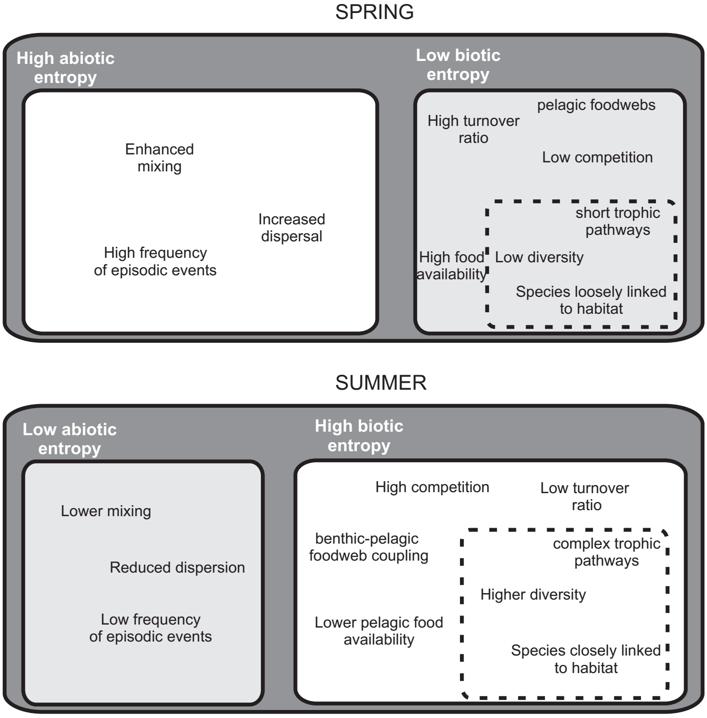

Figure 1.7. Conceptual diagram of the spring and summer differences in biotic and abiotic entropy and related fish strategies.

Under the summer scenario, the organisation of the ecosystem is driven by the incoming low-entropy energy flow and the response of biota as an entropy producer. Summer is more complex and organised (or less random), and the global entropy decreases due to increased organisation. During this period, phytoplankton and zooplankton biomass are lower. Phytoplankton biomass is concentrated at the deep chlorophyll maximum (DCM) level (below the thermocline), and the vertical distribution of micro- and mesozooplankton biomass also shows maximum abundances at the DCM (Alcaraz, 1985; Sabatés et al., 2008).

During the summer, biology is the prevailing driving force: biological rates control the system dynamics. If the optimisation principle is followed (or organisation seeking maximum resilience), spawning in summer is closely related with faster metabolism, higher larval growing rates and low dispersal. Low dispersal from protective habitats (structured seafloors) and fast development would minimise predation, and therefore, less abundant progeny would be required. Different studies have suggested that higher growth rates during the larval and juvenile stages could result in lower mortality (e.g., Houde, 1987; Hare and Cowen, 1997; Wilson and Meekan 2002). Furthermore, in the life cycle of coastal resident fishes, particularly in the case of those inhabiting seagrass beds, recruitment to adequate habitat is critical. Juveniles of some of these species show a high degree of fidelity to nursery areas (Macpherson, 1998).

In our case, these changes in ecosystem organisation most likely comprise a shift in the trophic pathway from the pelagic environment, in which oligotrophic conditions prevail during the summer season, to the more productive benthic system represented by rocky bottoms and seagrass meadows (*Posidonia oceanica*). *P. oceanica* seagrass beds, rocky zones and muddy bottoms are characteristic of the sampling area. Seasonality in the biomass of epiphytes, suprabenthos and detritus in *Posidonia* meadows has been described (Borowitzka and Lethbridge, 1989; Alcoverro et al., 1997; Tomas et al., 2005). Also, higher suprabentonic biomass in muddy bottoms is typical in summer (Fanelli et al., 2009).

Benthopelagic families of fish such as Labridae, Scorpaenidae, Serranidae or some Sparidae, constituting over 80% of the biomass associated to *P. oceanica* (Deudero et al., 2008), and feed on invertebrates inhabiting the canopy. Seasonal variability in feeding has been demonstrated for some of these species (Stergiou and Karpouzi, 2002), and the food sources in summer are more varied than in winter, generally including benthic microalgae, detritus, epifaunal crustaceans, molluscs, polychaetes and small fish. The temperature (and/or photoperiod) increase that is associated with benthic spawning is probably linked to a feeding signal coming from a change from pelagic to benthic food sources. The final composition of the larval assemblages is thus the result of different responses to an important change in energy flows.

During summer, however, most larvae of benthopelagic species will face a different trophic environment than their adults. Most larvae are located above the thermocline (Olivar and Sabatés, 1997), and only after some weeks their vertical active positioning may enable feeding at thin concentration layers. Trophic resources at the surface layers could be low and might be shared by a large number of larvae and a great diversity of species. It has been suggested that in oligotrophic systems, in which mixing is restricted by stratification, the pelagic production in summer can be dominated by the microbial loop, with microzooplankton being a key component of the food web dynamics (Tian et al., 2003). In the NW Mediterranean, Calbet et al., (2002) have already suggested that during the summer, when the densities of autotrophs are low, heterotrophs are a significant part of the zooplanktons' diet. Furthermore, Rossi et al., (2006) used lipid biomarkers to infer that anchovy larvae, *Engraulis encrasicolus*, probably complemented their zooplankton diet with protists. Some studies have even mentioned that protists are an important part of the fish larvae diet, either directly (Govoni and Chester, 1990; Fukami et al., 1999; Pepin and Dower 2007) or indirectly through predation on appendicularians or cladocerans (Morote et al., 2008; Catalán et al*.,* 2011) that exploit the microbial food web. This suggests that fish larvae may be more closely tied to the microbial food web than previously assumed. In oligotrophic areas such as the Mediterranean, this trophic link is probably of major importance, resulting in a higher efficiency of biomass and energy transfer from primary producers to higher trophic levels (such as fish) (Calbet and Saiz, 2005).

In conclusion, the diversion of energy flow from pelagic to benthic ecosystems during the spring-summer transition could partly explain the observed differences in the spawning strategies of coastal resident fish species. While the spring spawning species present a certain degree of coupling to plankton dynamics, coastal resident species most commonly funnel energy through coupling to the benthic seasonality in which seagrass habitats are key contributors to fish maintenance.

ACKNOWLEDGEMENTS

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CHAPTER 2

Dynamic regulation of larval fish self-recruitment in a marine protected area.

Abstract

The factors that regulate the self-recruitment of fish larvae were explored in Cabrera National Park (CNP), an insular Marine Protected Area (MPA) located off southern Mallorca (Western Mediterranean). Our study attributes the regulation of larval arrival to the MPA to a combination of retention by topographically generated circulation patterns around the island and shelf break frontal dynamics. Specifically, within this shelf, interaction of the wind-induced oscillatory flow with the island was shown to generate ephemeral recirculation patterns that, over time, favor larval retention in the proximity of the MPA. According to our measurements, oscillatory flows produced by wind forced island-trapped waves (ITWs) dominate the flow around CNP. ITW-forced dispersion simulations were in agreement with the observed distributions of several typical fish species that breed in the CNP. A second regulator of environmental variability is the influence of boundary currents and open ocean mesoscale structures at the shelf break. These structures generate frontal zones that are comparatively more long-lived than inner-shelf circulation patterns, and they were shown to act as barriers to the offshore dispersion of coastal fish larval assemblages. Finally, inferences from larval size distributions around the MPA together with particle-tracking model simulations suggested the relevance of behavioral processes for larval recruitment to the MPA. Based on these observations, the waters around the CNP can be viewed as a relatively stable system that allows breeding fish populations to rely on self-recruitment for their long-term persistence, independent of other source populations along the coast of Mallorca.

2.1. INTRODUCTION

The dispersion of coastal fish larvae from their natal habitat and their subsequent recruitment are prominent issues in the ecology, conservation, and management of fish populations. To understand the underlying mechanisms requires elucidation of the numerous participating biotic and abiotic processes operating at varying spatiotemporal scales. In an ecological context, these scales, despite their broad range, are non-random, as they are modulated by the degree of coupling between ocean dynamics and the speciesspecific biological characteristics of the regional fish populations, such as larval phase duration, larval physiology and behavior, and adult behavior. According to the classical theory, reproductive strategies have evolved such that offspring hatch and develop at times and in areas favorable for their growth and survival (Cushing, 1990). Indeed, larval fish assemblages are the result of convergent spawning strategies by multiple species responding to the same environmental driver. For example, in shelf areas of the Mediterranean Sea, life-cycle strategies often include summer spawning, when oligotrophy prevails in the water column (Antoine et al., 1995; Sabatés et al., 2007) but the probability of dispersal to the open sea by enhanced physical forcing episodes is reduced (Chapter 1, Alvarez et al., 2012). This adaptation to local conditions also allows marine fish populations to maintain a spatial persistence. However, evidence from numerical models and genetic data suggest that, even within a given species, the scale of dispersal in marine organisms can vary widely at different locations in space and time (Cowen et al., 2003; Sotka et al., 2004).

The traditional view of a potentially high dispersal for marine propagules has been challenged by the increasing evidence showing that self-recruitment is more common than previously thought (Jones et al., 1999, 2005; Almany et al., 2007). In coastal environments, the local retention of pelagic eggs and larvae may determine the success of early life stages, which in turn influences survivorship to adulthood and the persistence of the population (James et al., 2002; Bradbury et al., 2008). At this scale, the magnitude of self-recruitment is influenced not only by large drivers such as seasonality but also by small-scale variations in the physical environment and their coupling to the behavior of adult and larval phases. Generally, species inhabiting coastal regions have developed strategies to control dispersal from home habitats, such as the selection of favorable areas and spawning times, a shortened duration of the planktonic phase, an increased number of reproductive events, and larval behavior (Parrish et al., 1981; Cowen et al., 1993; Huggett et al., 2003; Leis, 2007).

The combination of physical and biological factors, even in species with a shared habitat and similar behavior, produces considerable spatial heterogeneity and variability in the distribution and diversity of fish larvae in shelf waters. While important clues on regional ichthyoplankton assemblages can be obtained identifying water masses (e.g., Muhling et al., 2008; Leon-Chavez et al., 2010), hydrography yields limited results in regions where significant small-scale circulation occurs within the same water mass (Cowen et al., 1993). Among the physical factors that increase local larval retention within a water mass, both the persistent convergent flows and eddies associated with coastal topographic features and sea-bottom irregularities are of primary importance for coastal spawning species (Sabatés et al., 2004; Sponaugle et al., 2005). Recruitment is known to be higher in the vicinity of topographic discontinuities such as inlets, headlands, islands, and submerged features, e.g., marine banks and canyons (Bolz and Lough, 1984; Boehlert et al., 1992; Shepherd et al., 1992; Nishimoto and Washburn, 2002).

Over the past decades the patterns of topographically steered flows and their influence on larval retention have been investigated using field, numerical, and remote-sensing techniques (e.g., Roughan et al., 2005; Banas et al., 2009). These studies provided insight into the physical aspects of larval accumulation; yet, most of them focused on highly dynamic systems such as tidally stirred areas or regions with dominant currents. However, in systems with weaker ocean dynamics, which are predominately wind-driven, transport pathways and the relative importance of biotic versus abiotic processes in larval distributions may be markedly different. For instance, whereas in highly dynamic systems larval dispersion is generally assumed to be assive (e.g., Rooper et al., 2006), under weaker flows, active habitat selection by late-stage larvae becomes effective (Pattrick and Strydom, 2009).

Due to their relative isolation, islands offer a particularly interesting opportunity to analyze self-recruitment. Previous studies in Cabrera National Park (CNP), an insular Marine Protected Area (MPA) located in SE Mallorca (39.15oN, 2.96oE; le. 1.1), suggested that the interaction of coastal flow with the island's topography enhances retention of the larvae of coastal-spawning fish species (Basterretxea et al., 2012). As in other Mediterranean areas with microtidal regimes, the Mallorcan coastal circulation in summer is generally weak and mainly windforced. Alvarez et al. (2012, Chapter 1) showed that, despite the occasional intrusions of oceanic species, ichthyoplanktonic assemblages in this area typically correspond to coastal species with a strong dependence on habitat. The majority of these species spawn in early summer, when the water column is stratified and larval food availability is relatively low (Sabatés et al., 2007). It is hypothesized that in the absence of important processes that stimulate primary productivity during this season (i.e., coastal upwelling), topographically steered flows favoring retention, concentration, and larval fish feeding would promote plankton accumulation, and retention would enhance larval survival, therefore increasing recruitment (e.g., Bakun, 1996; Lopez-Sanz et al., 2009). However, the extent to which increased larval recruitment is determined by physical processes controlling offshore dispersal, the increased productivity associated with local-scale flow patterns, and larval behavioral responses is not well understood.

It is also largely unclear how the unique characteristics of CNP regulate the distribution of fish larvae. Thus, to assess the potential areas of larval retention in CNP and to identify the mechanisms favoring self-recruitment in this MPA, we evaluated its larval fish assemblages, specifically, in an area extending across the shelf to offshore waters. The study was carried out during summer, when most coastal species spawn. In addition, we examined the key processes driving recruitment around CNP. The information contributed by this study widens our knowledge of fish larval dispersal in CNP and therefore also on fish population dynamics in this MPA and their biogeography.

2.2. METHODS

2.2.1. Study area

The geographic region of interest was the southeastern shelf of Mallorca. Centered in this region, CNP,comprising two main islands and a number of islets, is located some 9 km off the coastline of the island of Mallorca (Fig. 2.1). The passage between Mallorca and CNP is relatively shallow and narrow (~9 km), with depths of <50 m. Summer wind conditions on Mallorca are characterized by a mild breeze regime with a marked day/night pattern only episodically disrupted by the stronger Tramontane (N–NE winds; Basterretxea et al., 2005). The flow of shelf water around CNP responds to a combination of meteorological and oceanographic forcings that result in a variety of scenarios of along-shelf currents, the penetration of oceanic water, and offshore-directed flow. Generally, the weak and oscillatory currents of the inner shelf are highly decoupled from offshore flows associated with the propagation of island-trapped waves generated by the wind forcing (Jordi et al., 2009b). However, occasional intrusions of oceanic waters with well-differentiated larval assemblages are observed even at more coastal sites (Alvarez et al., 2012, Chapter 1).

This offshore water penetration is determined by shelf-break flows resulting from the dynamics in the Algerian basin (Perkins and Pistek, 1990; Millot, 1991) and by density fronts generated between the less saline 'recent' Modified Atlantic Waters in the south and the denser 'aged' Modified Atlantic Water over the Balearic and Liguro-Provençal basins (Jordi et al., 2009a). These fronts can form meanders and long-living structures that interact with other open-ocean features such as eddies detached from the Algerian current (Millot, 1999; Puillat et al., 2002). Since the term 'Modified Atlantic Water' is systematically used to refer to the surface water in the Mediterranean Sea independently of its salinity, we hereafter conveniently use mode 1 and mode 2 when referring to these 'recent' or 'aged' water masses, respectively.

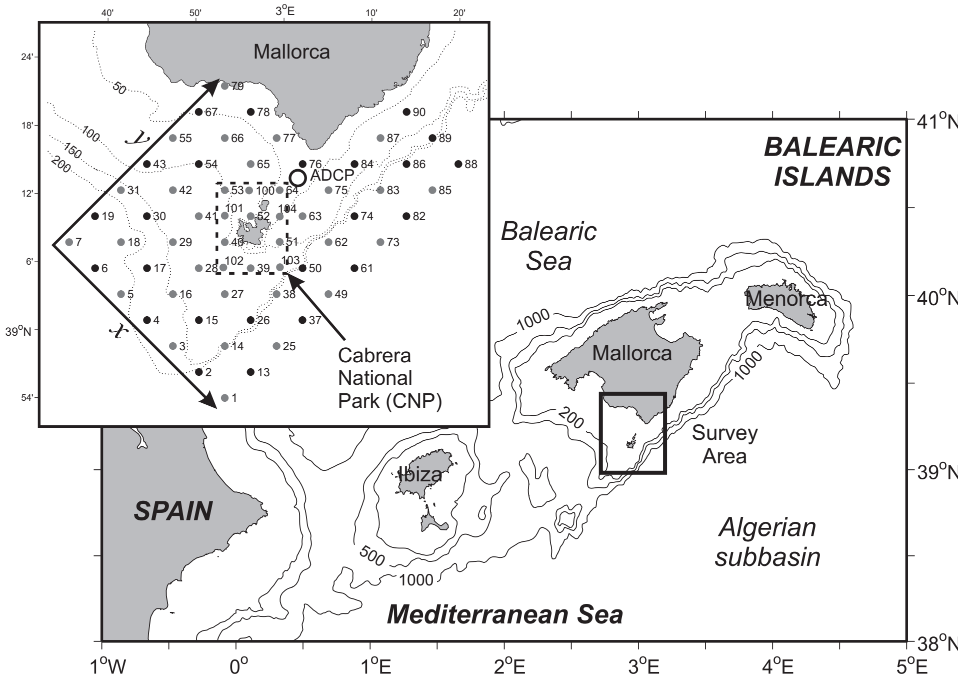

Figure 2.1. Location of the survey area in the NW Mediterranean Sea. Inset showing shelf bathymetry (m) and station locations. Black and gray circles correspond to CTD stations, and gray circles indicate biological sampling. The MPA limit considered in particle-tracking model simulations is marked by the dashed line. The rotated x and y axes (45° clockwise) shown in the figure are conveniently used in following figures to display results.

2.2.2. General circulation and shelf currents

General circulation patterns were depicted from sealevel anomaly (SLA) fields created by merging TOPEX/Poseidon, ERS1/2, Geosat Follow-On, Jason- 1, TOPEX/Poseidon interleaved, and ENVISAT altimeter measurements, obtained from AVISO (http://www.aviso.oceanobs.com/). SLA, as measured by altimetry, is particularly difficult to interpret with respect to characterizing the circulation because of the lack of accurate information on the mean dynamic topography (MDT). Therefore, in this study the MDT was derived from a high-resolution ocean general model of the Mediterranean Sea based on temperature/salinity climatology data (Jordi and Wang, 2009). Geostrophic currents were determined based on finite differences of the sea surface height (SSH), which is computed as the sum of the MDT and the SLA. Currents in the Balearic Sea are in good geostrophic balance and the use of the geostrophic approximation to estimate the circulation is thus valid (Pascual and Gomis, 2003). In addition, tidal currents are very weak and inertial oscillations only occur after severe storms, mainly in autumn and winter (Jordi and Wang, 2008).

During summer 2007, the shelf circulation in southern Mallorca was monitored using a bottom-mounted acoustic Doppler current profiler (ADCP, 1 MHz Nortek Aquadopp, Nortek AS, Vangkroken, Norway) placed to the NE of the CNP at a depth of 25 m (Fig. 1.1). Vertical profiles of current velocities were measured every 30 min at 4-m depth intervals within the first 25 m above the bottom. Wind data at Palma Airport were provided by the National Meteorology Agency (AEMET).

2.2.3. Field sampling

From 9 to 13 July 2007, a grid of 63 stations was sampled onboard the RV Regina Maris. The grid consisted of seven transects perpendicular to the coast and placed at intervals of ~4 km around Cabrera and 6 km elsewhere (Fig. 2.1). Vertical profiles of temperature, salinity, and fluorescence from the surface to a maximum depth of 250 m were obtained at each station using a CTD SBE-25 equipped with a Sea-Tech fluorometer. Water samples for chlorophyll-a determination were collected using a rosette system to calibrate the fluorometer. The measured seawater variables were interpolated using the objective analysis from the CTD stations and a regular grid of 30 9 42 points separated by 1.5 km in both directions. In the vertical, the grid consisted of 81 uniform sigma-levels from the surface to a maximum depth of 250 m.

Zooplankton and fish larvae were collected during the daytime from 39 selected ‘biological’ stations (see Fig. 2.1). Zooplankton was collected by means of vertical hauls from a depth of 70 m to the surface using a net with a 40-cm diameter ring net with a mesh size of 53 µm, and equipped with a flowmeter. Although the net was intended for microzooplankton, size-selection was not performed during sample processing. All samples were immediately fixed in 5% borax-buffered formalin. In the laboratory, aliquots that included at least 200 individuals (plus nauplii of copepods) collected from a single station were classified in large functional groups (e.g., appendicularians, chaetognaths, cladocerans, and copepods). Abundances were scaled up and transformed to individuals (ind.) m^{-3}. The use of nonsize fractioned zooplankton samples derived from a net designed for microzooplankton impeded the use of zooplankton information at any taxonomic level of aggregation. However, the use of total zooplankton is still an informative variable for a description of the biotic environment at the horizontal scale.

Ichthyoplankton was sampled using oblique Bongo net tows at each biological station (the same as for zooplankton). The net had a 60-cm diameter opening, a mesh size of 335 µm, and was towed from a maximum depth of 200 m to the surface or from 5 m above the sea floor at shallower depths. The volume of filtered water was estimated using a flowmeter positioned in the center of the mouth of the net. Samples were fixed as described for zooplankton. In the laboratory, all fish larvae were sorted and identified to the lowest taxonomic level possible. Larval abundances were expressed as the number of larvae per 10 m^2 of sea surface. In selected species, the standard length (precision = 0.1 mm) was measured in up to 30 individuals randomly selected from the sample by examination under a binocular microscope. Although size-selectivity is well-described in standard bongo samples, a preliminary inspection of the data showed that no station-biased size selectivity occurred, which might be the only case that could invalidate the interpretation on retention processes.

2.2.4. Statistical analyses

Two multivariate descriptive analyses were performed with the aim of describing the main environmental and larval assemblage features. First, a principal components analysis (PCA) and a cluster analysis (unweighted pair group method with arithmetic mean UPGMA) were carried out considering only the environmental data, which included depth (DEPTH, m), distance to coast (DIST, m), temperature (°C) at 10 m (T10), salinity at 10 m (S10), σt (kg m3) at 0 m (D10), Simpson’s stratification index (STR), integrated chlorophyll-a (CHLINT, mg m^{-2}), and total zooplankton abundance (ZOO, ind. m^{-3}). Simpson's stratification index was calculated every 2 m to characterize the strength of the thermocline (Simpson and Bowers, 1981). Secondly, the ichthyoplankton matrix was subjected to a multivariate description through PCA, using Hellinger's distance (Borcard et al., 2011) and a cluster analysis (UPGMA) on centered and log (x + 1)-transformed values. Hellinger's distance provides a common ground that allows the subsequent combination of multivariate analyses, and yields, in the case of biological variables, a metric that is similar in performance to the Bray–Curtis similarity.

The ichthyoplankton matrix was built after excluding rare species based on a constancy (C) criterion, i.e., the percentage of stations occupied by a particular taxon. Only taxa with C > 10% were considered for the analysis which, as shown in Table 2.1, produced a final matrix of 41 taxa. The stations grouped through the cluster analysis were further examined through a SIMPER routine from PRIMER 6.0 (Plymouth routines in multivariate ecological research). Species in which the ratio of average dissimilarity to the standard deviation of the similarity (r) was >2 were considered typical of the cluster group (Clarke and Warwick, 1994).

2.2.5. Larval dispersal estimations

To analyze the effect of ITWs on larval trajectories, estimates of current velocity and direction were obtained using a parallel version the Princeton ocean model (sbPOM; Jordi and Wang, 2012). sbPOM is a three-dimensional, primitive-equation, sigma-coordinate, hydrostatic model (Mellor, 1993). The model domain includes the entire Balearic Islands in order not to impede the generation and propagation of the ITWs around Mallorca. The horizontal resolution varies from 200 m within CNP to 2000 m near the boundaries. The bathymetry is realistic, although the maximum water depth is truncated to 1500 m. In the vertical, the model uses 31 non-equidistant (sigma) vertical levels concentrated towards the surface and the sea bed.

ITWs were generated by forcing the model with a constant wind of 10 m s1 blowing during 1 day. After this day, the model was run over 10 days without any forcing, to allow the propagation of the ITWs. A total of eight simulations were performed by varying the initial wind direction. The resultant three-dimensional currents of these 10-day simulations were stored at hourly intervals and then used in a post-processing mode to drive a separate particle-tracking model. Fish larvae were considered as passive particles and advected by the three-dimensional currents (Basterretxea et al., 2012; Casabianca et al., 2012). We based our dispersal analysis on average fields from the eight simulations of 25280 passive tracers that were uniformly released from seagrass⁄rocky bottoms around the CNP (<40 m depth). At each time-step (1 h), the final position of each particle was estimated from the particle speed at the initial position. Speed was determined by interpolating the model currents with the particle position. A random walk term was also used to approximate the effects of the sub-grid scale processes on particle trajectories as in Xue et al. (2008). In addition, we evaluated the effect of active larvae swimming directed towards the nearest coast (as suitable habitat) at modest speeds. This behavioral term was added to the passive drift in the particle-tracking model. Three cases were simulated: (i) no swimming capability; (ii) sustained shoreward swimming at a speed of 5 cm s^{-1}; and (iii) shoreward swimming at 5 cm s^{-1} only when currents were offshore-directed. Shoreward swimming was implemented at each time step, first by releasing the particles with no swimming capability (passive drift) and then prescribing an oriented swimming capacity towards the nearest land gridpoint.

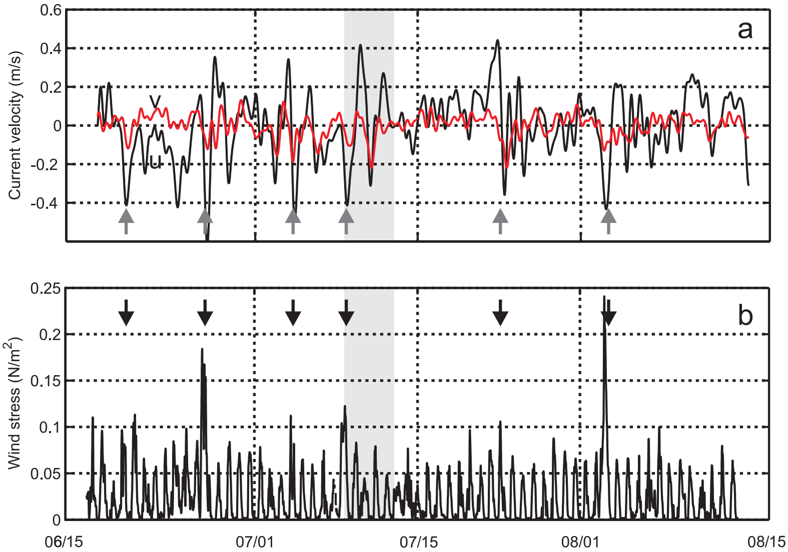

Figure 2.2. (a) Alongshore (u, black line) and cross-shore (v, gray line) components of near-surface alongshore flow speeds (m s^{-1}) in the mooring site. Vectors have been rotated 8^o counter-clockwise into the direction of maximum variance. Gray arrows indicate oscillatory intensification episodes corresponding to island trapped waves associated with increases in local wind stress (black arrows) shown in the lower panel (b). The gray band indicates the dates of the cruise.

2.3. RESULTS

2.3.1. Environmental setting

Figure 2.2 shows the current velocity and associated wind stress in the shelf during summer. As the currents were quite homogeneous through the water column, only near-surface measurements are shown. The mean currents were low (<6 cm s^{-1}); but velocities of up to 46 cm s^{-1} were registered in response to enhanced wind events. These oscillatory episodes, with periods of 57 h, were associated with ITWs, a particular albeit more energetic case of coastal-trapped waves (Jordi et al., 2009). One of these oscillatory episodes occurred during the cruise (Fig. 2.2a), following a notable intensification in response to winds of ~9 m s^{-}1 from the northeast. It is noteworthy hat while ITWs mainly produce shore-parallel displacement around Mallorca, the flow is cross-shore to the east and west of CNP, which would allow the interaction of larvae hatched in this area with the nearshore environment.

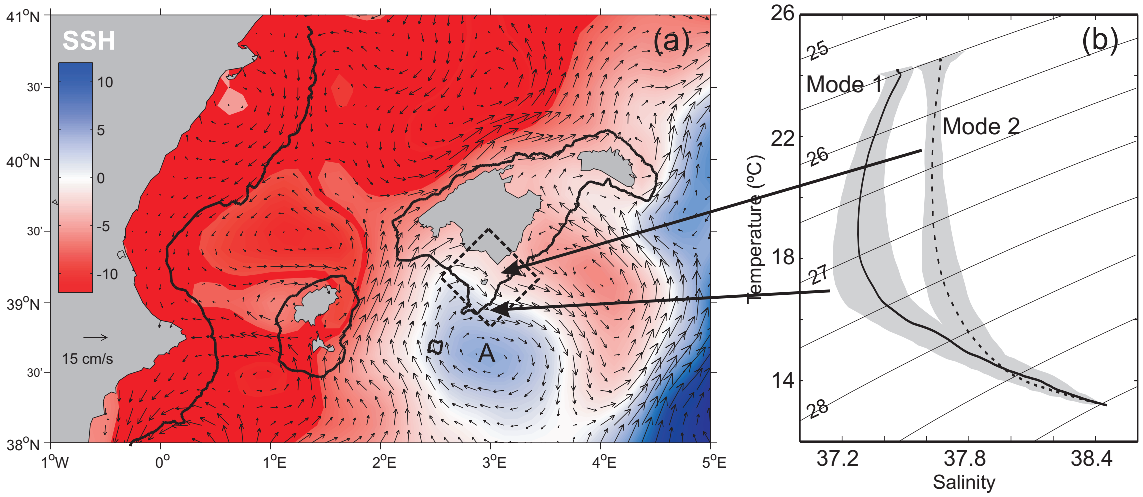

Figure 2.3.(a) Sea surface height (SSH, cm) and derived oceanic circulation patterns (cm s^{-1}). Note the NE-SW transition area across the Balearic Islands and eastward flow along the study area (dashed line) generated by an anticyclonic eddy (A). The black line marks the 200 m isobath. (b) T-S diagram depicted from CTD data during the survey. The solid line in b indicates the water mass contained in the gyre to the south of the sampling area (mode 1), and the dotted line corresponds to waters mass on the shelf (mode 2). Gray shading shows 1 S.D. of each water mass.

The oscillatory dynamics over the shelf contrast notably with current patterns further offshore. Figure 2.3 shows the regional circulation pattern around the Balearic Islands during the survey, depicted from SSH data. The most conspicuous feature of the open ocean circulation was the presence of an anticyclonic eddy about the size of Mallorca, entrained in the transition area between the denser waters of the Balearic Sea and those in Algerian sub-basin. This eddy structure interacted with the southern shelf of Mallorca at about the position of CNP. The clockwise circulation of the eddy was associated with currents of some 12 cm s^{-1} located at its periphery, inducing an eastward flow along the southern shelf of Mallorca. To the north of this eddy, the northward-directed slope circulation was strongly deflected offshore, returning to the shelf further to the north.

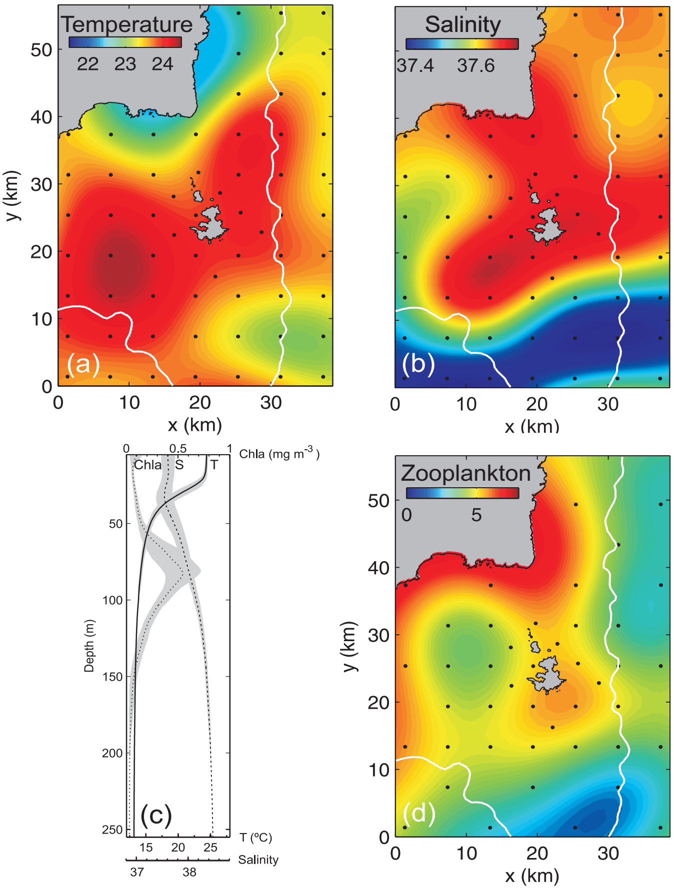

Figure 2.4. a) Near surface (20 m) temperature (ºC), (b) salinity field and (c) mean profiles of temperature, salinity and chlorophyll-a. Gray shading represent 1 S.D. for each variable. (d) Distribution of zooplankton abundance (ind m^{-3} x1000). The white line in the maps indicates the position of the 200 m isobath.

Table 2.1. Descriptors of the main taxa of fish larvae in Cabrera National Park during summer.

Taxa	Nº of larvae	Abundance (%)	C (%)	Range of standardized ab. (ind 10m^{-2}) in positive stations	Taxa	Nº of larvae	Abundance (%)	C (%)	Range of standardized ab. (ind 10m^{-2}) in positive stations
Anguilliformes* (ANG)	10	0.16	13.95	3-7	Ophidiidae * (OPH)	73	1.15	67.44	2-42
Apogonidae _Apogon_ imberbis* (AIM)	28	0.44	27.91	2-21	Paralepididae _Lestidiops jayakari_ *(LJA)	17	0.27	20.93	2-29
Argentinidae _Glossanodon leioglossus_	1	0.02	2.33	6	_Notolepis rissoi (Arctozenus risso)_*(AR)	22	0.35	13.95	4-64
Blenniidae * (BLE)	48	0.76	46.51	2-20	_Paralepis_ sp *	6	0.09	11.63	5-7
Bothidae _Arnoglossus_ spp *(ARN)	217	3.41	67.44	2-157	Phosychthyidae _Vinciguerria_ sp	4	0.06	6.98	4-10
Bramidae _Brama_ brama	4	0.06	9.30	3-4	Pomacentridae _Chromis chromis_ *(CCH)	608	9.56	79.07	5-179
Callyonimidae _Callionymus_ spp* (CALY)	6	0.09	11.63	3-9	Serranidae _Anthias_ anthias	3	0.05	6.98	2-5
Caproidae _Capros aper_	2	0.03	4.65	2-3	_Serranus cabrilla_ *(SCA)	66	1.04	46.51	3-24
Carangidae _Seriola_ sp	6	0.09	9.30	2-7	_Serranus hepatus_ *(SHE)	198	3.11	48.84	2-95
_Trachurus mediterraneus_* (TRA)	54	0.85	44.19	2-22	Scomberescocidae _Scomberesox saurus_* (SSA)	33	0.52	37.21	2-14
Trachurus spp	2	0.03	4.65	4-5	Scombridae _Thunnus thynnus_ *(TTHY)	330	5.19	37.21	2-254
Cepolidae _Cepola rubescens_ * (CRU)	82	1.29	44.19	2-67	_Thunnus alalunga_ *(THA)	35	0.55	20.93	3-30
Clupeidae _Sardinella aurita_ * (SAU)	199	3.13	41.86	2-189	_Auxis rochei_ *(ARO)	46	0.72	25.58	3-111
Cygnoglossidae _Symphurus_ spp* (SYM)	15	0.24	23.26	2-17	Other Scombridae	9	0.14	9.30	2-13
Engraulidae _Engraulis encrasicolus_ (ENG)	89	1.40	60.47	2-57	Scorpaenidae _Scorpaena porcus_	3	0.05	4.65	2-5
Gobiidae* (GOB)	629	9.89	72.09	2-236	_Scorpaena_ sp.	2	0.03	2.33	5
Gobiesocidae	3	0.05	4.65	2-5	Soleidae _Buglossidium luteum_	2	0.03	4.65	2-6
Gonostomatidae _Cyclothone braueri_ * (CBR)	1800	28.32	100.00	2-758	Other soleidae	2	0.03	2.33	4
Labridae _Coris julis_ * (CJU)	407	6.40	69.77	2-124	Sparidae _Pagellus erythrinus_ *(PER)	43	0.68	39.53	2-24
Other labridae * (LAB)	16	0.25	23.26	2-13	Other Sparidae*(SPA_NI)	41	0.64	30.23	2-39

Table 2.1. *(Continued)*

Taxa	Nº of larvae	Abundance (%)	C (%)	Range of standardized ab. (ind $10m^{-2}$) in positive stations	Taxa	Nº of larvae	Abundance (%)	C (%)	Range of standardized ab. (ind $10m^{-2}$) in positive stations
Merlucciidae					Sphyraenidae				
Merluccius merluccius * (MER)	6	0.09	11.63	3-6	*Sphyraena sphyraena*	1	0.02	2.33	2
Mullidae					Sternoptychidae				
Mullus spp. * (MUL)	57	0.90	51.16	2-48	*Argyropelecus hemigymnus**(AHE)	11	0.17	18.60	4-17
Myctophidae					Stomiidae				
Ceratoscopelus maderensis * (CMA)	262	4.12	65.12	2-132	*Stomias boa*	4	0.06	9.30	2-5
Hygophum hygomii * (HHY)	371	5.84	55.81	2-277	Sygnathidae	2	0.03	4.65	2-3
					Trachinidae				
*Benthosema glaciale** (BGL)	37	0.58	34.88	2-52	*Trachinus draco**(TDR)	124	1.95	65.12	2-48
					Triglidae				
Lampanyctus pusillus *(LPU)	140	2.20	51.16	2-106	*Lepidotrigla cavillone**(LCA)	26	0.41	27.91	2-17
*Lampanyctus crocodilus** (LCR)	32	0.50	39.53	2-27	*Trigla* spp *(TRI)	15	0.24	18.60	2-17
					Uranoscopidae				
*Lobianchia dofleini**(LDO)	53	0.83	37.21	2-26	*Uranoscopus scaber*	3	0.05	6.98	2-3
					Xiphiidae				
*Myctophum punctatum**(MYC)	16	0.25	23.26	2-28	*Xiphias gladius*	1	0.02	2.33	3
Symbolophorus veranyi	11	0.17	16.28	2-13					
Other Myctophydae* (MY_NI)	24	0.38	32.56	2-23					

C, constancy. (*) species selected for the multivariate analysis. The abbreviated name used in the multivariate analyses is given in parantheseslarvae in Cabrera National Park during summer.

The near-surface temperature was quite uniform throughout the survey area and most variations were attributable to changes produced by diurnal warming or to the nearshore upwelling along the eastern coast of Mallorca responding to the northeasterly winds (Fig. 2.4a). Contrastingly, near-surface salinity showed a pronounced front between the eddy and the waters around Mallorca (Fig. 2.4b). As seen in the temperature-salinity (TS) diagram (Fig. 2.3b), two distinct water modes were distinguishable; the presence of recent Atlantic Water (mode 1), with a lower surface salinity entrained in the eddy, and a higher-salinity water mass (>37.5) on the shelf corresponding to aged AtlanticWater (mode 2).

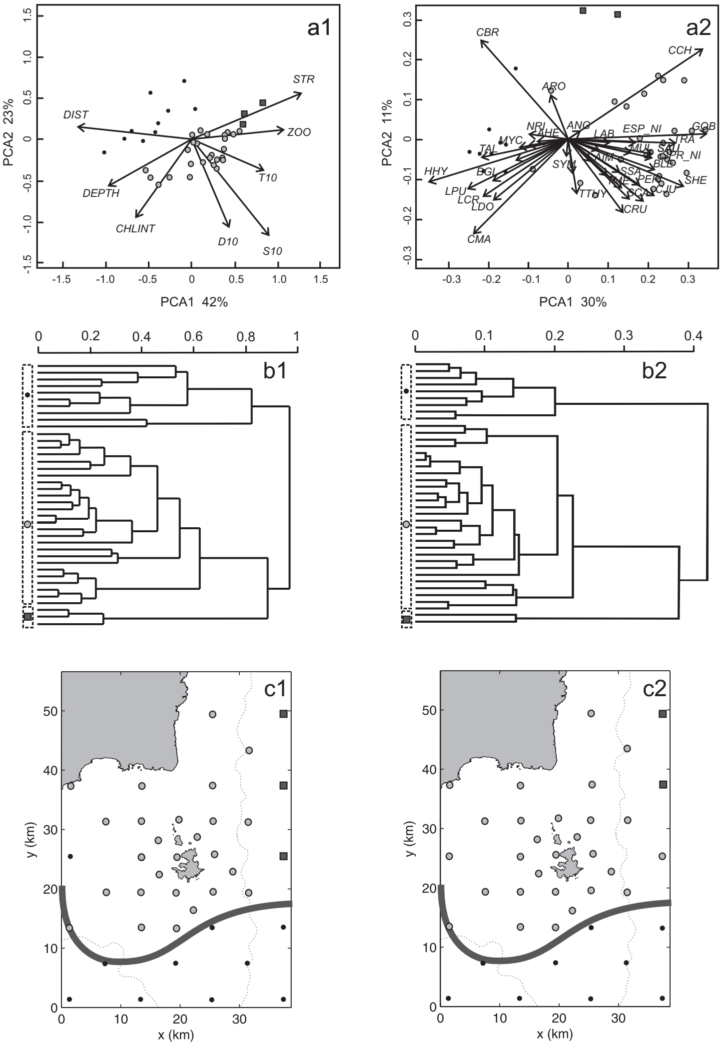

Figure 2.5. PCA, cluster and distribution map for environmental variables (a1,b1 and c1) and for larval fish taxa (a2, b2 and c2).

The vertical structure of the water column was dominated by thermal stratification, typical of full summer, with a marked thermocline beginning at ~20 m depth (Fig. 2.4c). Phytoplankton biomass displayed a characteristic non-uniform distribution in the water column, i.e., low (<0.1 mg chl a m3) surface values and a deep chlorophyll maximum located well beneath the pycnocline, at depths of some 75 m. Mixed-layer fields were modestly enhanced (~0.02 mg m^{-3}) in the shallower areas (<50 m, data not shown).

Patterns of total zooplankton abundance also showed coastal enhancements, with higher abundances generally observed over the shelf (Fig. 2.4d). The mean zooplankton abundance was 4425 ± 1490 ind. m^{-3}. Copepods comprised the dominant group, representing 21 ± 11% of total zooplankton counts, but chaetognaths, scaphopod mollusks (Dentalium sp.), and doliolids were similarly abundant (18, 16, and 14%, respectively).

The multivariate ordination of the stations enabled a more in-depth analysis of the environmental setting. The first three axes of the PCA were significant (broken stick model) and explained 79% of the variance, while 65% was explained by the first two (Fig. 2.5a1). The first axis was highly correlated with DIST and ZOO, and the second axis with differences in water masses (D10 and S10). The resulting environmental cluster separated stations in mode 1 waters, offshore, from those influenced by mode 2 waters, i.e., inshore, plus a separate station located to the east, in deep waters (Fig. 2.5b1). The environmental cluster-derived station grouping corroborated that mean zooplankton abundance was significantly higher at inshore stations (see below).

2.3.2. Larval fish assemblage composition and size structure

A total of 7023 fish larvae were collected, of which 89.5% could be assigned to 60 taxa (Table 2.1). The remaining individuals were unidentifiable because they were either too small or damaged. The most abundant and frequent species was the mesopelagic fish *Cyclothone braueri*, which accounted for 25% of all the larvae and was detected at all sampled stations. This species and other mesopelagic taxa were very abundant at the oceanic side of the front. Larvae of coastal fish species such as *Chromis chromis* and *Coris julis* comprised 9 and 6%, respectively, of total larvae, but represented >13% of coastal species abundance.

These species were particularly abundant at the western boundary of the front.

In the PCA performed on the larval matrix, the first axis explained 30% of the total variance and discriminated between coastal and oceanic species, whereas the second axis discriminated among only a few stations, i.e., those with low species numbers and located over high depths (Fig. 2.5a2). The resulting cluster discriminated three groups of stations: (i) oceanic (O), mainly including stations within the eddy characterized by mode 1 waters; (ii) coastal (C), comprising most of the stations within the shelf, characterized by mode 2 waters; and (iii) a final group consisting of only two stations, with mode 2 waters and situated in deep (D) open ocean waters at the northeast boundary of the sampling area (Table 2.2). The number of species and the diversity (H') were significantly higher in the coastal assemblage, followed by the oceanic assemblage, and finally by group D (ANOVA for H' index: F = 44.1, d.f. = 2, P < 0.001; ANOVA for number of species: F = 10.35, d.f. = 2, P < 0.001; *post-hoc* tests not shown).

Comparisons between clusters C and O yielded higher mean zooplankton abundances at the coastal stations (t-test = -3.4, mean = 4884 ± 1284, versus 3468 ± 1154 ind. m^{-3}, d.f. = 41).

The SIMPER analysis (Table 2.2) revealed that the typifying species (r > 2) of group O included mesopelagic fish such as Cyclothone braueri, various myctophids (*Hygophum hygomii, Ceratoscopelus maderensis* and *Lampanyctus pusillus*), and *Thunnus alalunga* (Table 2.2). Notably, *C. braueri* was detected at all stations, although with higher abundances in the oceanic assemblage, being a key species in cluster definition. Stations in group C were characterized by a high abundance of *Chromis chromis*, Gobiidae, *Coris julis* or *Trachinus draco*, but also by the presence of *C. braueri*. In group D, both the abundance and the number of species were very low.

The joint spatial distribution of O and C larvae is shown in Fig. 2.6(a, b). These representations clearly demonstrated that larvae included in the first group showed high abundances in the southern part of the studied area. The spatial distribution of the coastal assemblage was characterized by high larval concentrations at the eastern and, particularly, western boundaries of CNP. However, within this general pattern, the relative contribution of the different taxa varied notably. For example, while maintaining higher abundances around CNP, C. chromis and *Serranus hepatus* markedly differed in their distributions (Fig 2.6c, e). Likewise, differences were observed in oceanic taxa (Fig. 2.6 d, f).

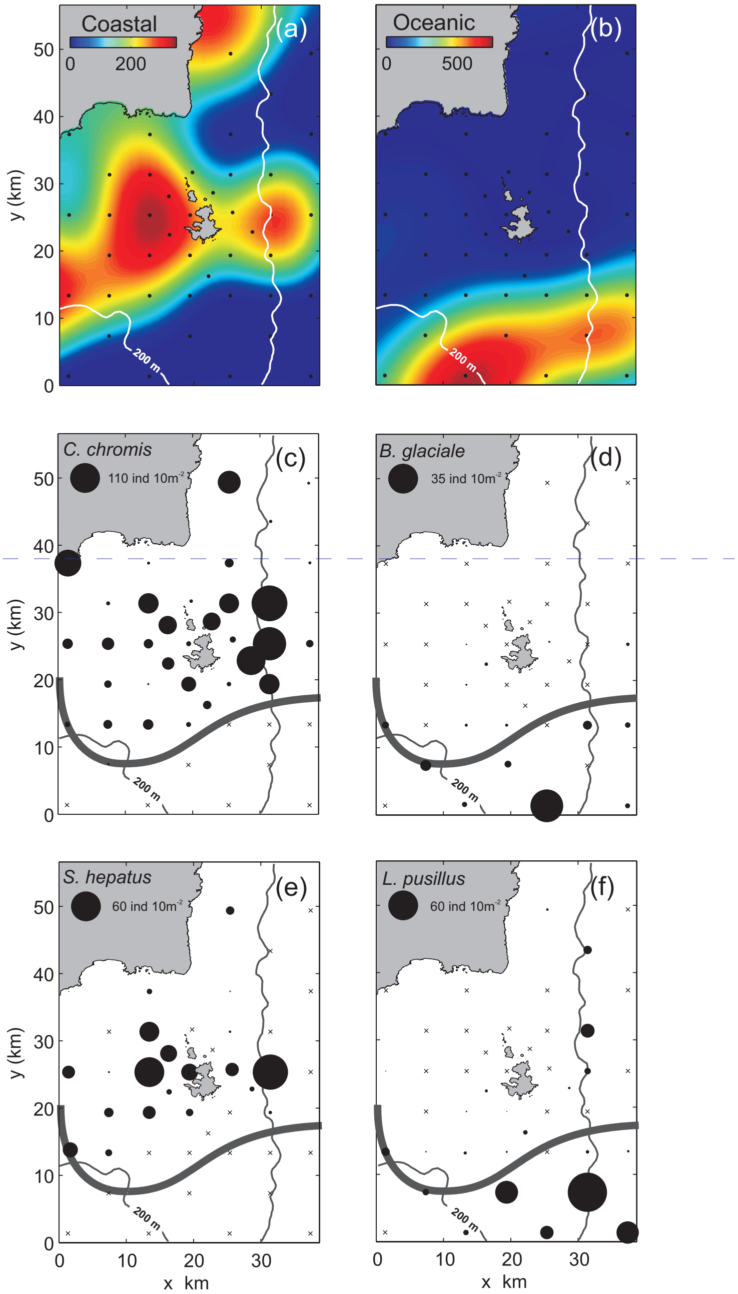

Figure 2.6. Distribution of (a) coastal and (b) oceanic fish larval species (ind. 10 m^{-2}) as clustered in Table 2.2 (groups O and C) and abundances of 2 coastal (*C. chromis* and *S. hepatus*) and 2 oceanic taxa (*B. glaciale* and *L. pusillus*). The thick gray line marks the approximate position of the front between the two water masses

Table 2.2. Description of the community structure at each predefined cluster groups, and SIMPER analysis using Bray-Curtis similarity (similar to Hellinger's distance, Borcard et al. 2011).

Taxa	Cluster O					Cluster C					Cluster D				
	H'=2.0 ± 0.52 S = 12.6 ± 4.54					H'= 3.2 ± 0.45 S = 18.9 ± 5.38					H'= 1.4 ± 0.79 S = 3.5 ± 2.12				
	A	C	s	r	%	A	C	s	r	%	A	C	s	r	%
C. chromis						47.7	100	7.7	**3.1**	14.6	7.1	100	22.9	-	38.5
C. braueri	276.8	100	16.5	**6.3**	29.6	40.3	100	6.0	**2.7**	11.5	14.9	100	36.6	-	61.5
Gobiidae						50.1	93	5.6	**2.0**	10.7					
C. julis						36.5	90	4.5	1.6	8.5					
T. draco						11.3	87	3.1	1.5	6.0					
Ophidiidae						6.7	87	2.7	1.5	5.1					
Arnoglossus						22.6	83	3.4	1.4	6.5					
S. hepatus						23.4	70	2.4	0.9	4.6					
Blenniidae						5.5	67	1.4	0.8	2.6					
Mullus spp.						7.0	67	1.4	0.8	2.7					
T.mediterraneus						6.9	60	1.2	0.7	2.3					
S. cabrilla						7.1	63	1.4	0.7	2.6					
Cepola						9.9	60	1.2	0.7	2.2					
S. aurita						25.3	57	1.3	0.6	2.5					
P. erythrinus						6.1	57	0.9	0.6	1.8					
S. saurus						4.9	53	0.8	0.6	1.6					
H. hygomii	69.8	100	9.9	**5.2**	17.7										
C. maderensis	44.9	91	7.4	1.8	13.3	9.2	60	1.0	0.7	1.9					
L. crocodilus	7.6	82	3.0	1.2	5.3										
L. pusillus	26.0	82	4.3	1.1	7.7										
B. glaciale	10.7	73	2.6	0.9	4.7										
T. alalunga	9.0	73	2.3	0.9	4.1										
L. dofleini	7.6	73	2.6	1.0	4.7										
E. encrasicolus	14.4	64	2.1	0.8	3.8	8.3	63	1.5	0.7	2.8					

Only taxa contributing >2% to within-station similarity in standardized abundance are used. For each group: H'= Shannon diversity index. S = number of species. For each species, A = mean abundance only in positive stations (ind. 10 m^{-2}, untransformed); C = constancy (% of station where the taxon appears); s = mean similarity contribution (%); r = s · SD-1 (where SD = standard deviation of s). The percentage individual contribution to within-group S is given by (%). For each group, values of r > 2 are in bold, indicating the main typifying species. Taxa are ranked approximately by the value of r in each group.

2.3.3. Observed and modeled larval dispersion

Two of the most frequent species that spawn in the shelf, *Serranus cabrilla* and *C. julis*, were selected for dispersion analysis (simulation experiments). The observed sizes, expressed as the standard length (SL) structure, of these two species are displayed in Fig. 2.7. Minimum sampled sizes were 2.0 and 1.7 mm, respectively.

The cumulative distribution revealed an inflection at approximately 6 mm SL, which in these species roughly matches the flexion size of the notochord (Bertolini et al., 1956). Notochord flexion and the concomitant development of the caudal fin are associated with important changes in larval capabilities, particularly substantial improvement in endurance swimming (Clark et al., 2005; Somarakis and Nikolioudakis, 2010). Thus, we assumed a higher capability of movement for larvae over 6 mm in size. The spatial distribution of larvae above and below this size threshold indicated that, as development progresses, larval abundance decreases, such that larger larvae would have been captured almost exclusively in the vicinity of CNP (Fig. 2.8) and at a station in the slope front (St. 31).

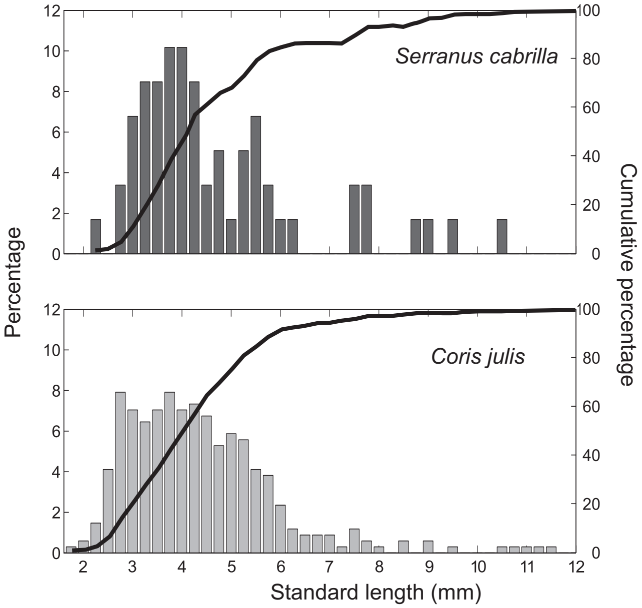

Figure 2.7. Comparison of length-frequency (bars) and cumulative frequency (line, right axis) distributions of *Serranus cabrilla* and *Coris Julis*

Current measurements (Fig. 2.2) showed that the bidirectional flows produced by ITWs dominated the dispersion dynamics of particles released in CNP. After the 10-day drifting period, the interaction between CNP and this oscillatory along-shore flow produced a pattern consistent with the observed distribution of neritic species larvae, albeit in the modeled case, accumulation occurred somewhat closer to the coast (Fig. 2.9a). A large percentage of the particles (29%) remained at a reasonable distance (<10 km) from the release area, suggesting that a number of larvae were kept very close to or within the settling region. Notable connectivity between the CNP and the coast of Mallorca was also depicted by this simulation.

In addition, the effect on advanced developmental stage larvae of a modest (5 cm s^{-1}), sustained swimming ability in the shoreward, direction was tested. These examples assumed orientated swimming, although, despite the obvious importance of orientation, it is in most cases an unproven factor. As shown in Fig. 2.9b, dispersion was notably reduced and the majority of larvae returned to the settling region in the MPA (41% of the particles remained close, i.e., <10 km from CNP).

Given the oscillatory nature of the currents, the simulation indicated that sustained swimming is not necessary for recruitment. The dispersal resulting from a swimming behavior that is activated only when currents are directed offshore was also simulated. As shown in Fig. 2.9c, this behavior, which involves swimming 46% of the time, produced similar results (37% of the particles remained close, i.e., <10 km, to CNP), but with a highly reduced energetic cost.

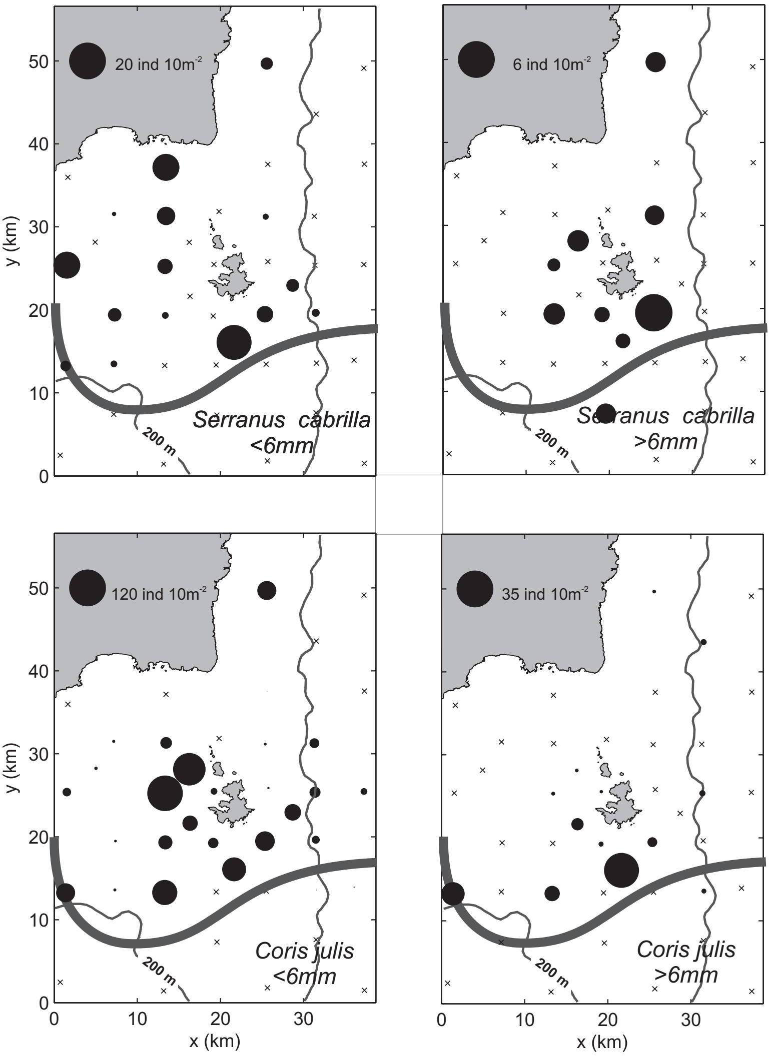

Figure 2.8. Larval abundances for <6 mm and >6mm size classes in *Serranus cabrilla* and *Coris julis*. The gray line marks the approximate position of the front between the two water masses.

2.4. DISCUSSION

Our analysis revealed that, despite being at the intersection of two oceanographic domains (coastal and oceanic), the waters around CNP provide a relatively stable ecosystem regulated by different, albeit interacting, forcings such as retention by topographically generated circulation patterns and shelf-break frontal dynamics, over which larval behavior operates. Nonetheless, the final outcome of these concurrent drivers of larval variability is species- and water mass-dependent. In the present work, two distinct, coastal and oceanic, larval fish assemblages were clearly identified. As in other studies, oceanic and neritic larval fish assemblages were delimited in analyses of the characteristics of water masses in different geographic regions (e.g., Cowen et al., 1993; Govoni, 2005; Olivar et al., 2010). However, only rarely have either the peculiarities associated with protected insular spots or their importance to conservation or fisheries been addressed with respect to temperate areas (Lopez-Sanz et al., 2009).

Although the observed coastal ichthyoplankton assemblage examined in this study was well-differentiated in terms of its structure, significant differences were observed in the spatial distribution of the different taxa (as shown in Fig.2.6). This was not only attributed to the spawning behavior of the adults (i.e., variations in spawning habitat and timing among species) but could also be due to disparities in the impact of physiological tolerances and vulnerability to predator fields on individual survival and thereby on the population size and the range of the affected species (e.g., Neill et al., 1994). Generally, retention and dispersal patterns will depend upon the equilibrium of the dynamic action of these drivers but their relative contribution may vary. For example, it is unlikely that physiological tolerances play a major role in our case because hydrographic and food sources (zooplankton) are relatively homogeneous throughout the shelf, with differences instead being attributed to variations in spawning. The results of this study, together with available information on larval recruitment to CNP (Crec'hriou et al., 2010), and the results of genetic studies (MacPherson et al., 2009) and connectivity studies (Basterretxea et al., 2012), confirm that the interaction of these drivers results in the high stability of the coastal system, which is not as open as would be anticipated given its insular nature and geographic location. Hence, we suggest that the breeding population in the MPA relies on self-recruitment for its long-term persistence, independent of other source populations along Mallorca.

As revealed by the data obtained from the moored current-meter, a main driver of larval fish self-recruitment in CNP is the along-shelf oscillatory motions, operating at scales of days, which dominate flow variability in the inner shelf. Jordi et al. (2011) showed that wind-forced Ekman transport and ITWs are responsible for a large part of this variability. This forcing is mainly barotropic and therefore does not predict larval vertical behavior for position maintenance as a major determinant of reproductive success in this region. The interaction of these frequently reversing currents (i.e., each 57 h) with CNP produces short-lived oceanographic features with biological effects hat, although they could not be spatially resolved by the present sampling, produce a bulk effect on larval retention. Consistent with our data (Fig. 2.2), the most efficient generators of trapped waves are transient alongshore winds, with this forcing having a predominant effect on shelf circulation in the down-wave direction, which is right-bounded in the northern hemisphere (Csanady, 1997). Trapped waves, while facilitating larval retention, do not appear to significantly increase phyto- or zooplankton biomass at this scale. Consequently, differences in food availability did not appear to be a major factor for the observed larval fish distributions. Although our zooplankton observations indicated a higher-than-average abundance in shelf waters, our sampling design did not permit a finer analysis of zooplankton-ichthyoplankton relationships.

Largier (2003) stated that in estimates of population- level settlement it is not the planktonic period of a single cohort that must be averaged but rather the length of all the planktonic periods of the season. For most coastal fish species resident in the Mediterranean Sea, the spawning season often spans more than 3 months (Tsikliras et al., 2010; Alvarez et al., 2012 (Chapter 1)). Therefore, despite the ephemeral nature of these circulation patterns, the integrated result is larval retention at both sides of CNP. This was the case in hydrodynamic simulations (Fig. 2.9) and it was particularly evident for indicator fish species such as *Serranus cabrilla*, whose distributions are markedly associated with the MPA. Moreover, the larvae of the selected species were found to mostly occur within 10 km of CNP. Certainly, not all these taxa follow the same larval pattern. Rather, there are likely to be differences in distributions that reflect disparities in adult ecology, larval life history or the coupling between oscillatory flow and spawning timing that provoke pulsed dispersal patterns.

A second regulator of environmental variability is the presence of boundary or upper-slope circulation. The position of the Balearic Islands, i.e., in a transition zone between different water masses, favors the persistence of slope currents and associated

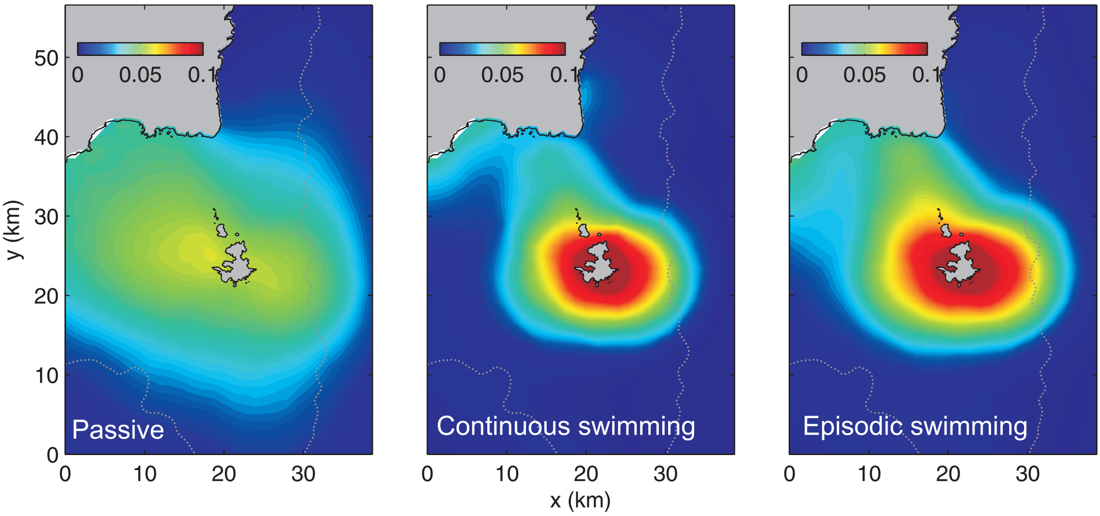

Figure 2.9. Modeled distribution of passive particles released around CNP (a). Distribution assuming 1 week of continuous shoreward larval swimming at speeds of 5 cm/s (b). Pattern assuming 1 week of larval swimming only when advected in offshore direction (c). Units are in particles per unit.

mesoscale instabilities, both of which are important in driving the exchange of water and organisms between the shelf and ocean (Sabatés et al., 2004). Also, open-sea eddies in this basin are associated with the Algerian current instability (Millot, 1985; Millot et al., 1990). These features are relatively frequent in southern Mallorca and they exert significant effects on the cross-shore distribution of shelf taxa (Alemany et al., 2006) in addition to being relevant for typically oceanic species, including tuna, as reported by Torres et al. (2011). The effect of these eddies may also differ in accordance with their origin and age. While mesoscale anticyclonic eddies that develop in the vicinity of continental margins may transport large quantities of shelf water and larvae to the open ocean (e.g., Holliday et al., 2011), the role of long-lived oceanic eddies interacting with the shelf, as in our case, has yet to be clearly defined. There is evidence that, although their trajectories can be altered, warm core oceanic eddies remain remarkably robust when interacting with shelf-slope walls (Wei and Wang, 2009). The frontal zones derived from this interaction could play an important role in the confinement of larvae in the shelf, and the seasonal and interannual variations in self-recruitment to the MPA could be related to the presence and variability of these boundary fronts, which are ultimately driven by basin-scale processes.

Since the flux along the southeastern coast of the Balearics is rather unstable, boundary currents may be characterized by marked intensity variations and even reversals, produced by meridional large-scale watermass adjustments in the Western Mediterranean. These changes in boundary flows may even be the main drivers of the anticyclonic eddies in the Algerian basin, as proposed by Testor et al. (2005), which in turn would modify their effectiveness in shelf retention.

However, the time scale of these variations is comparatively long-lived such that their overall effect on fish larval dispersal would be expected to be dependent on the relationship between their spatial persistence and the length of the fish spawning period. When the slope front is intensified, larval dispersal to offshore, unfavorable waters is dramatically reduced, as shown by the distribution of the taxa analyzed in this study, in which there was limited exchange across the front. Indeed, in our case, larvae of coastal species were very rarely observed within the eddy (<10%) and the percentage of mesopelagic taxa in shelf waters did not exceed 20%, even though most stations were located in the domain influenced by mode 2 water. This marked separation between systems not only involves fish larvae but also extends to the entire planktonic community, as commented on above. Similar shelf–ocean transitions are frequently seen in other Mediterranean areas (e.g., Sabatés and Olivar, 1996; Maso et al., 1998), yet their cross-shore location varies depending on factors such as shelf width, amount of riverine inputs or general circulation patterns (e.g., Somarakis et al., 2002). This leads to the conclusion that exchange is heavily dependent upon transport across the confluence zone rather than between water masses.

Finally, the third regulating factor of larval distribution and abundance is larval survival and the associated behavioral responses that, although not a main objective of this study, should be mentioned to understand the observed patterns and their consequences for the MPA. The eventual return of larvae into an adult area is a major requirement in coastal benthic species if persistence of the population is to be ensured; therefore, each species must employ strategies that guarantee the return of sufficient larvae. One of the difficulties in evaluating larval behavioral capabilities is that they encompass a wide variety of biophysical interactions (Paris and Cowen, 2004). This especially applies to species in oligotrophic areas, where larval assemblages are composed of a high number of species but at abundances low enough to hamper the assessment of behavioral patterns.

In contrast to other regions where relationships between spawning areas and hydrodynamics have been examined (e.g., Parrish et al., 1981), fish spawning in CNP seems to be conditioned by factors such as habitat selection rather than by adaptation to beneficial larval transport. This is attributed, among other reasons, to the variable nature of the shelf currents. Also, the response to food may well be a driver of larval behavior. However, according to our data, zooplankton abundance in this region seems to be linked to the presence of the coast, and zooplankton variability in open waters does not explain the observed fish larval patterns. In addition, evidence suggests that enhancements in primary and secondary production at the deep chlorophyll maximum generate an important food source for fish larvae (Sabatés et al., 2008). Consequently, an effect of this sort cannot be ruled out, since trophic components have been identified as essential for the structuring of fish assemblages at the beginning of the summer period (Olivar et al., 2010). Differences in the distribution between recently hatched larvae and post-flexion larvae could be a function of a better swimming capacity. In reef areas, late-stage fish larvae were shown to be strong swimmers able to maintain a speed of tenths of a cm per second for several days and to be capable of orienting themselves to their settlement habitat from considerable distances (Leis and Carson-Ewart, 1997; Stobutzki and Bellwood, 1998; Dudley et al., 2000). Although the larvae of reef fishes are much better swimmers than their non-reef relatives (Montgomery et al., 2001), the mean currents measured around CNP were a few cm s^{-1}, which is a reasonable speed attainable by many larval groups (Leis, 2007). Indeed, although the interaction between ITWs and CNP may be such that larvae are retained in the vicinity of the latter, active swimming may be necessary to facilitate significant recruitment to the coastal environment. It is plausible that, in our case, differences in the distribution of large larvae among species reflect variations in ontogenetic development but also the availability of habitat for recruitment. Similarly, differences in orientation cues can give rise to strong differences in the ability for self-recruitment.

In conclusion, the present study provides evidence for the hydrodynamic regulation of larval distribution around an MPA. Boundary circulation at the slope and oscillatory wind-induced currents interacting with the islands (CNP) are major drivers of recruitment to CNP over which specific larval behavior may operate. With some variations, this provides a stable yet dynamically regulated system that efficiently favors self-recruitment to the MPA.

ACKNOWLEDGEMENTS

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CHAPTER 3

Interaction between spawning habitat and coastally steered circulation regulate larval fish retention in a temperate Bay.

Abstract

Larval retention plays a fundamental role in the persistence of coastal fish assemblages. Here, we examine larval fish distribution and abundance patterns in Palma Bay, a large (~20 km) wind-driven microtidal bay in the southern coast of Mallorca (Spain, NW Mediterranean Sea). Larval fish assemblage structure in the bay were analyzed during July 2010 and interpreted in the context of the observed circulation patterns, adult habitat distribution and spawning traits. Acoustic Doppler Current Profiler (ADCP) observations showed the presence of retentive flow patterns in the middle of the bay enhancing local larval accumulation and self-recruitment. In consequence, larval abundances were higher in this central part of the bay (~ 40 m depth, mean abundance 607.6 ± 383 ind. 10 m^{-2}) than along the coastal fringe (< 35 m 113.7 ± 91 ind. 10 m^{-2}). Also, a multivariate predictive approach based on Redundancy Analysis (RDA) revealed differences between the larval fish assemblages in areas inside the bay, constituted by small pelagic and benthopelagic taxa (gobids, *Chromis chromis* and *Serranus hepatus*) and offshore larvae, mostly from meso and large pelagic fish. These larval fish assemblages were structured according to depth variations and zooplankton abundance, and remained relatively unmixed because of the circulation patterns in the mouth of the bay that uncouple its dynamics from along-shelf circulation. Even larvae of typically pelagic species that spawn close to the coast (*Sardinella aurita*, *Auxis rochei*) were associated with the retentive effect of the bay. Our study highlights the important role of coastal bays in the regulation of coastal fish population dynamics and as hotspots for the maintenance of diversity in the Mediterranean Sea.

3.1. INTRODUCTION

Bays, sounds, inlets and other semi-enclosed coastal geomorphological features are considered preferential areas for larval fish accumulation and retention, being important in the reproduction of local demersal species and of migrant pelagic fish that have evolved to hatch in favorable areas for growth and survival (e.g. Cushing, 1990). Retention of pelagic eggs and larvae in suitable areas for development may determine early life stage success, therefore influencing the rates of survivorship to adulthood and self-maintenance of the population (Bradbury et al., 2008). As a consequence, bays are regarded to play, through recruitment differences, a significant role in shaping the spatial distribution and population structure of organisms, as well as controlling the species diversity along the coast (e.g. Archambault and Bourget, 1999).

The spatial distribution of the larval fish populations are generally determined by a compound of factors such as spawning location of the adult, passive transport, behavior (mainly active swimming), predation and food availability (Stanley et al., 2012). During the egg and early larvae stages, the horizontal location of propagules is determined fundamentally by spawning location and physical transport processes. In many aspects, the importance of bays for larval development relies in the existence of weakened, stable and predictable marine dynamics. Likewise, the re-circulatory features within bays reduce advection and can entrap larvae reducing dispersal and favoring return to home habitat of coastal dwellers therefore strongly influencing the probability of survival of the early life stages of these organisms (e.g. Drake and Arias, 1991). The influence of terrestrial nutrient inputs through their watersheds can also be enhanced at bays sustaining increased coastal productivity (Newton et al., 2013). Moreover, reduced wave energy provides refuge and the larval settlement success is guaranteed by the quasi-continuous coastal habitat presence at relatively short distances and favorable swimming environment (Swearer et al., 1999). Moreover, these factors, including water exchange between the coastal water and the open ocean are strongly affected by their geometry and other boundary conditions.

In temperate seas, the study of early stages of fish in the coast has been traditionally approached in terms of statistical description of larval fish assemblages (herein LFAs) and their potential drivers (Sabatés et al., 2003; Azeiteiro et al., 2006; Borges et al., 2007; Basterretxea et al., 2013, Chapter 2; Kent et al., 2013; Pattrick et al., 2013). Small-scale empirical information on LFA also exists for estuaries (e.g. Hoffmeyer et al., 2009; Kruger and Strydom 2010), isolated oceanic islands (Macedo-Soares et al., 2012) and coastal lagoons (e.g. Pérez-Ruzafa et al., 2004). However, the assemblage dynamics (and specifically the transport effects on LFA) in temperate nearshore areas have been studied less frequently, in part owing to the need for high resolution models. It has been studied for alongshore rocky nearshore LFAs (Roussel et al., 2010) but not in complex temperate areas, where small scale variability in topographic and oceanographic features (e.g. coastal gyres) may influence the metapopulation connectivity and dynamics (Di Franco and Guidetti, 2011; Garavelli et al., 2014; Rogers et al., 2014).

Larval fish assemblages of Mediterranean bays are typically composed by resident species such as gobids, labrids and sparids, preferentially spawning in spring and summer (Tsikliras et al., 2010; Álvarez et al., 2012, Chapter 1). In these areas, ichthyoplankton diversity is generally high and bays are also regarded as important nursery areas for several marine organisms. Despite their ecological importance, the contribution of coastal embayments to the maintenance of early life stages of coastal resident fish is only poorly known. Palma Bay (Mallorca Island) is a rather productive coastal zone in the otherwise oligotrophic waters of the Western Mediterranean (Jordi et al., 2009a). Major circulation patterns in this coastal area can be explained in terms of the interaction between wind driven currents and oscillatory motions induced by the island-scale flow, which interact with topographic constrains that frequently generate submesoscale coastal gyres (Jordi et al., 2011). Reduced mean flows during summertime potentially favour retention both of eggs and larvae from fish assemblages inhabiting the bay (Hernández-Carrasco et al., 2013). Onshore surface transport induced by diurnal sea breeze which is intensified in the bay (Jordi et al., 2011), also represents a potential phenomenon affecting the recruitment of organisms spawned in nearby coastal areas and transported to the bay. The recognition of a double functional mechanism that both increases local recruitment but also incorporates larvae dispersed from other areas is a critical aspect for the understanding of the ecological role of bays in the persistence and connectivity of coastal fish populations (Stanley et al., 2012).

Previous works in this region anticipated, through numerical modelling, that Palma Bay is a highly retentive area in which maintenance of local fish populations could largely rely upon self-recruitment (Basterretxea et al., 2012); however, the mechanisms though which this retention takes place have not been addressed to date. Determining the role of bays in the reproductive cycle of various fish species, and the particular function of temperate microtidal coastal zones, is necessary to accurately define and quantify the mechanisms that promote larval retention. The hypothesis to be tested in the present work is that mechanisms regulating summer larval fish retention in a Mediterranean Bay can be attributed to an identifiable combination of biological and physical mechanisms.

3.2. MATERIAL AND METHODS

3.2.1. Study Area

Palma Bay is approximately 20 km wide and is located in the southern coast of Mallorca Island between Punta Cala Figuera and Cabo Blanco (Fig. 3.1). Depth smoothly varies from the shore to ~50 m and the bathymetry nearly parallels the coastline. The bay experiences a microtidal regime (amplitude up to 20 cm) and is opened to seas from the southwest (Basterretxea et al., 2004). Meteorological conditions in Mallorca during summer are characterized by stability and warm temperatures; in July and August, the weather is often almost identical from one day to the next, with scarce rainfall and weak winds dominated by sea breeze with intensities rarely exceeding 8 m s^{-1} (Ramis et al., 1990). Even though there are no permanent water courses discharging in the bay, nearshore productivity is sporadically increased by torrent outflow during occasional heavy rain episodes and by groundwater discharges along the shoreline (Rodellas et al., 2014).

The shallow areas of the bay contain extensive seagrass meadows that extend down to 34 m interspersed with patchy sand and rocky bottoms (Gazeau et al., 2005; March et al., 2013). This habitat shelters a large fraction of the spawning coastal fish usually found in the adult fish surveys (e.g. Sparidae, Labridae and Serranidae; García-Rubíes and McPherson 1995; Deudero et al., 2008). Most of these fish species remain

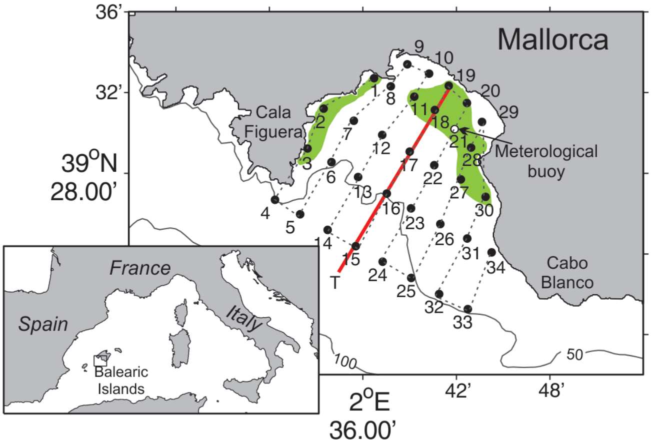

Figure 3.1. Bathymetric map of the study area indicating the presence of seagrass covered bottoms (green) and zooplankton sampling points. CTD casts were obtained along T transect (5 stations, red line). The ADCP track is indicated by the dashed line. The position of the meteorological buoy is also indicated.

sedentary throughout their adult life and dispersal is reduced to their pelagic larval phase (e.g. March et al., 2010, 2011; Palmer et al., 2011).

3.2.2. Field measurements

Sampling at Palma Bay (Fig. 3.1) was conducted from 21-24 July 2010 onboard the IMEDEA coastal research vessel, coinciding with the period of maximum abundance and diversity of coastal fish larvae in Mallorca (Álvarez et al., 2012, Chapter 1). A spatial survey consisting of a grid of 34 biological stations covering the bay was sampled for zooplankton between July 22 and 23 (see below in this section). The grid was designed to enable sampling in a quasi-synoptic fashion, with a slightly increased spatial resolution at the inner part of the bay (distance between stations varying 1 to 3 nm).

Bounding the biological sampling period (days 21 and 24), two additional surveys were conducted to characterize the coastal circulation patterns. Temperature, currents and backscattering values were recorded with a 1200 kHz RDI Workhorse Sentinel Acoustic Doppler Current Profiler (ADCP) mounted on an Endeco/YSI 703 V-Fin towed along the stern of the vessel, which followed the transect in Fig. 3.1. Currents and backscattering values were despiked and averaged in 1 min intervals and 1 m depth bins from 6 to 17 m during post processing.

Meteorological data (wind and atmospheric temperature at 10 minute intervals) was obtained from an oceanographic buoy located within the survey area (Fig. 3.1). Near surface (1.5m) winds were corrected to u10 following Large and Pond (1981). Satellite daily maps for sea surface temperature and chlorophyll in the Balearic Sea during the survey were obtained from MODIS-A (MODerate Resolution Imaging Spectroradiometer-Aqua), MODIS-T (MODIS-Terra) and MERIS (Medium Resolution Imaging Spectrometer) sensors from NASA›s OceanColor Web (http://oceancolor.gsfc.nasa.gov/) and averaged for the sampling period (days 14 to 26 July 2010).

Conductivity, temperature and depth (CTD) profiles were obtained along an inshore-offshore transect (5 stations, Fig. 3.1) with a Seabird SBE-25 CTD on day 22 concurrently with biological sampling.

Zooplankton and ichthyoplankton sampling was conducted on the 34 stations (Fig. 3.1) by means of double oblique bongo hauls, with a 40 cm mouth opening, 335 µm nets and a total net surface designed for green waters to prevent clogging (Smith et al., 1968). A mechanical flowmeter (General Oceanics) was attached at the center of each net mouth to estimate filtered volumes. The 40 cm diameter was considered appropriate to collect the smallest ichthyoplankton stages. The depth of the selected stations ranged from 10.5 to 67 m. In order to filter a similar water volume (~100 m^3) at all stations, the hauls were performed from surface to 2 m above the bottom at the deeper stations and through a series of up and down tows until a 5 min fixed period for the shallower stations. On board, samples were immediately fixed in 4% buffered formalin for preservation. Once in the laboratory, one of the bongo net samples for each station was used to determine the mesozooplankton dry weight (only the fraction above 335 μm, after removing fish and jellyfish) following Lovegrove (1966). Values were standardized to mg m^{-3} and represent a relatively large mesozooplankton fraction. From the other bongo sample, eggs and fish larvae were sorted and identified to the lowest possible taxonomic level under a stereomicroscope. Abundances were transformed to individuals per 10 m^2 of seawater (ind. 10 m^{-2}).

Two abundant taxa presenting different adult habitats (*Chromis chromis* and *Sardinella aurita*) were selected and classified according to pre-flexion, flexion or post-flexion stage to further inspect environmental drivers with respect to pelagic drift time. Each of the individuals was measured to the nearest 0.1 mm.

3.2.3. Derived environmental variables

The obtained currents from ADCP for the two surveys were decomposed in principal modes through Empirical Orthogonal Function (EOF) analysis. The depth-averaged currents for the two surveys are considered as Mode 0. The first two modes (Modes 1 and 2) explain 84% of the currents variability. We use these three modes as explanatory variables to determine relationships between transport processes and larval locations (see further in the text).

One environmental variable related directly or indirectly to almost all predictors of spawning habitat in fronts and gyres is the dynamic height (Asch and Checkley, 2013). In studies close to the coast, it is not adequate to use dynamic height as a descriptor of fronts and gyres because the effect of low depth. Therefore we used vorticity (see further in the text) and its sign to account for retention associated to small-scale gyres. Vorticity was calculated from the ADCP derived principal modes, following:

$$\mathbf{VOR= (\partial v/\partial x - \partial u/\partial y),}$$

Where u and v are the horizontal currents for the x and y depth level wanted. Vorticity values (s^{-1}) were normalized by the Coriolis parameter (f).

3.2.4. Statistical analyses

The statistical approach was based on i) an exploratory community ordination analysis based on cluster analysis and group classification, and ii) a Redundancy Analysis (RDA) to explain how environmental variables explain the taxonomic distribution (Borcard et al., 2011). Firstly, a raw taxonomic matrix was built based on fourth-root transformed abundances of the taxonomical groups discarding rare taxa (appearing in <10% of the samples; all were < 0.05 % of the total abundance). A cluster analysis (UPGMA) on the Bray-Curtis similarity matrix was first conducted. Coherent groups from the cluster were defined following permutational tests (SIMPROF test through 10 000 permutations, p<0.05, Clarke et al., 2008). The resulting groups were analysed for species composition and species contribution to within-group similarities through SIMPER analysis (Clarke & Ainsworth, 1993) using Primer v.6.

To explore the possible influence of environmental variables (predictive environmental matrix) on LFAs (response matrix, larval fish taxa) we used a multivariate predictive approach based on RDA) (Legendre and Gallagher 2001; Borcard et al., 2011). For the RDA, a distance matrix was built using Hellinger's distance, which produces similar results to Bray-Curtis similarity but it permits modelization through PCA and RDA analyses (Legendre and Gallagher 2001).

The RDA included only significant variables selected through forward method (Borcard et al., 2011) and the existence of spatial autocorrelation was assessed through Multiscale Ordination analysis (MSO) (Wagner, 2004). The environmental matrix included the following variables: depth (D, m), sea surface temperature from ADCP sensor (SST, 6m, °C), absolute velocity of the current modes 0, 1 and 2 (VM0, VM1, VM2 cm s^{-1}), vorticity associated to these modes (VOR0, VOR1, VOR2, f-normalized) and mesozooplankton biomass determined at the laboratory (MZB, mg m^{-3}). We also included the presence or absence of seagrass meadows (POS; Fig. 3.1), a key habitat for many local species that may condition spawning areas (Deudero et al., 2008). These values were extracted from March et al. (2013). All analyses were performed in R package (v.2.14.2., R core Team).

3.3. RESULTS

3.3.1. Environmental scenario

Atmospheric conditions recorded by the meteorological buoy during July are shown in Figure 3.2 (a and b). Temperatures reveal a regular, wind controlled cycle, with temperatures oscillating between 23 and 28 ºC. A well stablished breeze regime occurred throughout the study period with winds from the southwest reaching amplitudes below 8 m s^{-1} at noon and decaying at night to weak northeasterly land-breeze. Temperatures along the inshore-offshore transect were horizontally uniform (Fig. 3.2c). The water column structure showed a well-marked seasonal thermocline around 15 m depth that separated surface waters (~27.5 ºC) from deeper waters (<18.5 ºC). Salinity was rather homogeneous in the mixed layer although the offshore stations displayed slightly lower salinities suggesting higher evaporation within the bay (Fig. 3.2d). These conditions were consistent with the satellite depicted SST in the region which reveals a weak cooling (~ 1ºC) off the southern coast of Mallorca but not particularly relevant oceanographic features in the area (Fig 3.3). Likewise, ocean color data shows marked phytoplankton biomass decline off the Bay where chlorophyll concentrations reduce to <0.1 mg m^{-3}.

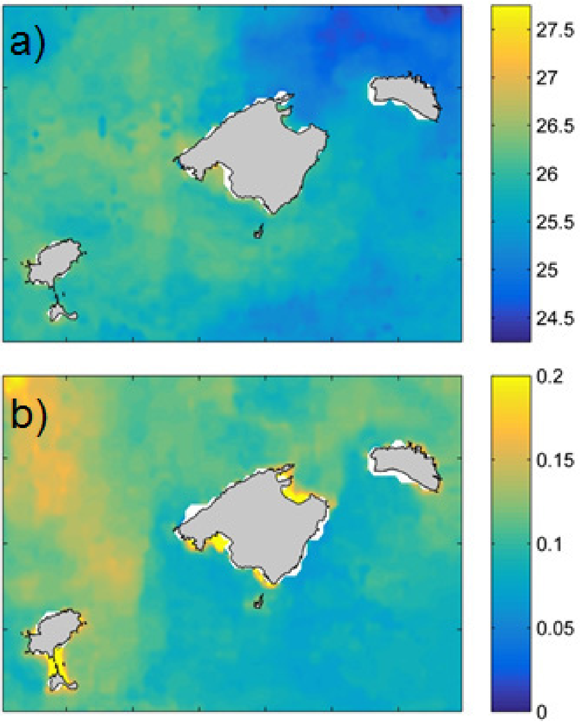

Figure 3.3. Satellite derived mean SST (ºC) and chlorophyll (mg m^{-3}). Average for the period July 14 to 26.

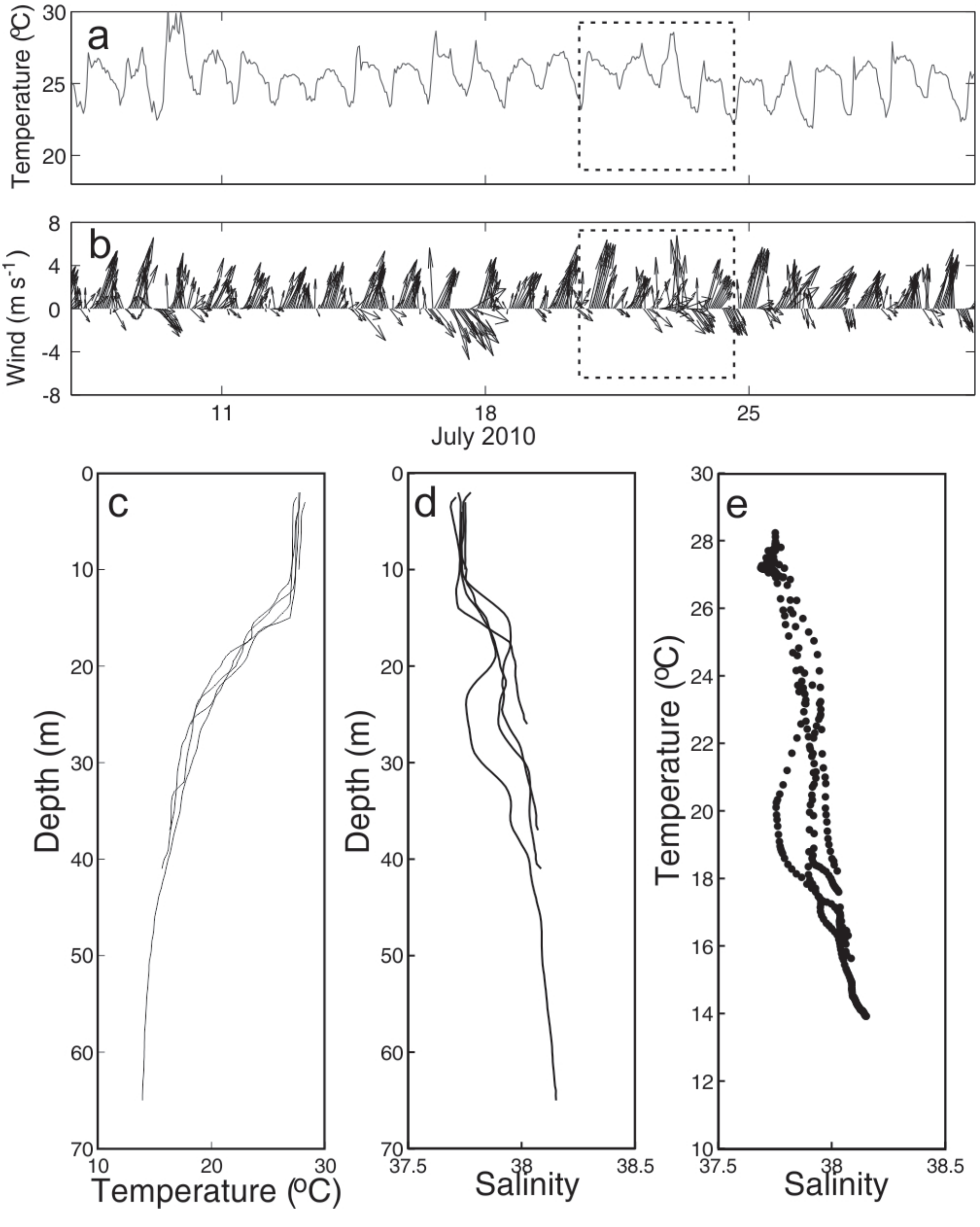

Figure 3.2. Meteorological (a and b) and hydrographic conditions (c, d and e) in Palma Bay during July. The dashed line indicates the dates of the survey. (a) Hourly atmospheric temperature (ºC); b) hourly U10 wind speed and direction. Vertical profiles of c) temperature (ºC), d) salinity from the CTD transect T (Stations 15 to 19; see Fig. 3.1), and e) corresponding T-S diagram.

The three principal modes derived from the ADCP currents modes show the circulation of offshore waters in the outer part of the bay and the interaction with coastal waters (Fig. 3.4). Mode 0 (the depth-averaged currents for the two surveys) represents a large counter-clockwise gyre located in the mid-west section of the bay and some exchange with offshore waters through two current systems. This mode, consisting in a recirculation pattern in about the middle of the bay and compensatory flows out of it, is consistent with the response of the Bay to breeze forcing obtained by Werner et al. (1993) through numerical modeling. In mode 1 (explaining 55% of the variability), offshore waters penetrate into the bay from the southeast boundary bifurcating into two main branches as they progress inshore. Mode 2 (explaining 31% of the variability) mainly shows the deflection of alongshelf circulation in the mouth of the bay, and weak currents inside the bay. Vorticity values associated with these modes were positive for counter-clockwise gyres and negative for the clockwise ones.

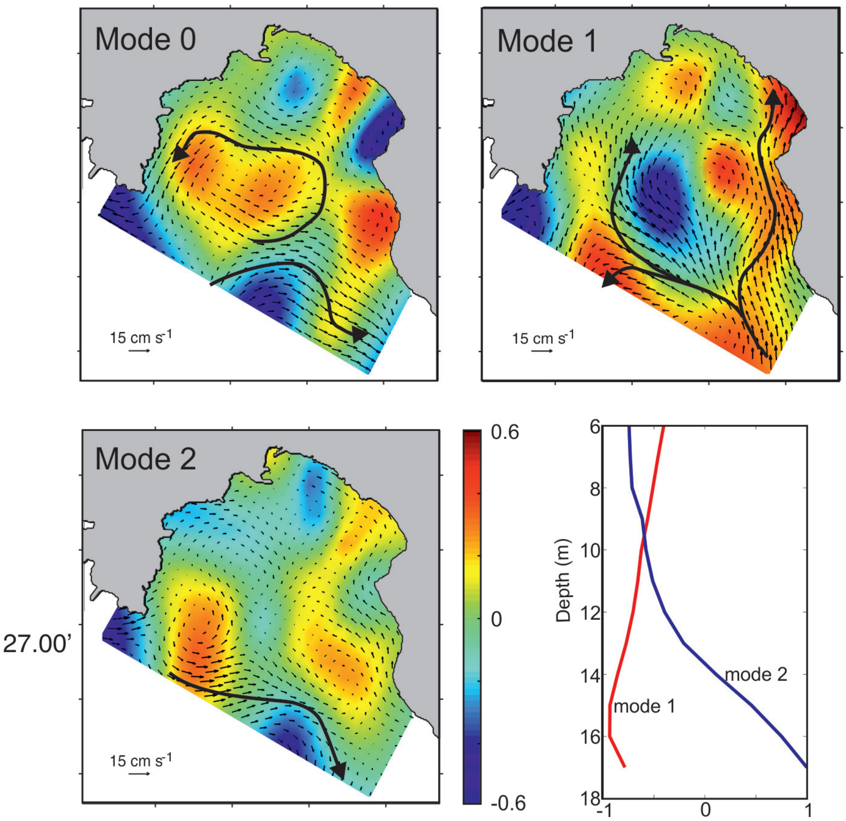

Figure 3.4. Maps: mean current (cm s^{-1}) obtained by EOF analysis of the two ADCP surveys carried out. The main flow paths are highlighted with thick lines. Colors indicate the vorticity (s^{-1}) associated to each mode. Arrow sizes are proportional to current velocities. Bottom-right graph: Vertical profile of mode 1 and mode 2 currents

The vertical distribution of current modes 1 and 2 for the first ADCP survey is also shown in Figure 3.4. Mode 1 currents displayed a highly barotropic response whereas mode 2 currents reversed with depth. Since mode 2 currents were relatively weak inside the bay, we assume that currents in the bay were essentially barotropic, at least above the thermocline. Both modes reversed in sign for the second survey while maintaining the same structure. This is attributed to a shift in the direction of the mean flow produced by island trapped waves which flow parallel to the coast and a periodicity of ~60 hours (Jordi et al., 2009b), approximately the time lag between both surveys.

The distribution of mesozooplankton biomass ranged from 0.9 to 9.2 mg m^{-3} (Fig. 3.5) Maximum values corresponded to the inner most part of the bay in the area influenced by the Port of Palma. A secondary maximum was observed at the middle of the bay.

3.3.2. Larval assemblage abundance and composition

A total number of 6949 fish larvae were collected, from which 87.4% could be classified into 61 taxa: 15 to the family level, 7 to genus and 39 to species. Generally, the stations in the center of the bay presented the higher values of coexisting taxa (up to 28 different taxa) and abundance (max. 1699 ind. 10 m^{-2}).

The most abundant taxa (Table 3.1) corresponded to epipelagic species like *Sardinella aurita* (19.55 % of the total abundance, TA) and *Auxis rochei* (15.96 % TA); benthopelagic species (Gobiidae family; 10.58 % TA and *Chromis chromis*; 4.35 % TA); and the mesopelagic species *Cyclothone braueri* (8.79 % TA). The most ubiquitous taxa, present in more than the 90 % of the stations, were Gobiidae spp. but *Trachurus mediterraneus* (85.29%)*, C. chromis* (85.29 %) and *S. aurita* (82.35 %) also occurred in most of the stations.

In general, the highest abundances and number of taxa were found in the center of the bay (Fig. 3.5). The eggs also appeared in a central position. The taxa were grouped depending on the habitat of their adults following Table 3.2, in Mesopelagic, Epipelagic and Benthopelagic. The mesopelagic group and, particularly, its most abundant taxa (*C. braueri* and *Ceratoscopelus maderensis*) occupied the offshore waters (depth > 50 m, Fig. 3.6). The epipelagic taxa (excluding *S. aurita*) followed a similar distribution to mesopelagics but with a higher occupancy of mid-bay areas. *S. aurita* was widely distributed in the bay except for some near shore areas whereas *A. rochei* remained in offshore waters (Fig. 3.6). The highest abundance of benthopelagic taxa appeared mostly in the center of the bay, with a small peak in the vicinity of Punta Cala Figuera (western area). Sparidae spA and *Symphodus* spp followed a different distribution than the other benthopelagic species, occupying nearshore areas.

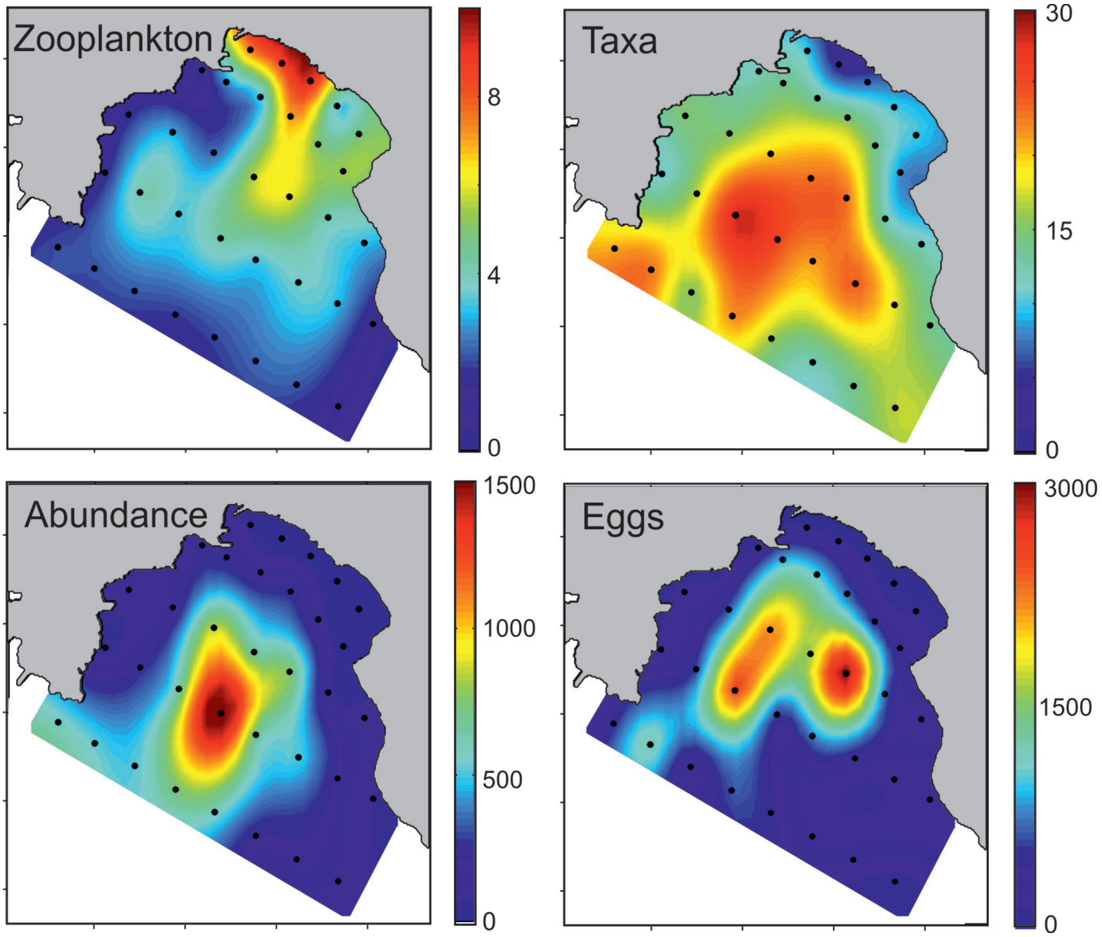

Figure 3.5. Mesozooplankton biomass (dry weight, mg m^{-3}). Horizontal distribution of number of taxa (S), total abundance of fish larvae (N, ind. 10m^{-2}) and total abundance of eggs (eggs 10m^{-2}).

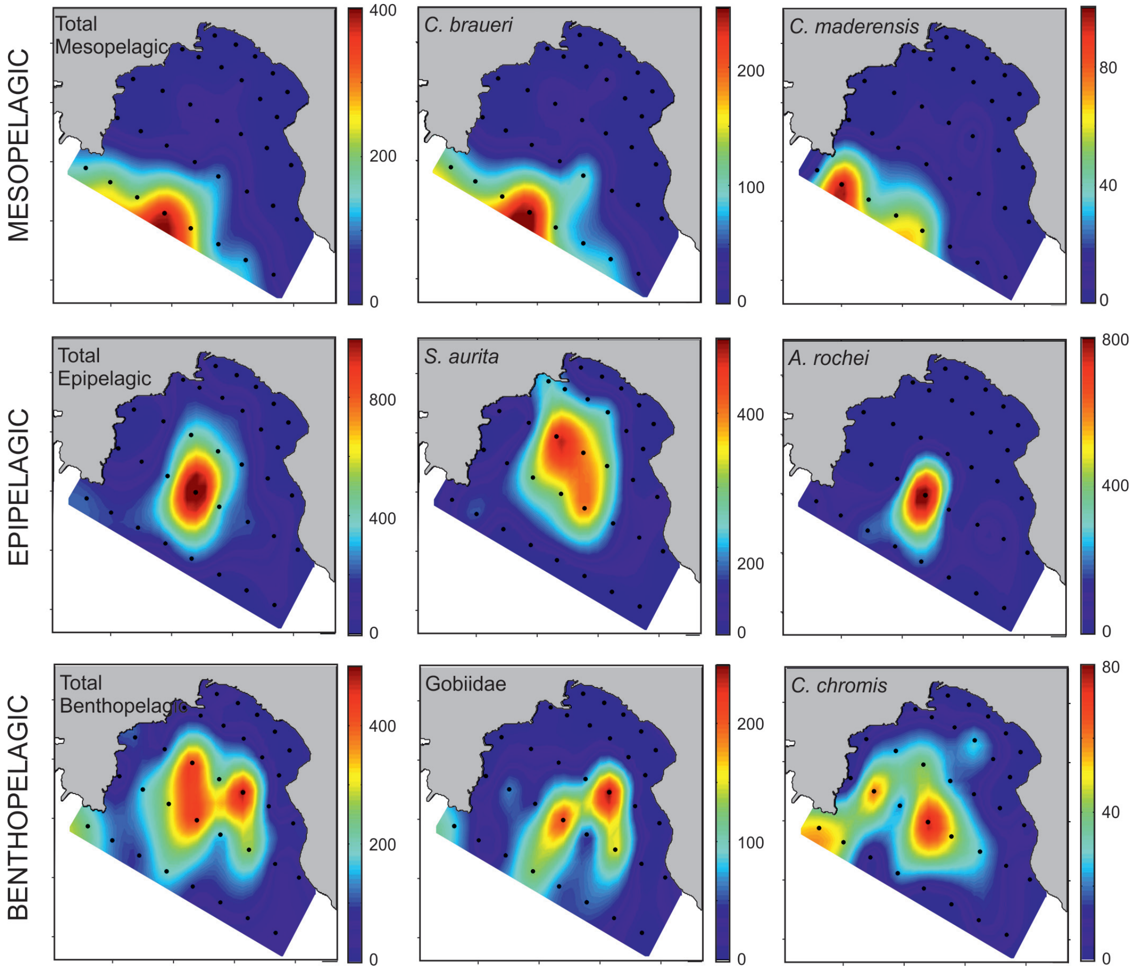

Figure 3.6. Horizontal distribution of the taxa abundances (ind. $10m^{-2}$) including the total numbers and the most abundant taxon of each group, ordered by the type of adult habitat (Mesopelagic, Epipelagic and Benthopelagic).

Table 3.1. Taxa composition. RDA code: codes used in the RDA analyses (only taxa fitting the a priori criteria were included); A: Mean abundance; SD: Standard deviation of A; A+: Mean abundance in the positive stations; SD+: Standard deviation of A+; F%: percentage of the stations where the taxa is present; %A: Percentage of the total abundance, *: rare taxa (%A < 0.05%) discarded for the multivariate analyses. All abundances expressed: ind. 10 m^{-2}

Taxa	**RDA code**	**A**	**SD**	**A+**	**SD+**	**F%**	**%A**
Apogonidae							
Apogon imberbis	Aimb	0.39	1.24	3.33	1.98	11.76	0.10
Argentinidae							
Glossanodon leioglossus		0.05	0.31	1.83		2.94*	0.01
Other Argentinidae spp		0.05	0.30	1.78		2.94*	0.01
Atherinidae							
Atherina boyeri		0.03	0.19	1.10		2.94*	0.01
Belonidae							
Cheilopogon heterurus		0.06	0.36	2.12		2.94*	0.02
Blenniidae							
Blennius ocellaris		0.05	0.31	1.80		2.94*	0.01
Blenniidae spp	Blen	4.52	9.04	7.69	10.79	58.82	1.15
Bothidae							
Arnoglossus spp.	Arno	1.89	3.89	4.95	5.03	38.24	0.48
Bothus podas	Bpod	0.51	1.14	2.50	1.16	20.59	0.13
Callionymidae							
Callyonimidae spp	Call	1.53	2.19	3.06	2.21	50.00	0.39
Carangidae							
Trachurus mediterraneus	Tmed	10.56	15.18	12.38	15.75	85.29	2.69
Seriola dumerili		0.03	0.18	1.08		2.94*	0.01
Other Carangidae spp		0.03	0.18	1.08		2.94*	0.01
Carapidae							
Carapus acus		0.05	0.27	1.57		2.94*	0.01
Centracanthidae							
Spicara smaris	Ssma	0.22	0.63	1.89	0.32	11.76	0.06
Cepolidae							
Cepola rubescens		0.11	0.46	1.92	0.12	5.88*	0.03
Clupeidae							
Sardinella aurita	Saur	76.82	102.59	93.28	106.16	82.35	19.55
Coryphaenidae							
Coryphaena hippurus		0.16	0.74	2.72	2.06	5.88*	0.04
Dactylopteridae							
Dactylopterus volitans	Dvol	1.49	4.40	4.59	6.94	32.35	0.38
Engraulidae							
Engraulis encrasicolus	Eenc	2.82	4.68	6.00	5.28	47.06	0.72
Gadidae							
Gadidae spp	Gadi	0.40	0.91	2.27	0.65	17.65	0.10
Gobiesocidae							
Lepadogaster sp		0.06	0.35	2.03		2.94*	0.02
Other Gobiesocidae spp		0.17	0.68	2.81	0.72	5.88*	0.04
Gobiidae							
Gobiidae spp	Gobi	41.57	62.19	44.17	63.24	94.12	10.58
Gonostomatidae							
Cyclothone braueri	Cbra	34.54	58.84	48.93	65.06	70.59	8.79
Labridae							
Coris julis	Cjul	1.75	3.44	4.26	4.31	41.18	0.45
Symphodus spp.	Symp	4.00	7.02	7.56	8.20	52.94	1.02
Other Labridae spp	Labr	0.25	0.74	2.15	0.71	11.76	0.06
Mugilidae							
Mugilidae spp	Mugi	0.81	1.59	2.74	1.84	29.41	0.21
Mullidae							
Mullus barbatus	Mbar	2.48	5.74	7.03	8.00	35.29	0.63
Muraenidae							
Muraenidae spp		0.07	0.39	2.30		2.94*	0.02

Table 3.1. (*Continued*)

Taxa	**RDA code**	**A**	**SD**	**A+**	**SD+**	**F%**	**%A**
Myctophidae							
Hygophum spp	Hygo	6.42	17.58	19.86	26.95	32.35	1.64
Ceratoscopelus maderensis	Cmad	11.75	21.65	21.02	25.56	55.88	2.99
Lampanyctus crocodilus	Lcro	0.83	2.76	7.05	5.02	11.76	0.21
Lampanyctus pusillus		0.35	1.30	3.93	2.57	8.82*	0.09
Ophididae							
Parophidion vassali	Pvas	1.49	2.93	4.61	3.54	32.35	0.38
Paralepididae							
Lestidiops jayakari	Ljay	0.54	1.28	3.06	1.26	17.65	0.14
Phosichthyidae							
Vinciguerria attenuata		0.05	0.31	1.83		2.94*	0.01
Pomacentridae							
Chromis chromis	Cchr	17.08	20.16	20.02	20.45	85.29	4.35
Sciaenidae							
Sciaena umbra		0.12	0.47	1.96	0.23	5.88*	0.03
Scombridae							
Auxis rochei	Aroc	62.72	168.61	82.02	189.42	76.47	15.96
Euthynnus alletteratus	Eale	0.76	2.60	4.31	5.12	17.65	0.19
Thunnus alalunga	Tala	2.70	6.36	9.18	9.06	29.41	0.69
Thunnus thynnus	Tthy	0.85	2.21	4.13	3.31	20.59	0.22
Scophthalmidae							
Lepidorhombus boscii	Lbos	0.45	1.21	2.53	1.84	17.65	0.11
Scorpaenidae							
Scorpaena porcus		0.21	0.75	2.34	1.30	8.82*	0.05
Other Scorpaenidae spp		0.05	0.30	1.78		2.94*	0.01
Serranidae							
Anthias anthias		0.03	0.18	1.06		2.94*	0.01
Serranus hepatus	Sheo	6.50	10.79	8.18	11.55	79.41	1.65
Serranus spp.	Serr	5.37	9.52	9.12	11.02	58.82	1.37
Soleidae							
Soleidae spp		0.16	0.55	1.87	0.44	8.82*	0.04
Sparidae							
Diplodus spp.	Dipl	2.76	11.26	18.77	25.89	14.71	0.70
Pagrus pagrus	Ppag	1.32	2.30	3.75	2.44	35.29	0.34
Sparidae sp A	SpaA	5.61	9.38	11.92	10.64	47.06	1.43
Other Sparidae spp	Spar	4.42	7.65	7.91	8.84	55.88	1.12
Sphyraenidae							
Sphyraena sphyraena	Ssph	11.17	54.45	37.98	98.68	29.41	2.84
Trachinidae							
Trachinus draco	Tdra	2.63	5.31	5.96	6.72	44.12	0.67
Other Trachinus sp.		0.06	0.36	2.09		2.94*	0.02
Triglidae							
Triglidae spp	Trig	0.50	1.22	2.44	1.62	20.59	0.13
Uranoscopidae							
Uranoscopus scaber		0.18	0.77	3.06	1.34	5.88*	0.05
Xiphiidae							
Xiphias gladius		0.05	0.31	1.80		2.94*	0.01

Table 3.2. Classification, adult habitat, egg development and summer presence of adults in P. oceanica meadows. Where: RDA: Code used for the RDA biplot (Fig. 3.8); C: Classification of taxa used throughout this work. The taxa were assigned to three categories according to their habitat when adults: E: Epipelagic (small pelagic, medium pelagic & large pelagic); B: Benthopelagic (demersal shelf/slope) and M: Mesopelagic (meso- and bathypelagic); Egg development and Typical adult substratum described by (1): Whitehead et al (1986). Summer presence of adults in P. oceanica meadows observed by (2): Deudero et al. 2008. Young Pos: Young individuals found on *P. oceanica*.

Taxa	**RDA code**	**C**	**Eggs development (1)**	**Typical habitat(1)**	**Summer presence (2)**	**Young Pos**
Anthias anthias		B	pelagic	sand and mud bottom	-	
Apogon imberbis	Aimb	B	Males buccal cavity	muddy or rocky bottoms and caves	x	-
Arnoglossus spp.	Arno	B	pelagic	mixed or muddy bottoms.	-	-
Atherina boyeri		E	fixed: plant or stone	water column	-	-
Auxis rochei	Aroc	E	pelagic	water column	-	-
Blenniidae spp	Blen	B	male guarded	depending on sp	-	-
Blennius ocellaris		B	male guarded	hard bottoms	-	-
Bothus podas	Bpod	B	-	sandy and muddy bottoms	x	-
Callyonimidae spp	Call	B	pelagic	sandy bottoms	-	-
Carapus acus		B	pelagic	comensal in holothurians	-	-
Cepola rubescens		B	pelagic	muddy sand bottom	-	-
Ceratoscopelus maderensis	Cmad	M	pelagic	water column	-	-
Cheilopogon heterurus		E	pelagic	water column	-	-
Chromis chromis	Cchr	B	nested on rock or sand	rocky reefs or above seagrass meadows	x	-
Coris julis	Cjul	B	pelagic	near rocks and eelgrass beds.	x	-
Coryphaena hippurus		E	pelagic	water column	-	-
Cyclothone braueri	Cbra	M	-	water column	-	-
Dactylopterus volitans	Dvol	B	-	sand, mud or over rocks in sandy areas	-	-
Diplodus spp.	Dipl	B	-	*seagrass,* sandy bottoms.	-	x
Engraulis encrasicolus	Eenc	E	pelagic	water column	-	-
Euthynnus alletteratus	Eale	E	pelagic	water column	-	-
Gadidae spp	Gadi	B	pelagic	depending o sp	-	-
Glossanodon leioglossus		M	-	near bottom	-	-
Gobiidae spp	Gobi	B	male guarded	high diversity	-	-
Hygophum spp	Hygo	M	-	water column	-	-
Lampanyctus pusillus		M	-	water column	-	-
Lampanyctus crocodilus	Lcro	M	-	water column	-	-
Lepadogaster sp		B	guarded by parent/s	-	-	-
Lepidorhombus boscii	Lbos	B	-	soft bottoms	-	-
Lestidiops jayakari	Ljay	M	-	water column	-	-
Mugilidae spp	Mugi	B	pelagic	over sand or mud bottom	-	-
Mullus barbatus	Mbar	B	-	gravel, sand and mud bottoms	-	-
Muraenidae spp		B	-	holes, under rocks or corals	-	-
Pagrus pagrus	Ppag	B	pelagic	rock, rubble, or sand bottoms. *s*	-	x
Parophidion vassali	Pvas	B	pelagic (gelatinous mass)	demersal	x	-
Sardinella aurita	Saur	E	pelagic	watercolumn	-	-
Sciaena umbra		B	-	rocky and sandy bottoms,	x	-
Scorpaena porcus		B	-	rocks and algae	x	-
Seriola dumerili		E	pelagic	watercolumn	-	-
Serranus hepatus	Sheo	B	-	seagrass, sand, mud and rocks	x	-
Serranus spp.	Serr	B	pelagic	rocks, *Posidonia* , sand & mud bottoms	x	-

Table 3.2. *(Continued)*

Taxa	**RDA code**	**C**	**Eggs development** (1)	**Typical habitat**(1)	**Summer presence (2)**	**Young Pos**
Soleidae spp		B	pelagic	on muddy bottoms	-	-
Sparidae sp A	SpaA	B	pelagic	over rock, rubble, or sand bottoms	-	-
Sparidae spp	Spar	B	pelagic	over rock, rubble, or sand bottoms	x	-
Sphyraena sphyraena	Ssph	E	-	water column	-	-
Spicara smaris	Ssma	B	nests in sandy bottoms	*Posidonia* beds and muddy bottoms	x	-
Symphodus spp.	Symp	B	nest of seaweed	rocks or eel-grass beds	x	-
Thunnus alalunga	Tala	E	pelagic	water column	-	-
Thunnus thynnus	Tthy	E	pelagic	water column	-	-
Trachinus draco	Tdra	B	pelagic	sandy, muddy or gravelly bottoms	-	-
Trachurus mediterraneus	Tmed	E	pelagic	watercolumn	-	-
Triglidae spp	Trig	B	pelagic	sand, muddy sand or gravel bottoms	-	-
Uranoscopus scaber		B	pelagic	buried in the sand or mud	-	-
Vinciguerria attenuata		M	-	water column	-	-
Xiphias gladius		E	pelagic	watercolumn	-	-

Cluster analysis of the abundance matrix (Fig. 3.7a) resulted in two groups of stations at 40% similarity. One of the groups could be significantly split in two sub-groups cut at 55% similarity according to simproof test.

The contribution of the different taxa to the grouping of stations from the taxa cluster (SIMPER test) is displayed in Table 3.3 and the distribution pattern of the cluster groups is shown in Fig. 3.7b. From the 3 assemblages differentiated by the Cluster, the first group (a1) comprised 7 offshore stations with an average similarity in taxa composition of the 62.8 %. This group was mainly characterized (displaying Sim/SD>2) by the presence of mesopelagic species: *C. braueri,* C. *maderensis* and *Hygophum* spp. The epipelagics *A. rochei* and *Thunnus alalunga* and the benthopelagics *Serranus hepatus* and the Gobiidae family were also representative of the group. *C. braueri* was also present in group a2, formed by 10 stations located between the 35 and the 50 m isobath with an average similarity of 62.8 %. This group also included *A. rochei*, the Gobiidae family and *C. chromis*. Although not characterizing the cluster (Sim/SD < 2), average abundance of *S. aurita* in these stations was high (177 ind. 10m^{-2}) and the number of benthopelagic taxa was also important (12 taxa). Group b (16 stations, 51.31 % average similarity) was distributed along the shore and included epipelagic species like *S. aurita* and *T. mediterraneus* as well as the Gobiidae family.

Regarding larval stages, 99.2% of the *C. chromis* captured belonged to pre-flexion stage (2.5-4.4 mm; Leis and Carson-Ewart, 2000). In the case of *S. aurita* 94.16% of the *S. aurita* caught in our study belonged to first-feeding stage (<6 mm; Morote et al., 2008); 5.26% to pre-flexion (6-9.9 mm; Morote et al., 2008) and 0.58% to post-flexion stage.

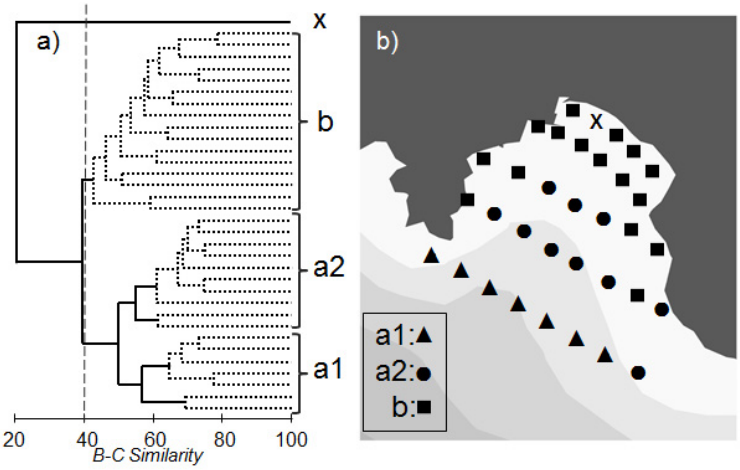

Figure 3.7. a) Hierarchical clustering of the stations. b) Spatial representation of the cluster groups in the bay.

Table 3.3. SIMPER Results for the groups resulting from the taxa cluster. The symbols for each group are consistent with those in figure 3.7. Av. Ab.: mean abundance (ind $10m^{-2}$) of the taxa in the stations of each group. Av. Sim: average similarity between samples. Sim/SD: similarity/standard deviation. %: percentage of each species contribution to the average similarity between samples.

		Group a1 Average similarity: 62.78				Group a2 Average similarity: 62.80				Group b Average similarity: 51.31			
	Taxa	**Av.Ab**	**Av.Sim**	**Sim/SD**	**%**	**Av.Ab**	**Av.Sim**	**Sim/SD**	**%**	**Av.Ab**	**Av.Sim**	**Sim/SD**	**%**
MESO-	*Cyclothone braueri*	128.91	9.68	**7.09**	15.42	24.09	4.42	**4.18**	7.04				
	Ceratoscopelus maderensis	44.19	6.84	**7.19**	10.9	8.40	3.12	1.89	4.96				
	Hygophum spp	28.93	5.75	**3.42**	9.15								
	Lampanyctus crocodilus	4.03	1.09	0.61	1.73								
	Lestidiops jayakari	2.00	1.01	0.61	1.61								
EPI-	*Auxis rochei*	102.81	6.02	1.48	9.59	128.28	5.07	**4.17**	8.07	8.13	2.52	0.74	4.92
	Thunnus alalunga	11.07	4.43	**4.74**	7.06								
	Thunnus thynnus	2.51	2.6	1.5	4.14								
	Sardinella aurita					177.03	5.85	1.73	9.31	43.01	9.04	**2.27**	17.62
	Engraulis encrasicolus	2.35	1.14	0.61	1.82	7.02	2.47	1.2	3.94				
	Trachurus mediterraneus	9.44	2.05	0.89	3.27	21.69	3.57	1.88	5.69	4.75	6.55	**2.18**	12.76
BENTHOPELAGIC	Gobiidae spp	62.31	7.88	**5.17**	12.56	89.34	6.06	**4.44**	9.64	5.25	6.39	**2.14**	12.46
	Serranus hepatus	8.29	4.15	**4.6**	6.6	12.95	3.03	1.8	4.82	2.09	2.88	0.88	5.61
	Chromis chromis	20.23	3.37	1.44	5.37	32.17	5.06	**5.04**	8.05	7.33	4.67	1.32	9.09
	Arnoglossus spp	1.93	0.94	0.62	1.5								
	Coris julis					4.90	2.53	1.83	4.03				
	Trachinus draco					7.79	2.99	1.74	4.76				
	Blenniidae spp					9.78	2.5	1.17	3.98	1.73	2.04	0.63	3.98
	Serranus spp					12.10	2.21	1.25	3.52	3.44	2.25	0.75	4.38
	Mullus barbatus					6.90	2.2	1.22	3.5				
	Symphodus spp					6.90	2.2	1.14	3.5	3.88	1.48	0.54	2.89
	Parophidion vassali					3.78	1.63	0.91	2.59				
	Sphyraena sphyraena					37.00	1.59	0.9	2.53				
	Bothus podas					1.29	0.94	0.69	1.49				
	Sparidae spA									7.6	3.59	0.85	6.99
	Other Sparidae spp									7.13	3.83	1.06	7.46
	Callyonimidae spp									1.80	2.23	0.75	4.35

3.3.3. Environment-species relationships

The RDA selected a parsimonious model to explain multivariate larval composition in which only four variables were significantly included (R^2adj=0.19, $F_{4,29}$=3.001, p<0.001). By order of contribution to explained variance these variables were depth (D), velocity of Mode 2 current (VM2), vorticity depicted from Mode 0 current (VOR0) and mesozooplankton dry weight (MZB) . Thus, the model can be expressed as follows:

***Fish assemblages* ~ D + VM2 + VOR0 + MZB.**

A multiscale ordination analysis (MSO) showed that there was no spatial autocorrelation in our data. Three canonical axes were significant, explaining 90.8 % of the total constrained (explained by the model) variance which enabled a good 2D representation of the data (78% of the variance explained, Fig. 3.8). The RDA biplot (Fig. 3.8) revealed the relationships among the selected environmental variables and the larval fish taxa constituting the assemblages in each area. Most taxa typical from offshore (e.g. *Hygophum* spp, *C. maderensis*, *T. alalunga*) waters were bounded to deepest areas whereas benthopelagic taxa (e.g. Sparidae, Blenniidae, and Callyonimidae) generally occurred at shallowest depths. Mesopelagic taxa (except *C. maderensis*) and the large epipelagic species (large and medium tuna larvae) appeared closely related to Mode 2 velocities (VM2). The benthopelagics and small epipelagics were split in several clusters. Sparidae spA, Blenniidae, Sparidae spp, *T. mediterraneus* and Mugilidae spp, were more close to mesozooplankton dry weight (MZB) and shallow depths (D); *Callyonimus* spp, *Diplodus* spp, *Symphodus* spp, *Mullus barbatus*, *C. chromis* and *Serranus* spp were explained by Mode 0 vorticity and *S. aurita* showed positive relationship to a combination of MZB, VOR0 and opposite to VM2 (higher with increasing depth). Some benthopelagics were close to a combination of the mean vorticity of the bay (VOR0) and depth.

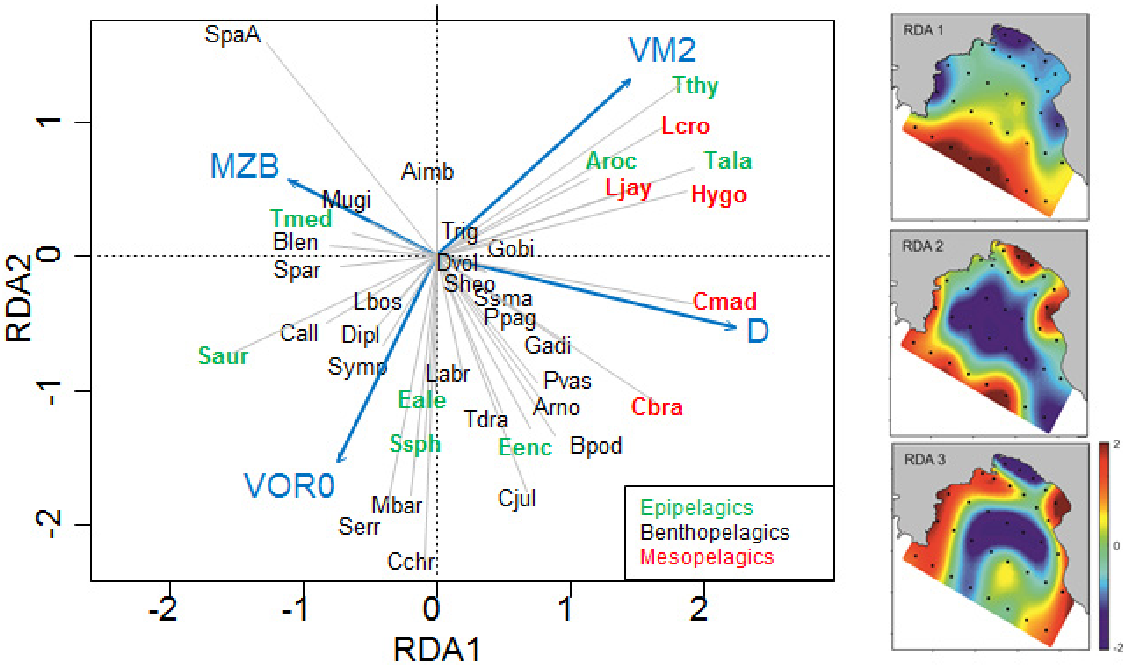

Figure 3.8. a) RDA triplot, sites not shown where: D: depth; VOR0: associated vorticity to Mode 0 current; MZB: mesozooplankton dry weight (mg m^{-3}) determined at laboratory and VM2: velocity of the Mode 2 current (cm s^{-1}). Taxa code as in Table 3.1. Epipelagic taxa are typed in green, mesopelagic taxa in red and benthopelagic taxa in black. b) Spatial distribution of RDA1, RDA2 and RDA3 scores.

3.4. DISCUSSION

Retention of fish larvae, when relative to a particular area or location, results from a combination of biological parameters of adult fishes as well as of pelagic larvae (stage of development, pelagic larval duration and behaviour) together with physical variables such as site isolation, coastal complexity and flow variability (Sponaugle et al., 2002). Our study reveals the mechanisms regulating larval fish dynamics in a typical Mediterranean Bay during summer when coastal conditions are stable, facilitating larval survival. Topographically steered cyclonic circulation (see Mode 0 currents) was a major feature of the circulation of the bay during the survey. As observed in previous studies, this closed circulation pattern seems to be a rather permanent feature that, owing to the prevalent forcings (e.g. ITWs, changes in alongshelf flow, variations in wind forcing), may experience flow reversals (see Gazeau et al., 2005). Despite these variations in flow direction, the center of the bay seems to be an area of weakened flow favoring accumulation. Our data reveals accumulation of fish eggs in the center of the bay (three times more abundant than in other areas) and also increased abundance and diversity mainly of epipelagic and benthopelagic species. The relationship between vorticity and larvae also confirms this passive retention of the early stages of fish larvae.

Observed larval abundances are greater than in other nearby enclosed areas (Pérez-Ruzafa et al., 2004), particularly in the center of the bay where abundances exceed 76 % offshore values. However, the bay is not an isolated realm and a number of individuals could be attributed to spawning from other areas since alongshelf flow in the mouth of the bay only represents a semi-permeable barrier for larvae dispersal.

Occasional intrusions of oceanic water masses may occur in the coastal waters of the Balearic Islands and influence LFAs (Jordi et al., 2009a; Álvarez et al., 2012, Chapter 1). Our data shows that oceanic species (e.g. *C. braueri*) are not rare in the bay but they only represent 23 % of observed taxa (35% of the total abundance). Likewise larvae from nearby areas could also contribute to the LFAs in the Bay. Basterretxea et al. (2012) estimated that surrounding zones could contribute in as much as 25% of the larvae.

Even though retention in the bay can favor mixing among different assemblages, our analysis reveals clear inshore-offshore structuring. According to RDA analysis, different factors explain the spatial structure of these LFAs. Besides the obvious influence of depth, we observed that variables describing bay hydrodynamics are associated with these assemblage patterns. Several studies describe variations in coastal fish assemblages associated with different water masses (e.g. Cowen et al., 1993; Olivar et al., 2010; Basterretxea et al., 2013, Chapter 2). However, our study emphasizes the importance of flow patterns (through flow associated indicators such as current modes and vorticity) moulding the larvae distributions within the same water mass. These flow characterizers reveal preferential transport/retention pathways rather than environments in which larvae were originally spawned. Retentive patterns do not only restrict larval dispersal but, also, other components of the food web are affected, therefore altering the spatial correlations among organisms. For example, the a2 assemblage, retained in the middle of the bay is benefited by the higher mesozooplankton biomass retained in this area potentially favoring larval development. In temperate rocky shores in NW Mediterranean, depth, wind, current direction and topography of the coast where described as the most influential factors for ichthyoplankton abundance and for the relative differences between nearshore and continental shelf LFA (Roussel et al., 2010). Our analysis confirms that these factors are also relevant for the structure and abundance of LFA Palma Bay. However, in the case of semi-enclosed areas topographically steered current veering and the associated recirculation patterns may be a predominant factor.

It is difficult to assess to what extent larvae distribution within the bay is determined by adult spawning sites. Assumedly, adults of mesopelagic species do not spawn in the shallow waters of the bay and, hence, larvae of these taxa should have dispersed either passive or actively to the bay. Meso and epipelagic fish have broad capacities to swim long distances finding the most adequate spawning locations that ensure survival of their breed (Lavett-Smith et al., 1987). Species like *A. rochei* and *S. aurita* usually choose areas near to the coast to spawn whilst large tuna (*Thunnus thynnus*, *T. alalunga*) follow environmental cues, usually density fronts, as signal to spawn (Sabatés et al., 2009; Alemany et al., 2010; Reglero et al., 2012). Conversely, the most abundant benthopelagic adults in the area may present very narrow home rages and generally spawn in nearshore waters (March et al., 2010, 2011; Alós et al., 2012). Thus, the larvae of these species will be sensitive to retention within the bay. Nevertheless, the fraction of local versus allochthonous hatched larvae can only be approximated from larval size and/or developmental stage. The small larvae are locally hatched whereas larger larvae can both correspond to local and remote subpopulations, the same happens to pre-flexion larvae (locally hatched) and flexion and post-flexion (unknown origin).

From the size-spectra of fish larvae collected by bongo nets during late spring- summer in the area (mode of ca 2.5 mm, maximum size of 7 mm, Catalán et al., 2014) and the very early developmental stages presented by the measured taxa in the present study, it is reasonable to infer that, our results mainly describe the influence of passive processes on the spatial distributions for the early stages of fish in Palma Bay. The stage of development at hatching and pelagic larval duration determines the degree of sensitivity of hatched larvae to these passive processes. Species with non-pelagic eggs have larvae that hatch at a more advanced development stage and larger size than those of pelagic spawners, and are more capable of avoiding drift but that does not necessarily mean they cannot be dispersed (Lavett-Smith et al., 1987; Swearer et al., 1999; Hickford and Schiel, 2003; Kent et al., 2013; Pattrick et al., 2013). In the case of species with pelagic eggs such as the Gobiidae and *Engraulis encrasicolus* in our study, the pelagic larval duration will determine the sensitivity of hatched larvae to passive processes (dispersion, retention). Differences in number of eggs released may also be a strategy to ensure offspring survival. Meso and epipelagic species, whose offspring has to be specialized for long transport by ocean currents, release higher number of eggs than benthopelagic taxa that usually are spawned very close to the settlement areas (Lavett-Smith et al., 1987).

The retention mechanism by the main gyre (VOR0) was indistinctly used by taxa with pelagic or demersal eggs. *C. chromis* larvae, coming from nested eggs (Table 3.2), appeared distributed at intermediate depths rather than nearshore. Similar distribution was found for the Gobiidae family, most of their species coming from male guarded eggs. The taxa with a distribution nearest to the coast were *Shymphodus* spp. (from nested eggs) and the Sparidae spA (from pelagic eggs), Their distribution might reflect recent spawning associated to seagrass meadows and shallow rocky areas. The horizontal and vertical swimming ability and the sensory capabilities will be determinant for these larvae to return to settle to adult habitats.

3.5. CONCLUSIONS

Our results highlight the importance of bays as retention areas for some fish larvae. In Palma Bay, a high number of local summer-spawners species and some epipelagic taxa take advantage of this mechanism. Other factors not accounted for such as food-related and behavioral mechanisms should be further investigated but it is anticipated that they become more relevant with increasing larval size. This study opens new questions such as the processes involved in niche partitioning, which would require resolving vertical distributions of larvae, or small-scale recruitment dynamics.

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CHAPTER 4

Environmental forcing and the larval fish community associated to the Atlantic bluefin tuna spawning habitat of the Balearic region (Western Mediterranean), in early summer 2005.

Abstract

The Balearic region is a highly dynamic area located in the Western Mediterranean, straddling the transition between the Algerian and Provencal basins and constitutes one of the main spawning grounds or the large, migratory Atlantic bluefin (*Thunnus thynnus*) and other medium and small tuna species (*Thunnus alalunga*, *Auxis rochei*, *Euthynnus alleteratus* and *Katsuwonus pelamis*). In summer, despite been considered an oligotrophic region as the whole Mediterranean Sea, it harbors a relatively abundant and diverse larval fish community (LFC). In this study, we analyze the composition, abundance and the influence of abiotic and biotic factors on the horizontal structure of the LFC in the Balearic region, in early summer 2005, during the spawning season of Atlantic bluefin tuna. Hydrographically, 2005 was an unusual year with a summer situation of relatively lack of mesoscale features, weak surface currents and a general situation of high stability. A total of 128 taxa of fish larvae, belonging to 52 families, were identified. The average abundance was 1770 larvae 1000 m−3. Multivariate statistical analysis revealed LFC to have a strong horizontal structure. Cluster analysis and non-metric multidimensional scaling ordination identified two larval fish assemblages. These assemblages were mainly delineated by depth and, therefore, by the spawning location of adult fish. Our results also suggest that anticyclonic eddy boundaries constitute favourable habitats for fish larvae. Also, the scenario of higher than unusual hydrographic stability found during the cruise would be responsible for the relatively lack of mesoscale features and, consequently, for the lack of influence of these features on the horizontal distribution of fish larvae and on the horizontal structure of the LFC.

4.1. INTRODUCTION

The Balearic region is a highly dynamic area located in the Western Mediterranean (Fig. 4.1). The Balearic Archipelago straddles the transition between the Algerian and Provencal basins and plays a key role in the water mass dynamics in the Central Western Mediterranean, by conditioning water mass exchange between the two basins, through the island channels (Lopez-Jurado et al., 1995; Pinot et al., 2002). The input flow of Atlantic Water (AW), through the Gibraltar strait, cross the Alboran Sea and enters the Algerian basin following the North African coast, forming the Algerian Current (AC). A thermohaline front, the Almeria–Oran front (Fig. 4.1), is formed by the convergence of surface Atlantic waters, less saline, and Mediterranean surface waters, more saline (Tintore et al., 1991). The unstable character of the AC sometimes leads to the generation of cyclonic and anticyclonic eddies (Millot, 1985, 1999). Anticyclonic eddies have a lifetime of weeks to months, move freely within the Algerian Basin and some of them reach the Balearic Islands (Font et al., 2004; Millot, 1987).

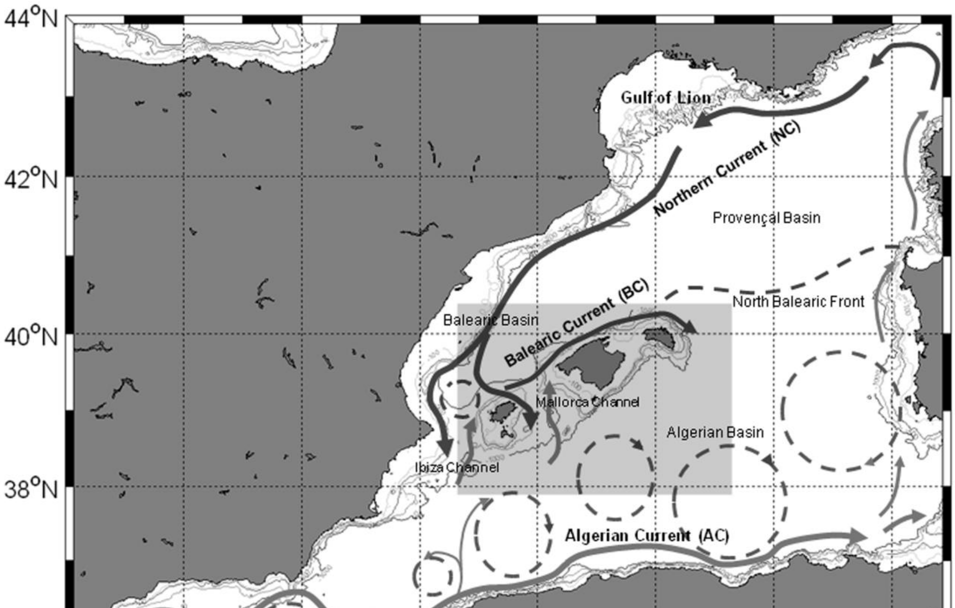


Figure 4.1. Map of the western Mediterranean Sea showing the study area (shadow zone) and the main hydrographic features of the region

Filaments of AW, generated when the thermohaline Almeria–Oran front becomes unstable (Tintore et al., 1988), can also reach and even surpass the Balearic archipelago through the island channels (Fig. 4.1). In the Provencal basin, the Northern Current (NC) flows southwestward, along the continental slope (Fig. 4.1). A branch of the NC forms the Balearic Current (BC) that flows northeastward, along the northern slope of the Balearic Islands (Fig. 4.1). A surface front, the Balearic Front, associated with the BC, and continued in the east by the North Balearic Front (Fig. 4.1), separates fresher AW of the Algerian basin from colder and saltier resident AWof the Provencal basin (Salat, 1995). The surface circulation is mainly driven by density in the Algerian basin while in the Provencal basin is mainly driven by atmospheric forcing, largely wind (Hopkins, 1978). As consequence, hydrodynamic conditions in the north and south of the islands are quite different (Lopez-Jurado et al., 2008).

The Balearic region, as the whole Mediterranean Sea, is considered an oligotrophic region during the summer stratification period (Estrada, 1996; Fernandez de Puelles et al., 2007). During summer, in the absence of riverine nutrient input (it must be pointed out that there are no permanent freshwater streams in the Balearic Islands), the biological production is mainly associated with mesoscale oceanographic features, fronts and eddies (Alcaraz et al., 2007; Estrada et al., 1993; Jansa et al., 2004, 1998). Also, the vertical distribution of chlorophyll shows a deep chlorophyll maximum (DCM), typical of oligotrophic regions, located below the thermocline (Estrada et al., 1993; Jansa et al., 1998). The maximum concentration of zooplankton coincides with the DCM, where zooplankton is feeding (Alcaraz et al., 2007; Saiz et al., 2007).

Despite its oligotrophy, the Balearic region harbors a relatively diverse and abundant summer larval fish community (LFC) (Alemany, 1997, 2006; Sabatés et al., 2007). In addition, this region is recognized as one of the main spawning areas for the eastern Atlantic stock of the large migratory Atlantic bluefin (*Thunnus thynnus*), other medium and small tuna species (*Thunnus alalunga, Auxis rochei, Euthynnus alleteratus, Katsuwonus pelamis*) and other large pelagics, such as, *Xiphias gladius or Coryphaena hippurus* (Alemany et al., 2010). The presence of larvae of these species, the reproductive strategy of most of fish species in the northwestern Mediterranean, which reproduce in spring–summer (Olivar et al., 2010; Sabatés et al., 2007), and the mesoscale oceanographic features, enhancing biological productivity, may account for the relatively high species richness and larval fish abundances recorded in the area. On the other hand, processes such as currents, fronts and eddies influence the distribution, abundance and survival of fish larvae and, accordingly, define the abundance, structure and diversity of the LFC (Bakun, 2006; Holliday et al., 2011; Lobel and Robinson, 1988; Mullaney et al., 2011; Rodriguez et al., 2004; Sabatés and Olivar, 1996).

The summer LFC of the Balearic region has been previously studied but at a short spatial scale. In this study, the most geographically widespread carried out on the ichthyoplankton in the region, we analyse the composition, abundance and the horizontal structure of the LFC of the Balearic region, in early summer 2005. We also analyse the influence that abiotic (depth, sea surface salinity, dynamic height and geostrophic velocity and biotic environmental factors (phytoplankton and microzooplankton biomass) have on the horizontal structure of the LFC. We hypothesized that the horizontal distribution of fish larvae and, consequently, the horizontal structure of the LFC would reflect the mesoscale oceanographic features of the region.

4.2. MATERIAL AND METHODS

4.2.1. Data collection

This study is based on data collected during the Tunibal 05 oceanographic-ichthyoplankton survey, carried out in the Balearic region (NW Mediterranean), in summer (from June 27 to July 23) 2005 (Fig. 4.1). A total of 190 (183 for ichthyoplankton) stations, arranged in a regular sampling grid of 10_10 nm, were sampled.

At every station, vertical profiles of conductivity, temperature and fluorescence were obtained with a Sbe 911 CTD. Profiles were to 350 m in depth (160 stations), or to 650 m at selected stations (30 stations).

Zooplankton samples were collected with a Calvet net equipped with 55 µm mesh nets in vertical hauls, from 70 m depth to the surface. Samples were filtered immediately through 55 µm, 200 µm and 2mm mesh filters to separate the three zooplankton fractions. The macrozooplankton fraction was discarded and both, the micro and mesozooplankton samples where then placed in Petri dishes and frozen at -20 ºC. In the laboratory, the micro and mesozooplankton dry weight were obtained following Lovegrove (1966). Nonetheless, mesozooplankton was not considered because the Calvet net may undersample this zooplankton fraction. Microzooplankton dry weight biomass values were standardised to mg m^{-3}.

Ichthyoplankton samples were collected with a Bongo 60 net equipped with 200 and 335 µm mesh nets. Tows were oblique trying to reach 70 m depth, apart from three stations shallower than 70 m. At every station, the length of the wire was adjusted in function of the wire angle to reach 70 m depth. The volume of water filtered was measured by two flowmeters (General Oceanics) installed in the mouths of each net. Ichthyoplankton samples were immediately preserved in a 4% sodium-borate buffered solution of seawater and formaldehyde. In the laboratory, all fish larvae were sorted from the 335 µm mesh net samples, counted and identified to the lowest taxonomic level possible. Larval fish catches at each station were standardised to number 1000 m^{-3}.

4.2.2. Data analysis

Temperature, salinity and fluorescence records at each station were processed at their original sampling frequency and averaged at 1 m interval. Horizontal hydrographic fields were obtained with a standard optimal interpolation scheme, using an isotropic Gaussian correlation (Bretherton et al., 1976; Pedder, 1993). The dynamic height at 10 dbar was calculated by vertical integration of the specific volume anomaly from the level of 600 dbar, which was chosen as the level of no motion (Pinot et al., 2002). At shallow stations, or when data were recorded only down to 350 m, the density anomaly at the closer 600 m station was assigned to the deepest level sampled by the CTD. Geostrophic velocities were obtained using the first-derivative of the dynamic height fields (Pinot et al., 1996). Dynamic height was used as an indicator of eddies and frontal regions, because dynamic height should be higher than average in anticyclonic and frontal regions and lower than average in cyclonic eddy regions (Lindo-Atichati et al., 2012 and references therein). Geostrophic velocity at 10 m depth was used as an indicator of eddy boundaries and frontal regions, because geostrophic velocity should be higher in these regions (Bakun, 2006; Le Fevre, 1986; Sournia, 1994).

In early summer, the surface warming in the Mediterranean Sea is strong. Thus, sea surface temperature (SST) does not depend on the geographical position but on sampling date. As consequence, temperature was not useful for characterizing surface water masses. Sea surface salinity (SSS), salinity at 10 m depth, was considered the best parameter for this purpose.

The relation between environmental variables, SSS, dynamic height, geostrophic velocity, depth-integrated (5–200 m) fluorescence, as an estimate of phytoplankton biomass, microzooplankton biomass and larval fish concentration was tested using

Pearson's correlation coefficient in SPSS v. 19.0.

Taxon diversity was calculated for each station using the Shannon–Wiener diversity index (H′) in PRIMER v. 6.1.6 (Plymouth Routines in Multivariate Ecological Research).

Following Clarke and Ainsworth (1993) and Field et al. (1982), non-parametric multivariate techniques in PRIMER were used to study the horizontal structure of the LFC. Cluster analysis in conjunction with non-metric multidimensional (MDS) ordination was used to identify larval fish and taxa assemblages. Only "non rare taxa, those found in 45% of the stations and/or had a relative abundance of 40.04%, were included in the analysis. Cluster analysis and MDS were performed on a Bray and Curtis (1957) similarity matrix, generated from the loge (x+1) transformed data of larval fish abundances. Data were transformed to down-weight the influence of more abundant taxa (Clarke and Ainsworth, 1993; Field et al., 1982). Hierarchical agglomerative clustering with group-average linking, carried out on the similarity matrix, was used to delineate assemblages with distinct community structure. Arbitrary cut-off levels were chosen on dendrograms to produce ecologically interpretable clusters (Field et al., 1982; Auth and Brodeur, 2006). The adequacy of the classification analysis was checked by superimposing the results of the clustering on MDS plots generated from the same similarity matrices (Auth and Brodeur, 2006; Clarke and Ainsworth, 1993; Clarke and Warwick, 2001). A two-dimensional ordination approach was adopted because the stress level (≤0.16) was acceptably low (Clarke and Ainsworth, 1993; Clarke and Warwick, 2001).

The relationship between biological and environmental variables and "non rare" taxa was assessed with Canonical Correspondence Analysis (CCA) in CANOCO 4.5 (ter Braak and Smilauer, 2002). CCA is a multivariate method to elucidate the relationships between assemblages of species and their environment (ter Braak and Verdonschot, 1995). Rare species, as above, were not included in the analysis. Larval abundances were loge (x+1) transformed before analysis. The explanatory variables were station depth, SSS, dynamic height, geostrophic velocity, depth-integrated fluorescence and zooplankton biomass. SST was not included in the analysis because of is temporal variability, daily increase, as indicated above. Canonical axes were tested for significance with a Monte Carlo permutation test (9999 permutations) in CANOCO (ter Braak and Smilauer, 2002).

4.3. RESULTS

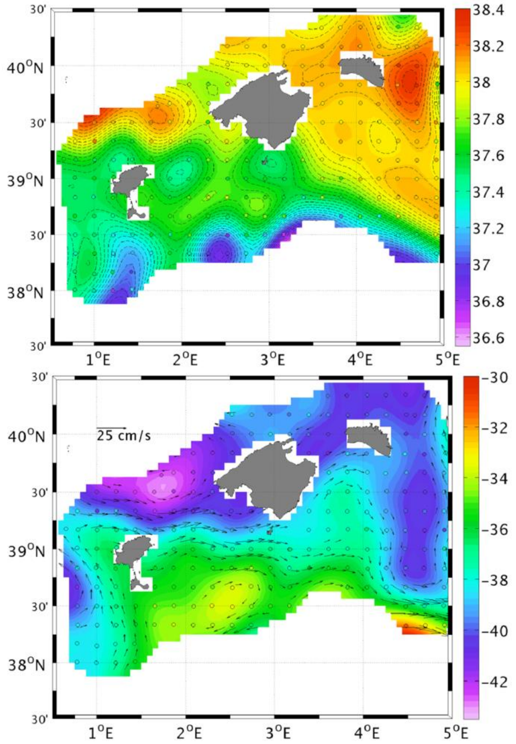
4.3.1. Hydrography and plankton

In summer, in the absence of the winter atmospheric forcing, the density gradient dominates and allows AW inputs to enter the Balearic region. Thus, the southernmost part of our study area was occupied by fresh AW (salinity o37.5) (Fig. 4.2a). Weak inputs of this water crossed the Ibiza channel and, surrounding the northern Ibiza Island, returned into the Algerian basin through the Mallorca channel. The northeastern corner was occupied by resident AW (salinity438), isolated patches of resident AW were also found in the north of the area, and the rest of the region was occupied by mixed AW (salinity 37.5–38) (Fig. 4.2a). Consequently, the boundary between fresh and resident AW was found south of the archipelago. The main hydrographic mesoscale features observed during the study were two anticyclonic eddies. A strong, fresh AW anticyclonic eddy was located south of the Mallorca Channel, centered at 38.51N (Fig. 4.2b). Another weak, mixed AW anticyclonic eddy was found at the east of Mallorca and the south of Menorca Island (Fig. 4.2b). Surface currents, including the BC flow, were also relatively weak (Fig. 4.2b).

The water column showed a strong thermal stratification. The mixed layer, defined as the layer where temperature and salinity were homogeneous due to solar heating and turbulence induced by weak easterlies, was 15 m of average thickness and with temperatures between 20 and 26 1C. It was followed by a strong thermal gradient to around 60 m depth. From this depth to 150 m, the temperature decreased gradually to reach ~13 1C, the deep-water temperature (Fig. 4.3). As mentioned above, SST depended on sampling date. Thus, the lowest SST was recorded at the beginning of the cruise and the highest SST was measured at the end of the cruise. In fact there was a significant correlation between SST and sampling dates ($r = 0.62$ for temperature at 5 m depth and $r = 0.34$ for temperature at 10 m depth, $p < 0.01$ in both cases).

The vertical distribution of fluorescence showed a deep fluorescence maximum (DFM) located at an average depth of about 75 m, below the thermocline (Fig. 4.3). The horizontal distributions of depth-integrated fluorescence and microzooplankton biomass showed irregular patterns (Fig. 4.4). The most noticeable feature of these distributions was that the highest values for both these biological variables were recorded in the oceanic region. In fact, the correlation of depth-integrated fluorescence and mesozooplankton biomass with depth was significant ($r =0.30$, $p < 0.01$ and $r = 0.16$, $p < 0.05$, respectively).

Figure 4.2. Horizontal distribution of (a) sea surface salinity (salinity at 10 m depth) and (b) dynamic height (cm) at 10 decibars (db) relative to 600 db and derived geostrophic currents at 10 m depth



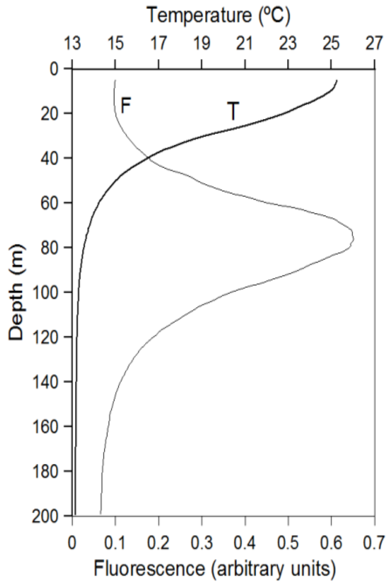


Figure 4.3. Average temperature (T) and fluorescence (F) profiles

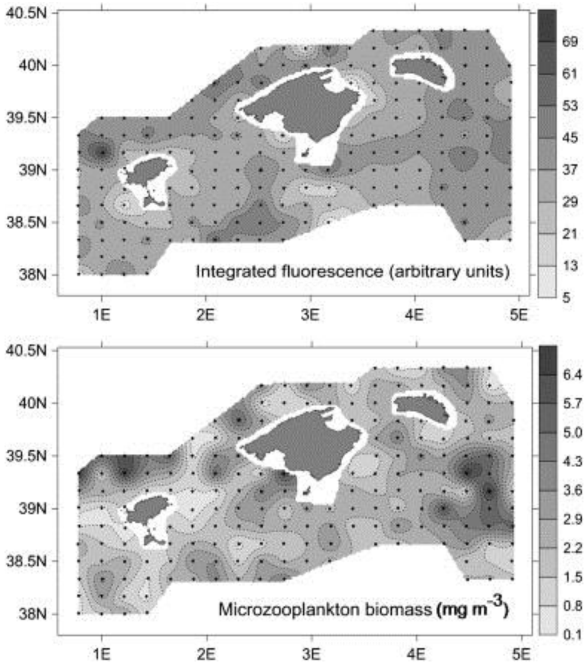


Figure 4.4. Horizontal distribution of depth-integrated (5-200 m) fluorescence and microzooplankton biomass

4.3.2. The larval fish community

A total of 54,545 fish larvae were caught in this study, including 128 taxa belonging to 52 families (Table 4.1). Myctophydae, with 17, and Gobiidae, with 12, were the families with the largest number of taxa. The abundance of fish larvae ranged from 90 to 5991 L 1000 m^{-3}, with a mean of 1770 L 1000 m^{-3}. Larvae of the families Myctophidae, which accounted for 50% of total catch, and Gonostomatidae, 33% of total catch, were the most abundant. *Hygophum* spp was the most abundant and one of the most common taxa, accounting for 25.1% of the total larval fish abundance and being caught at 95.1% of the stations. The second most abundant species was *Cyclothone braueri* (24.6%), which also was the most common taxa, appearing at almost all stations (98.9%). Other abundant and common taxa were *Ceratoscopelus maderensis*, 14.3% of the larval fish abundance and appearing at 97.8% of the stations, *Cyclothone pygmaea*, 7.6% of the larval fish abundance and captured at 91.8% of the stations and *Lampanyctus crocodilus* that accounted for 4.2% of the larval fish abundance and was captured at 89.1% of the stations. Only for three neritic species their relative abundances were above 1% of total larval catch. These species were *A. rochei*, which accounted for 2.3% of larval fish abundance and was caught at 44.8% of the stations, *Sardinella aurita*, 1.6% of the larval abundance and caught in 25.7% of the stations and *Engraulis encrasicolus*, 1.4% of the larval fish abundance and present in 33.9% of the stations. The horizontal distribution of fish larvae, with low concentrations around the islands and the highest recorded away from these (Fig. 4.5), showed similar pattern to that of depth-integrated fluorescence and microzooplankton biomass (Fig. 4.4). Individual species showed irregular patterns of horizontal distribution (Fig. 4.5). As expected, larvae of oceanic species showed higher concentrations in the oceanic region and larvae of neritic species showed higher concentration in the neritic region (Fig. 4.5). Nevertheless, larvae of oceanic species were caught in the neritic region, as were larvae of neritic species caught in the oceanic region (Fig. 4.5). Larval fish abundance was correlated with geostrophic velocity ($r = 0.16$, $p < 0.05$) and with the species diversity index ($r = -0.28$, $p < 0.01$).

The number of taxa per station ranged from 7 to 35, with the maximum values recorded around the islands (Fig. 4.6a). Larval diversity was relatively high, ranging from 0.92 to 2.98. Its horizontal distribution followed a similar pattern to the number of taxa, with the highest values also recorded around the islands (Fig. 4.6b). Larval diversity was correlated with SSS ($r = 0.34$, $p < 0.01$) and with larval abundance, as indicated above.

Table 4.1. Alphabetical list of larval fish families collected in the Balearic Sea, in July 2005, taxa code (Code), their relative abundance (RA, %) and their percentage of occurrence (%O).

Family and species	Code	RA	% O
Apogonidae			
Apogon (Apogon) imberbis		0.031	3.3
Argentinidae			
Glossanodon leioglossus		0.002	0.5
Blenniidae			
Parablennius pilicornis		0.002	0.5
Unidentified sp		0.02	
Bramidae			
Brama brama		0.004	1.1
Bothidae			
Arnoglossus imperialis		0.002	0.5
Arnoglossus laterna		0.009	1.6
Arnoglossus rueppelli		0.007	1.6
Arnoglossus thori	At	0.062	9.8
Bothus podas		0.019	4.9
Arnoglossus spp	Aspp	0.084	7.1
Callionymidae			
Callionymus spp	Cspp	0.048	9.3
Caproidae			
Capros aper		0.011	3.3
Carangidae			
Trachinotus ovatus		0.002	0.5
Trachurus mediterraneus	Tm	0.434	20.2
Trachurus spp	Tspp	0.871	13.7
Seriola dumerili		0.035	4.9
Carapidae			
Carapus acus		0.002	0.5
Cepolidae			
Cepola rubescens	Cr	0.299	15.8
Chlorophthalmidae			
Chlorophthalmus agassizii		0.002	0.5
Clupeidae			
Sardinella aurita	Sa	1.638	25.7
Centracanthidae			
Spicara flexuosa		0.002	0.5
Spicara smaris	Ss	0.42	8.7
Spicara spp		0.009	0.5
Centriscidae			
Macroramphosus scolopax		0.002	0.5
Congridae			
Ariosoma balearicum		0.002	0.5
Coryphaenidae			
Coryphaena hippurus		0.004	1.1
Dactylopteridae			
Dactylopterus volitans		0.007	1.6
Engraulidae			
Engraulis encrasicolus	Ee	1.365	33.9
Evermannellidae			
Evermannella balbo		0.03	6
Exocoetidae			
Hirundichthys sp		0.002	0.5
Gobiidae			
Aphia minuta	Am	0.1	6
Crystallogobius linearis		0.058	1.1
Gobius niger	Gn	0.11	7.7
Gobius paganellus		0.002	0.5
Lebetus guilleti	Lg	0.048	7.1
Pomatoschistus marmoratus		0.009	0.5
Pomatoschistus minutus		0.002	0.5
Pseudaphya ferreri	Pf	0.963	14.2
Gobiidae sp 1		0.032	0.5
Gobiidae sp 2		0.002	0.5
Gobiidae sp 3		0.004	1.1
Unidentified spp		0.036	4.9
Gonostomatidae			
Cyclothone braueri	Cb	24.615	98.9
Cyclothone pygmaea	Cp	7.584	91.8
Unidentified spp		0.005	1.6
Labridae			
Coris julis	Cl	0.582	31.1
Thalassoma pavo		0.018	2.7
Symphodus sp 1		0.007	1.1
Symphodus sp 2		0.007	1.6
Symphodus sp 3		0.021	3.3
Symphodus spp		0.002	0.5
Xyrichthys novacula		0.014	2.2
Lophotidae			
Lophotus lacepedei		0.002	0.5
Merlucciidae			
Merluccius merluccius		0.006	1.6
Mugilidae			
Mugil spp		0.011	2.7

Table 4.1. *(continued)*

Family and species	Code	RA	% O
Mullidae			
Mullus barbatus	Mb	0.04	6
Mullus surmuletus		0.005	1.6
Unidentified spp		0.035	4.4
Muraenidae			
Unidentified spp		0.002	0.5
Myctophidae			
Benthosema glaciale	Bg	1.936	60.7
Ceratoscopelus maderensis	Cm	14.297	97.8
Diaphus holti		0.038	9.8
Diaphus spp		0.003	1.1
Electrona rissoi		0.004	0.5
Hygophum spp	Hspp	25.06	95.1
Lampanyctus crocodilus	Lc	4.216	89.1
Lampanyctus pusillus	Lp	2.219	84.7
Lampanyctus spp		0.017	1.6
Lobianchiia dofleini	Ld	0.124	21.9
Lobiancha gemellarii		0.007	1.6
Notoscopelus kroeyerii		0.023	6.6
Notoscopelus bolini		0.027	4.9
Notoscopelus spp		0.017	3.3
Myctophum punctatum	Mp	0.18	18.6
Symbolophorus veranyi	Sv	0.711	53.6
Unidentified spp		0.15	14.8
Nomeidae			
Cubiceps gracilis		0.002	0.5
Ophidiidae			
Ophidion barbatum		0.002	0.5
Parophidion vassali		0.025	4.4
Ophididae			
Unidentified spp	Ophid	0.044	7.1
Ophichthidae			
Dalophis imberbis		0.006	1.6
Paralepididae			
Lestidiops jayakari	Lj	0.47	55.8
Lestidiops sphyrenoides		0.036	7.1
Notolepis rissoi	Nr	0.221	16.9
Paralepis coregonoides	Pc	0.598	36.1
Unidentified spp		0.215	22.4
Phosichthyidae			
Ichthyococcus ovatus		0.007	1.6

Table 4.1. *(continued)*

Family and species	Code	RA	% O
Vinciguerria attenuata	Va	1.364	74.9
Pleuronectidae			
Unidentified spp		0.002	0.5
Pomacentridae			
Chromis chromis	Cc	0.719	37.2
Scombridae			
Auxis rochei	Ar	2.251	44.8
Euthynnus alletteratus	Ea	0.064	5.5
Katsuwonus pelamis		0.002	0.5
Scomber japonicus		0.002	0.5
Thunnus alalunga	Ta	1.07	61.7
Thunnus thynnus	Tt	0.276	18.6
Unidentified spp		0.01	0.5
Scophthalmidae			
Lepidorhombus boscii		0.002	0.5
Scorpaenidae			
Helicolenus dactylopterus		0.002	0.5
Scorpaena notata		0.005	1.6
Scorpaena porcus		0.008	2.2
Scorpaena spp		0.014	3.3
Serranidae			
Anthias anthias		0.009	2.2
Epinephelus sp		0.002	0.5
Serranus cabrilla	Sc	0.411	22.4
Serranus hepatus	Sh	0.37	16.4
Sparidae			
Diplodus annularis		0.006	1.6
Diplodus spp		0.022	3.8
Oblada melanura		0.002	0.5
Pagrus pagrus	Pp	0.128	7.1
Unidentified spp		0.018	1.6
Sternoptychidae			
Maurolicus muelleri		0.011	2.2
Stomiidae			
Borostomias antarcticus		0.004	0.5
Chauliodus sloani		0.002	0.5
Stomias boa	Sb	0.215	35
Stomiidae			
Unidentified spp		0.002	0.5
Syngnathidae			
Nerophis ophidon		0.002	0.5

Table 4.1. *(continued)*

Family and species	Code	RA	% O
Synodontidae			
Synodus saurus		0.008	2.2
Trachinidae			
Trachinus draco	Td	0.209	15.8
Trachinus spp		0.005	1.6
Triglidae			
Eutrigla gurnardus		0.002	0.5
Lepidotrigla cavillone		0.032	3.8
Trigloporus lastoviza		0.002	0.5
Unidentified spp		0.008	2.2
Trichiuridae			
Trichiurus lepturus		0.026	3.3
Uranoscopidae			
Uranoscopus scaber		0.002	0.5
Xiphiidae			
Xiphias gladius		0.015	4.4
Unidentified larvae		2.089	

Cluster analysis identified two LFAs at a similarity level of 41% (Fig. 4.7a). MDS ordination produced the same results (Fig. 4.7b). Assemblages were named after the location of the stations they occupied. The neritic assemblage occupied almost exclusively stations located inside the 200 m isobath, while the oceanic assemblage occupied the stations located outside the 200 m isobath (Fig. 4.7c). This two group classification was reinforced by the formation by cluster analysis and MDS ordination of two taxa assemblages: a neritic and an oceanic one (Fig. 4.8). The neritic assemblage was formed by larvae of those taxa that as adults inhabit the neritic region and also reproduce there. The oceanic assemblage was formed by larvae of fish species that as adults live and reproduce in the oceanic region. The allocation of larval fish taxa into one of these two groups was quite accurate, only a taxon *Arnoglossus thori*, a flatfish inhabiting shelf bottoms, clustered with oceanic taxa.

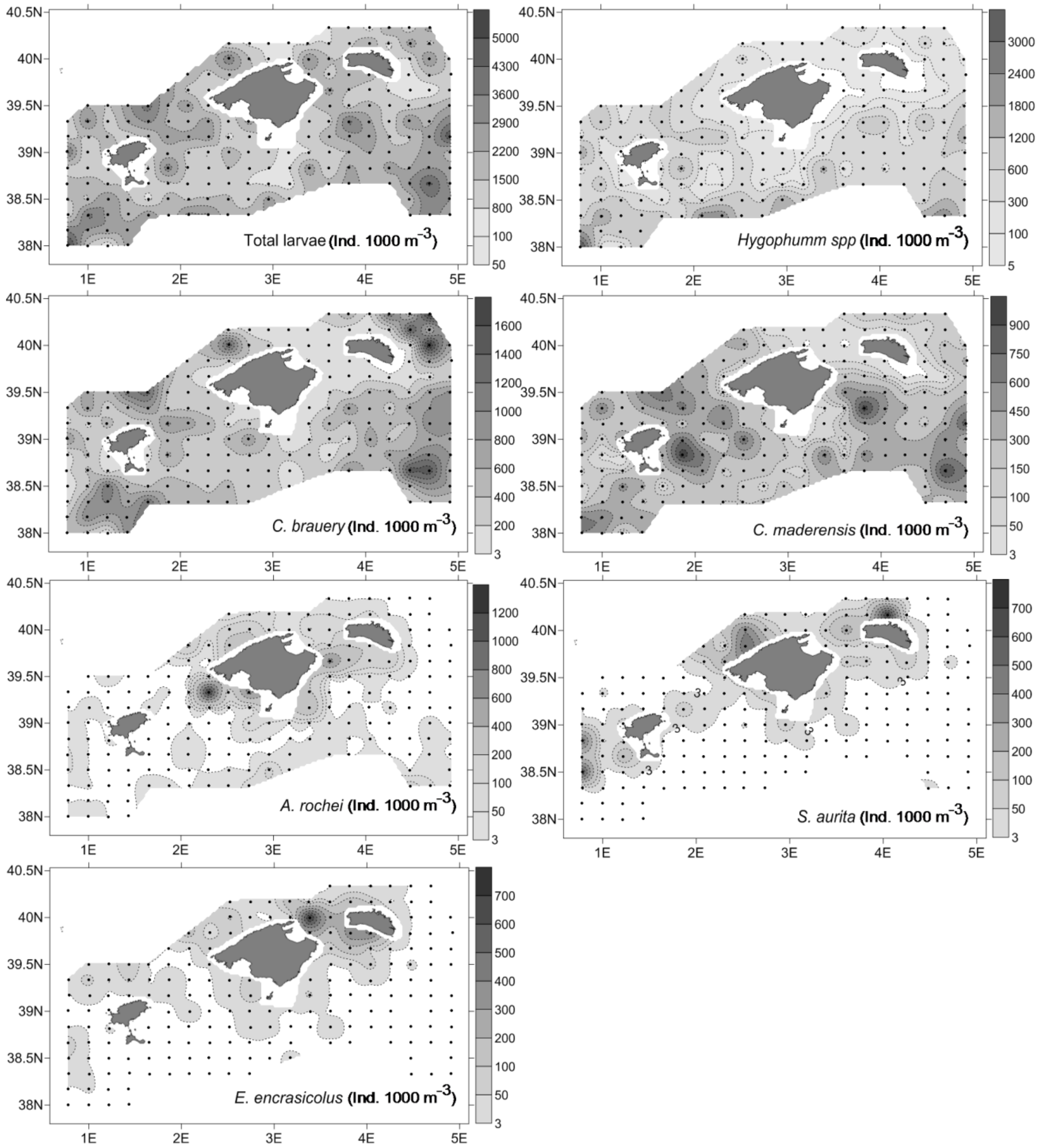


Figure 4.5. Horizontal distribution of fish larvae

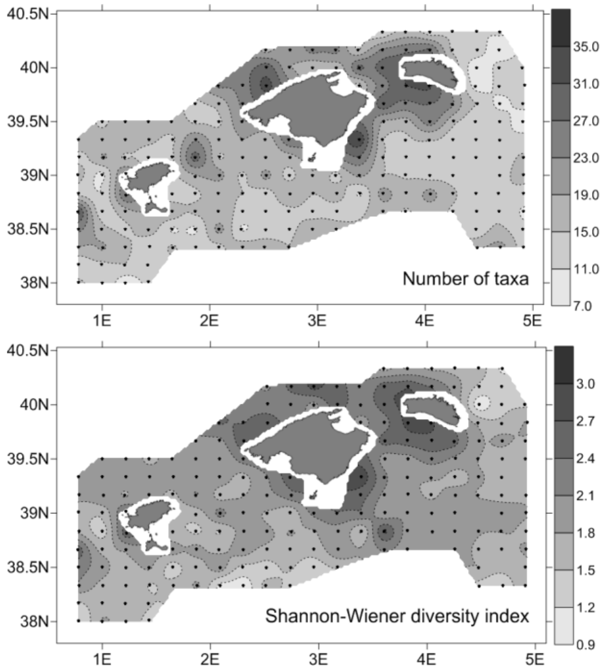


Figure 4.6. Horizontal distribution of taxon richness and diversity of fish larvae

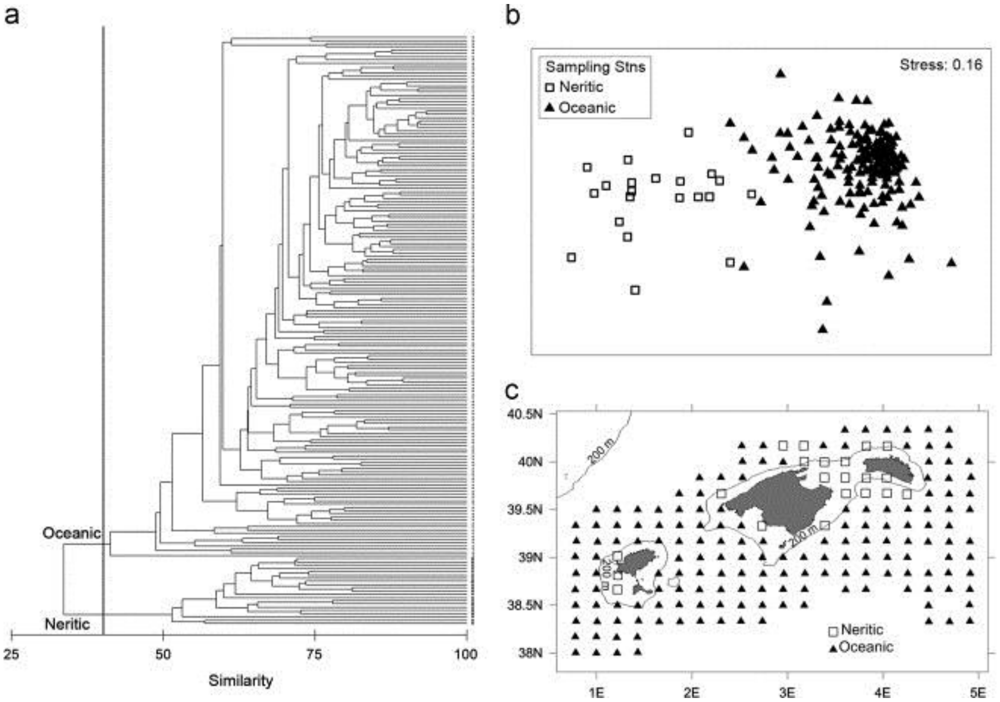
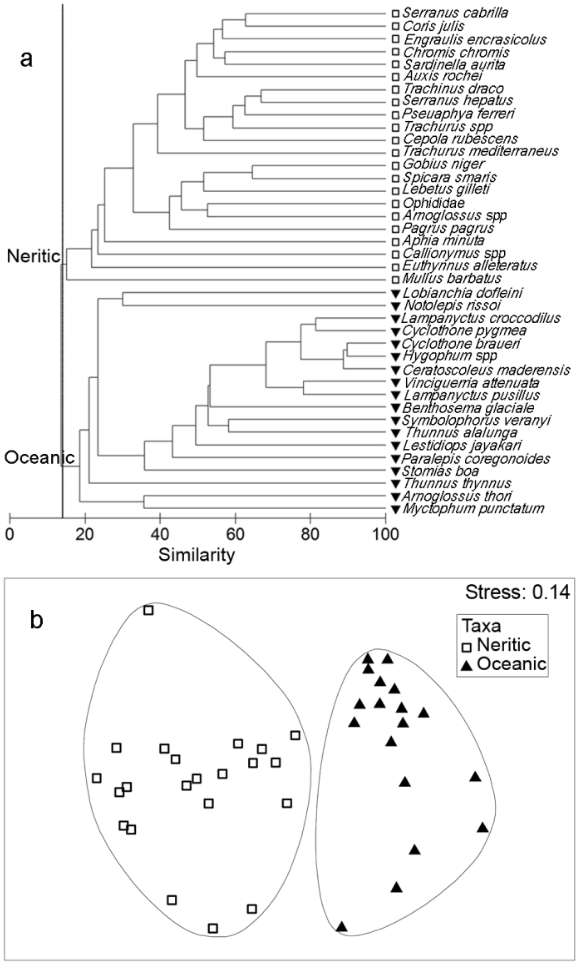


Figure 4.7. (a) Hierarchical clustering, (b) non-metric multidimensional scaling (MDS) ordination and (c) geographical location of the larval fish assemblages based on the Bray Curtis similarity matrix of Log_e (x+1) transformed abundance of fish larvae

4.3.3. Relationship between larval fish taxa and environment

The Monte Carlo permutation test showed that only the first two canonical axes were significant ($p < 0.05$). These two axes explained 88.0% of the variance of the species–environment relationship. The species-environment correlation coefficients for the first two CCA axes were 0.70 and 0.56, respectively. In the CCA biplot, environmental variables are represented by arrows, with origin at the centre of the biplot and pointing in the direction of its increase. The length of environmental arrows and their orientation on the biplot determine their relative importance to each axis (ter Braak and Verdonschot, 1995; ter Braak, 1986). Then, according to Fig. 4.9, depth was the most important variable in explaining taxa distribution. This variable, depth-integrated fluorescence, microzooplankton biomass, dynamic height and geostrophic velocity were negatively correlated with axis 1; only SSS was positively correlated with this axis (Fig. 4.9). The geographical representation of scores of each station confirms that axis 1 is a depth axis (Fig. 4.10a). Accordingly, oceanic taxa appeared on the negative side of this axis (Fig. 4.9). In general, these taxa clustered near the centre of the CCA biplot (Fig. 4.9). Only two neritic taxa, *A. thori* and *Mullus barbatus*, were located on the left side of axis 1, although very close to the right side region of the CCA biplot (Fig. 4.9). Most taxa that appeared at the very right side of the axis 1 are demersal fish species (e.g. *Gobius niger*, *Spicara smaris*, *Pagrus pagrus* or Ophididae) with relative littoral distribution. Larvae of neritic epipelagic taxa (e.g. *A. rochei, Trachurus mediterraneus* or *E. encrasicolus*) were located on the right side of Axis I but near of centre of the CCA biplot. Only the oceanic specie *T. thynnus* was located on the right side of the CCA biplot, although near its centre, as most of the oceanic taxa (Fig. 4.9). Axis 2 was positively correlated with depth and dynamic height (Fig. 4.9). The geographical representation of scores of each station shows that axis 2, unlike axis 1, could not be identified with any of the environmental variables (Fig. 4.10). *A. thori, Myctophum punctatum, Lobianchia dofleini* and *M. barbatus* were the species that showed the highest correlation with axis 2 (Fig. 4.9).

The groups of larval fish taxa formed by cluster analysis and MDS ordination (Fig. 4.8) also appeared in the CCA with little difference (Fig. 4.9). This indicates strong support of taxa grouping and their relationship with the considered environmental variables (Leps and Smilauer, 2003).



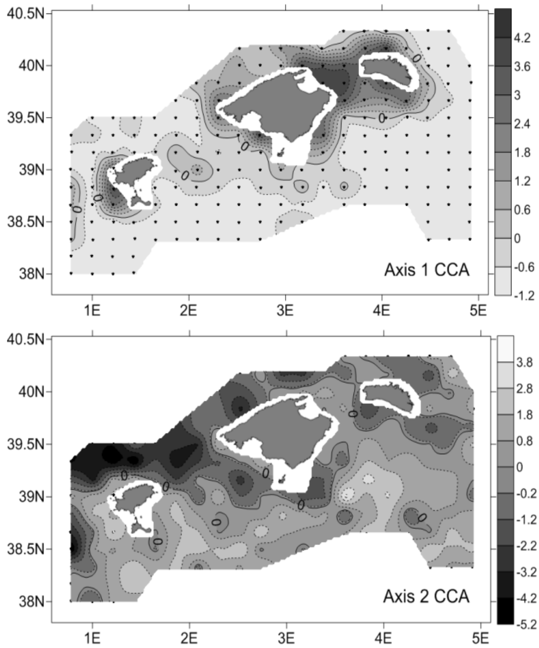
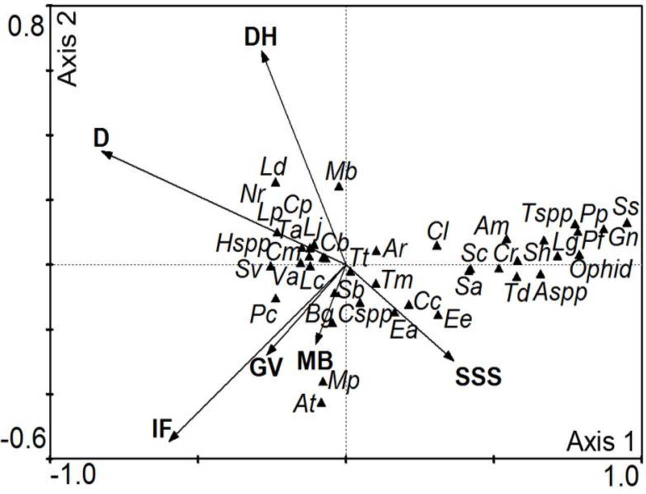


Figure 4.10. Geographical distribution of axes 1 and 2 CCA sample scores

Figure 4.8. (a) Hierarchical clustering and (b) non-metric multidimensional scaling (MDS) ordination of the species assemblages based on the Bray Curtis similarity matrix of Log$_e$ (x+1) transformed abundance of fish larvae

Figure 4.9. CCA biplot for environmental variables (arrows) and larval fish species (triangles). Environmental variables were depth (D), sea surface salinity (SSS), dynamic height (DH), geostrophic velocity (GV), depth-integrated fluorescence (IF) and mesozooplankton biomass (ZB). See Table 4.1 for larval fish species codes.



4.4. DISCUSSION

4.4.1. Hydrography

Hydrographically, 2005 was an unusual year because there were consecutive episodes of severe winter leading to violent convective events, with the development of a thermohaline anomaly in deep waters (Lopez-Jurado et al., 2005). Even so, no winter intermediate water (WIW) was formed, since all the surface water masses affected by the cold and intense winter winds became deep Mediterranean waters (Lopez-Jurado et al., 2005). In addition, the winter atmospheric forcing, which dominates in the Provencal basin (Hopkins, 1978), favoured that colder and saltier surface waters moved south of the Balearic archipelago (Lopez-Jurado et al., 2005). When this forcing decayed, the recent AW progressed northward generating oceanic fronts along 391N parallel. During summer, as surface currents were relatively weak, there was no intense inflow of oceanic surface waters towards coastal areas, or currents transporting shelf waters offshore. Also, the Balearic Current Balearic Current (BC) only received weak fresh AW inputs through the Ibiza Channel, because the anticyclonic eddy located south of Mallorca blocked its passage through the Mallorca channel. According to Alemany et al. (2010), the hydrodynamic scenario observed during this survey was more stable than those found in similar summer surveys carried out in previous years in the region. This stability would be responsible for the relatively lack of mesoscale hydrographic features found in the area at the time of the study.

During the stratified summer situation and in the absence of riverine nutrient input, the only nutrient source in the region has to be related with the mesoscale oceanographic processes in the region. The horizontal distribution of depth-integrated fluorescence and microzooplankton biomass, with relatively low concentrations around the islands and the highest values recorded in the oceanic region (Fig. 4.4), supports that biological production in the region during the study was not related with inputs of nutrients from the islands. It has been reported that Chl a maxima during summer in the Balearic region, are associated with hydrographic features, such as fronts and eddies (Estrada et al., 1993; Jansa et al., 2004, 1998), which constitute important fertilization sources (Alcaraz et al., 2007; Bakun, 2012). Concretely, during 2001–2003 summers, Jansa et al. (2004) found those maxima, of up to 8 mg L^{-1}, in subsurface strata, in the border of anticyclonic eddies.

In this study, the lack of significant correlation of the horizontal distributions of depth-integrated fluorescence with dynamic height and geostrophic velocities did no support the relationship between Chl a and mesoscale hydrographic features. Though, the significant correlation between depth-integrated fluorescence and SSS indicates that biological production was higher in resident AW waters, richer in nutrients than in the fresh, nutrient depleted AW (Estrada, 1996). This relationship of depth-integrated fluorescence with resident AW may mask the relationship of phytoplankton with mesoscale hydrographic features. The most noticeable were the above mentioned two eddies, one of them of fresh and the other of mixed AW (Fig. 4.2).

The vertical distribution of fluorescence, with a deep fluorescence maximum (DFM), is typical of the Mediterranean Sea during the stratification period (Estrada, 1996). In open waters off the Balearic Islands, Jansa et al. (2004) found significant concentrations of chlorophyll at the DCM level in summer. It has also been reported that during the stratification period, the main zooplankton peak coincides with the DCM (Alcaraz et al., 2007). Copepods nauplii and copepodites, the main food items for fish larvae, also concentrate at this depth (Olivar et al., 2010; Sabatés et al., 2009). So, our sampling to 70 m depth, may have not included zooplankton maximum leading to an underestimation of the true values of the microzooplanton biomass. This also may account for the lack of relationship between the horizontal distribution of depth-integrated fluorescence and mesozooplankton biomass.

4.4.2. The larval fish community

The number of larval fish taxa captured is higher than those found in previous ichthyoplankton studies carried out in our study area, in summer, (Alemany et al., 2006; Torres et al., 2011), off the nearby Catalan coast (Olivar et al., 2010; Sabatés, 1990) or in other regions of the Mediterranean Sea, such as the Aegean Sea (Somarakis et al., 2002, 2011), Gulf of Gabes (Zarrad et al., 2013) or the Alboran Sea (Rodriguez, 1990). Species richness was only slightly lower or comparable to that reported for subtropical areas (e.g. Keane and Neira, 2008; Moyano and Hernandez-Leon, 2011; Muhling et al., 2008). The higher species richness found in this study in relation with other previously carried out in the region, in summer, may be due to the fact that our study covered a larger area than Alemany et al. (2006) and a larger area and sampling deeper than Torres et al. (2011). In addition, larvae of large migratory tuna and other pelagic species that reproduce around the Balearic archipelago, the large area covered in this study, including the island shelves and the oceanic region, and the great number of stations sampled could explain the higher specific richness found in this study in relation with other . Mediterranean regions.

The patterns of horizontal distribution shown by species richness and diversity, with the highest values recorded around the islands, may be related with the narrowness of the island shelves that leads to an overlap of larvae of neritic and oceanic species in the proximity of the islands. Also, eddies found in the area could approach oceanic larvae to the islands, as reported for other marine regions (Franco et al., 2006; Lobel and Robinson, 1986; Olivar et al., 2010). For its part, the negative correlation between larval abundance and species diversity indicates that the increase in larval abundance is related with the proliferation of a single or a few taxa rather than with the increase in abundances of all taxa that made up the larval fish community.

Larval fish abundances were also higher than reported for the region by Alemany et al. (2006). But, the study of Alemany et al. (2006) was restricted to two small areas off the Mallorca Island, covering the coastal-slope region. So, the fact that larval abundances were higher in the oceanic region would account for the relatively higher larval abundance recorded in this study. Another characteristic of the LFC was that larval abundances were also higher than those found in other more productive marine regions, such as the Taiwan strait (Hsieh et al., 2012) or the California Current region (Auth and Brodeur, 2006). This finding is counterintuitive because the Mediterranean Sea in summer, as mentioned above, is considered oligotrophic. Nevertheless, during this season, in the Western Mediterranean, the DCM and the relatively high zooplankton biomass associated to it (Alcaraz, 1985) offers an important food source for fish larvae (Sabatés et al., 2007). Moreover, there may be deep zooplankton hotspots, located in the border of anticyclonic eddies and associated to the phytoplankton hotspots found in other studies (e.g. Jansa et al., 2004). These zooplankton hot spots may also constitute feeding regions for fish larvae. Furthermore, currents that flow through the islands and eddies may trap and transport neritic larvae off the island shelves (Leis, 1982; Lobel and Robinson, 1986; Olivar et al., 2010). In this sense, simulations suggest that during summer a relatively small proportion (~30%) of neritic larvae in the Balearic Islands could be advected offshore (Basterretxea et al., 2012, Chapter 2). All these factors may account for the relatively high larval fish abundance found in this recorded in the oceanic region.

In addition, the vertical distribution of larval food would also be favourable for the LFC found in the region. In stratified waters, fish larvae show a stratified vertical distribution.

With some exceptions, larvae of neritic species are distributed in the mixed layer and the upper region of the thermocline, while larvae of oceanic species show a deeper distribution, generally below the thermocline (Ahlstrom, 1959). Larvae of neritic taxa caught in this study, apart from e.g. Gobiidae and Callionymidae, show a shallow vertical distribution in the region (Olivar et al., 2010; Olivar and Sabatés, 1997; Torres et al., 2011), but also some of them perform daily vertical migrations. This is the case of larger *S. aurita* and *E. encrasicolus* larvae, the second and third most abundant neritic species caught in this study, that move downward during the daytime, to the DCM in the case of *E. encrasicolus* (Olivar et al., 2001; Sabatés et al., 2008). As for larvae of mesopelagic taxa, which widely dominated the LFC, show a deeper distribution, even below the thermocline (Olivar et al., 2010; Olivar and Sabatés, 1997; Rodriguez et al., 2006; Sabatés, 2004). Only two Gonostomatidae species *C. braueri* and *C. pygmaea* and the Myctophydae *C. maderensis* reach the surface mixed layer (Olivar et al., 2010; Rodriguez et al., 2006; Torres et al., 2011). That is to say, the vertical distribution of larval food would be favourable for most oceanic-mesopelagic larvae and also for larvae of neritic species, which are able to perform diel vertical migration. Also, the larvae of tuna and most neritic species, with shallow vertical distribution, would be favoured because they would not have to share the scarce trophic resources of the surface layers. The lack of correlation between larval fish abundance and microzooplankton biomass may be explained either by the consumption of zooplankton by fish larvae or the fact that, as indicated above, our sampling may have not included the zooplankton maximum.

Neritic larvae advected offshore do not necessarily have to get lost for the adult neritic fish populations of the islands. They may return to the island shelves, either passively transported by eddies (Franco et al., 2006; Lobel and Robinson, 1986) or actively swimming (Leis, 2007; Leis and Carson-Ewart, 1997; Stobutzki and Bellwood, 1997). In this case, eddies would also function as a nursery area for these larvae (Govoni et al., 2010; Lobel and Robinson, 1986; Logerwell and Smith, 2001; Sabatés et al., 2013). It has to be indicated that neritic larvae caught in the oceanic region were advanced larvae (even juveniles), in apparently very good condition (author's personal observation). Moreover, some of these larvae, e.g. *Mullus* and *Bothidae* species, have a long pelagic stage (Macpherson and Raventos, 2006; Russell, 1976). These two aspects would increase the chance of survival for those larvae.

Multivariate analysis indicates that depth and, consequently, the spawning location of adult fishes were the main factors in shaping the horizontal structure of the LFC. This is consistent with that reported in previous LFC studies in our study area (Alemany et al., 2006), other regions in the Mediterranean Sea (Sabatés, 1990; Somarakis et al., 2011) and elsewhere in the world (Auth, 2008; Muhling and Beckley, 2007; Rodriguez et al., 2009). The influence of depth on larval fish distribution is clear in the case of larvae of neritic species, which most of them clustered on the very right side of the CCA biplot, but not for oceanic taxa. The clustering of most of these taxa near the centre of the CCA biplot suggests that their distribution was little influenced by any of the environmental variables considered in this study (ter Braak, 1986). However, in the case of depth this may be an artefact caused by the narrowness of the island shelf. In fact, 88% of the ichthyoplankton stations were deeper than 200 m and 95% were deeper than 100 m. This would explain the high percentage of occurrences and the wide horizontal distribution shown by many oceanic taxa. For its part, the significant correlation found between larval abundances and geostrophic velocity suggests some accumulation of fish larvae in anticyclonic eddy borders. This agrees with Lindo-Atichati et al. (2012) who, in the Gulf of Mexico, found higher densities of *T. thynnus* and *Auxis* spp in the boundaries of anticyclonic eddy regions.

The apparently low influence that mesoscale oceanographic features had on the horizontal structure of the LFC in this highly dynamic region contrasts with the large influence that mesoscale features have on the horizontal structure of the LFC in similar regions, e.g. off the nearby Catalan coast (Olivar et al., 2010; Sabatés, 1990; Sabatés et al., 2007) and other places around the world (Franco et al., 2006; Holliday et al., 2011; Keane and Neira, 2008; Rodriguez et al., 2004). The scenario of relatively high hydrographic stability found during the cruise should explain the low influence of mesoscale oceanographic features on the horizontal structure of the LFC. Also, the presence of only two LFAs, a coastal and an offshore, reported for other regions with a narrow continental shelf (Auth and Brodeur, 2006; Richardson and Pearcy, 1977; Rodriguez et al., 2009), indicates that, despite the narrowness of the shelf, most neritic larvae remain in the neritic region and most oceanic larvae in the oceanic region. This would agree with the above mentioned Basterretxea et al. (2012, Chapter 2) simulation results that suggest most neritic larvae during summer, in the Balearic Islands, remain in the neritic region.

In summary, the Balearic region during early summer harbours a relatively abundant and diverse LFC dominated by larvae of oceanic mesopelagic species. Larval fish assemblages were mainly delineated by depth and consequently by the spawning location of adult fish. Thus, our hypothesis that the structure of the LFC should reflect the mesoscale oceanographic features of the region was not confirmed. The unusual, from the meteorological and hydrographical point of view, 2005 year and the scenario of higher-than usual hydrographic stability would be responsible for the relatively lack of mesoscale features and, consequently, for the lack of influence of these features on the horizontal distribution and structure of the LFC.

ACKNOWLEDGMENTS

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CHAPTER 5

Larval fish assemblage structure in the surface layer of the NW Mediterranean under contrasting oceanographic scenarios

Abstract

During the summer season, the relative influence of resident Atlantic Waters (AW) and new AW largely drives the mesoscale dynamics around the Balearic Islands (NW Mediterranean). Two principal summer hydrographic scenarios were identified in the region, mainly differentiated by the relative position of the density front between new and resident AW within the archipelago and its associated mesoscale activity. In this study we investigated how those early summer mesoscale scenarios influence the summer larval fish assemblages, by analysing data from two representing cruises of those two scenarios (2004 and 2005). Redundancy analysis (RDA) was used to assess the variance in the larval fish assemblage that could be significantly explained by the most parsimonious combination of available environmental variables in both years. While depth was the most important variable in explaining the larval fish assemblage structure variability observed under both scenarios, indicators of mesoscale activity (dynamic height, geostrophic velocity) contributed significantly to understanding the dynamics of the larval fish community. Mesoscale activity was higher in summer 2004, leading to higher larval fish abundances and zooplankton biomass and lower larval fish diversity than in the warmer than usual summer 2005, which showed lower mesoscale activity. The larval assemblage dynamics are discussed in terms of extrinsic and species-specific factors.

5.1. INTRODUCTION

The Mediterranean Sea is considered an oligotrophic deep basin with a dominant thermohaline circulation and high mesoscale activity (Antoine et al., 1995). In the NW Mediterranean (Fig. 5.1), this activity is particularly high in the Balearic region, considered a transitional zone in terms of hydrography between the fresher AW of the Algerian basin and the colder and saltier resident AW of the Provençal basin (Salat, 1995; Pinot et al., 2002; Millot, 2005). The regional circulation in the Western Mediterranean has been previously described by Millot (1987) and Millot and Taupier-Letage (2005). A major surface current of Atlantic waters entering the Mediterranean by the strait of Gibraltar (herein referred to as new AW), forming the Algerian Current, flows eastwards close to the coasts of North Africa (Fig. 5.1a). Due to its instability, filaments and eddies, which can reach the Balearic archipelago, are detached from this current. A branch of this current enters the eastern Mediterranean (outside of the figure 5.1a), and the other branch progresses northwards following an anti-clockwise pattern, returning to the westernmost Mediterranean Sea as the Northern Current (NC). The NC, formed by modified (saltier) surface Atlantic Waters (herein, resident AW), flows westwards and southwards along the continental slope of the north-western Mediterranean (Fig. 5.1a). Depending on the hydrodynamic scenario in the Mallorca and Ibiza channels, this current can cross the Ibiza channel or be deflected to the Balearic archipelago, reinforcing the so-called Balearic Current (BC), which flows north-eastwards along the NW Mallorca Island slope (Fig. 5.1a; Pinot, 2002).

The interannual variability of the summer circulation around the Balearic Islands mostly depends on the presence or absence of Western Intermediate Water (WIW) in the archipelago channels (Balbín et al., 2014). WIW is formed in winter over the northern Mediterranean continental shelf and slopes and transported by the NC, into the Gulf of Valencia and the Ibiza channel, between the end of winter and beginning of spring. WIW is not found in the Balearic channels every year and its presence or absence is the origin of the two main summer hydrographic scenarios: i) presence (Fig. 5.1b) or ii) absence (Fig. 5.1c) of WIW in the island channels. The presence of WIW in the island channels acts as a barrier to the northward flow of new AW in the Ibiza Channel. This new AW is therefore forced to progress north-eastward, south of Ibiza and Formentera Islands,

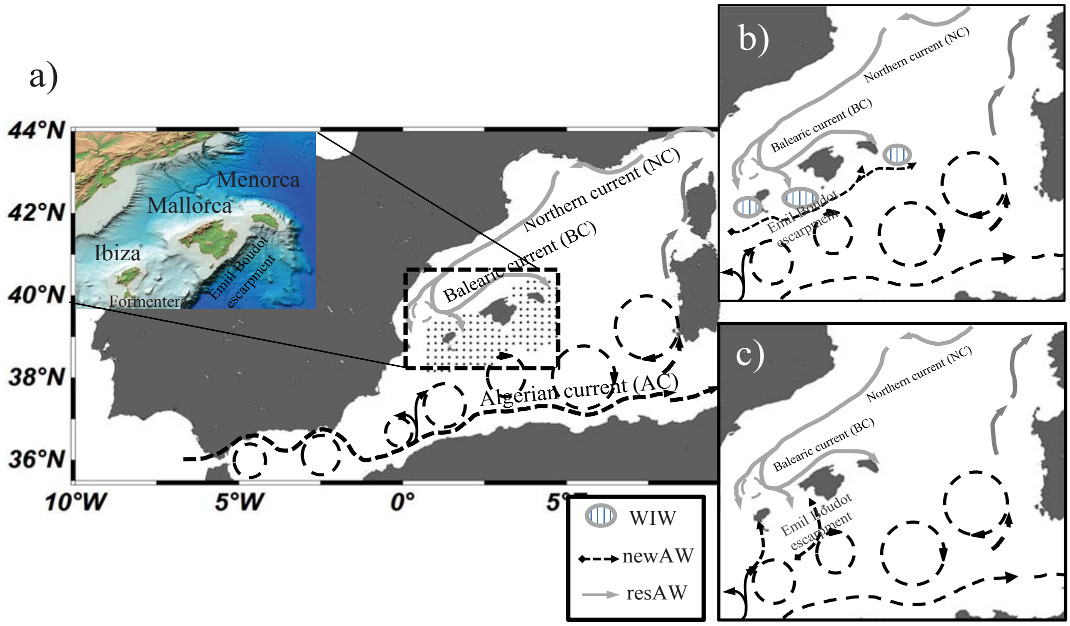


Figure 5.1. a) Study area, sampling stations and the general circulation scheme for the Western Mediterranean. b) Distribution of water masses under Scenario i and c) Scenario ii. (See text for descriptions of the scenarios).

towards Mallorca Island. In this scenario, the density front that separates the new AW (coming from the south) and resident AW (coming from the north) is located in the south of the archipelago usually along the Emil Baudot escarpment (Fig.5.1). Alternatively, the absence of WIW in the channels facilitates the southward flow of the NC, near the mainland continental slope, and the northward progression of new AW, through the eastern part of the Ibiza channel, close to the Ibiza Island slope (Fig. 5.1c). Under this scenario, the density front appears north of 39ºN in the western part of the Balearic region. Based on the available time-series in the literature (2001-2005 and 2012), scenario i was observed during the summers of 2002, 2003, 2004 and 2012, while scenario ii appeared in 2001 and 2005 (Balbín et al., 2014). Other mesoscale structures, such as eddies of new AW, occupying the southern part of the Ibiza channel, may constitute an obstacle to the southward flow of the NC, blocking its passage through the Ibiza channel. In this area and due to the presence of strong haline gradients, salinity is the most conservative variable, characterizing the different water masses.

Seasonality is a dominant feature in the region and largely drives productivity processes. Associated effects of seasonality are winter mixing and the formation in summer of the deep chlorophyll maximum (DCM) at open waters. The DCM can sustain higher than expected primary and secondary production (Estrada 1985; Sabatés et al., 2007; Macías et al., 2014). In the NW Mediterranean, this production is also influenced at different spatio-temporal scales by continental water inputs, currents, eddies, surface fronts and wind episodes (Sabatés et al., 2007). Frontal mesoscale events between new and resident AW and input of cold northern water into the channels can also act as external fertilization mechanisms that enhance productivity off the Balearic Islands (Pinot et al., 1995, Fernández de Puelles et al., 2004). Under scenario i, the productivity of the region is more dependent on the sub- and surface phytoplankton concentration in new AW, while under scenario ii, with higher areas occupied by resident AW, production patterns are more dependent on primary production at the DCM (Hidalgo et al., 2014).

In addition to these environmental factors, adult fish inhabiting particular depths/water masses respond to thermal cues and photoperiod to display a particular spawning period (Sabatés et al., 2007). Most fish species in the Mediterranean spawn in spring-summer (Tsikliras et al., 2010) and larval fish diversity during that season is relatively high, comparable to tropical regions (Thorrold and Williams, 1996; Álvarez et al., 2012, Chapter 1).

Currently there are no studies tackling how these two complex environmental scenarios affect the ichthyoplankton community. Summer larval fish assemblages have been previously described for the Balearic region, but most of these studies were conducted at scales smaller than that required to adequately address mesoscale dynamics (Alemany et al., 2006; Torres et al., 2011; Basterretxea et al., 2013; Chapter 2). At a regional scale, the temporal and spatial partitioning of the spawning habitat of Bluefin tuna (*Thunnus thynnus*), albacore (*Thunnus alalunga*) and bullet tuna (*Auxis rochei*) in the Balearic region have already been determined (Reglero et al., 2012). Covering a wide area in the archipelago, Rodríguez et al. (2013, Chapter 4) found that under the hydrographic scenario ii, the larval fish assemblages in the area are not significantly driven by any mesoscale structure but are related to the habitat of the adult fishes.

The aim of the present study was to investigate to what degree the structure of the summer larval fish community responds to extrinsic forcing (including mesoscale forcing) derived from the processes associated with the two well-differentiated scenarios. For this purpose, we extended the study conducted by Rodríguez et al. (2013, Chapter 4) for the summer of 2005 (scenario ii, low mesoscale activity) with data from a methodologically comparable survey carried out in the summer of 2004 (scenario i, high mesoscale activity, Balbín et al., 2014). The relevance of these extreme hydrographic scenarios for fish populations as well as the interacting effect of unaccounted variables such as adult habitat requirements and critical habitats for the spawning of different species is discussed. Moreover, mesoscale hydrographic features have been shown to influence the habitat and therefore the larval fish community structure (Bakun, 2006) although the ecological processes through which mesoscale processes affect larval assemblages are not clear. Therefore, we hypothesise that, in the presence of contrasting oceanographic scenarios (in terms of mesoscale processes), mesoscale-related variables should partly explain differences in larval fish assemblages between scenarios.

5.2. MATERIAL AND METHODS

5.2.1. Sample Collection and Treatment

This study is based on data and samples collected on the Tunibal 04 and Tunibal 05 cruises, conducted in the Balearic region, NW Mediterranean (Fig. 5.1). Tunibal 04 was carried out from June 18 to July 8, 2004 and Tunibal 05 was from June 27 to July 23, 2005.

A regular grid of stations, 10 nautical miles apart, was defined for the area, from which 165 stations were sampled in 2004 and 183 in 2005. For this comparative study and in order to maximise spatial coherence, we selected the stations sampled in both years (n= 143; Fig. 5.1a). At each station, vertical profiles, from the surface down to 350 m depth (or 650 m at selected stations), of temperature, conductivity and fluorescence were obtained with a SBE 911 CTD (Sea Bird Electronics).

To estimate the potential food available for fish larvae, microzooplankton samples were obtained with a 55-µm CalVet net hauled vertically from 70 m depth to the surface. Samples were immediately sieved through a device consisting of two nets: a 200-µm mesh net to separate the macro and mesozooplankton fraction (which were discarded) and a 55-µm mesh net to retain microzooplankton, which was stored in Petri dishes at -20 ºC. Upon reaching the laboratory, the dry weight biomass was obtained following Lovegrove (1966). Microzooplankton biomass values were standardised to mg m^{-3}.

Ichthyoplankton samples were collected with a Bongo net (60 cm of mouth diameter) equipped with 200-µm and 335-µm mesh size nets. Oblique tows were performed down only to 70 m depth, as surveys were designed for tuna larvae sampling and these larvae inhabit the upper layers of the water column (Olivar et al., 2010; Olivar et al., 2014). The volume of water filtered was measured with a General Oceanic flowmeter placed in each mouth of the net. The 335-µm fraction was preserved in a 4% sodium tetraborate-buffered formaldehyde solution . All fish larvae from the 335-µm net samples were sorted in the laboratory. Due to the large number of samples, they were split and sent to two different laboratories for the identification of fish larvae. Each laboratory received the samples from one complete survey. All fish larvae were counted and identified to the lowest taxonomic level possible. For each station, larval fish catches were standardised to the number of larvae per m^{-2}. To avoid any bias caused by differences in the level of precision in the taxonomic identifications between laboratories, the two resulting faunistic lists were standardised to the lowest taxonomic level common to both laboratories. Note that the key differences in the structures of larval fish assemblages can be detected even at the family level (Carassou et al., 2012b). Moreover, a third ichthyoplankton taxonomist (Dr. F. Alemany) was consulted for doubtful specimens.

5.2.2. Data treatment

a) Hydrography

The CTD profiles, obtained at every station, were processed at the original sampling frequency and averaged at 1 m intervals. Hydrographic horizontal fields (see the Multivariate analyses section for descriptions of selected variables) were calculated from CTD casts. Vertical integration of the specific volume anomaly from the level of 600 dbar, chosen as the level of no motion (Pinot et al., 2002), was used to calculate the dynamic height (DH) at 10 dbar. For the shallower stations (<600 m depths, ~25% of the stations), the DH anomaly was extrapolated from the nearest deep stations (>600 m). DH profiles were interpolated into a regular grid following a standard optimal interpolation scheme, using an isotropic Gaussian correlation (Bretherton et al., 1976; Pedder 1993). The first derivative of the resulting DH field was used to calculate the module and direction of the geostrophic velocity (GV) at 10 dbar. DH was used as an indicator of eddies and frontal regions because DH should be higher than average in anticyclonic and frontal regions and lower than average in cyclonic eddy regions (Lindo-Atichati et al., 2012). Also, this variable integrates the effects of multiple other hydrographic variables (Asch and Checkley, 2013). GV was used as an indicator of eddy boundaries and frontal regions, as the geostrophic velocity should be higher in these regions (Bakun, 2006).

Brunt-Väisälä Stratification Index (N, Hz) was calculated following Mann and Lazier (1996) at every meter for each station, discarding the upper 2 meters of the water column. The maximum N value for each station was selected as the stratification index. Sea surface temperature (SST) data were not used in statistical tests because a preliminary analysis indicated that this variable could not be considered synoptic for the surveys. Therefore, it was not valid for the identification of water masses.

b) Biological data: Fluorescence and fish larvae

Fluorescence data from CTD casts were only available for 80% of the stations in 2004. Hence, this variable was excluded from the multivariate analyses. However, these data were employed in the discussion of the observed patterns in the areas where they were available.

For each taxon and survey, the frequency of occurrence (FO, percentage of stations where a taxon occurred) and numerical frequency (NF, percentage contribution of a taxon to the total number of individuals) were also calculated.

5.2.3. Multivariate analyses: Environment-larval fish relationships

a) Identification of the main environmental variables and the main larval fish assemblages

First, an exploratory principal component analysis (PCA) was performed with the aim of describing the main environmental processes observed during the surveys. We performed the PCA on the correlation matrix of environmental variables, which included station depth (D, m), mixed layer depth (ZM, m), dynamic height at 10db (DH, J kg^{-1}), geostrophic velocity at 10 db (GV, cm s^{-1}), sea surface salinity (SSS, salinity at 10 db), Brunt-Väisälä stratification index (N, Hz), Solar Elevation (SUN, degrees) and microzooplankton biomass (MB, mg m^{-3}). The solar elevation was included to detect any significant influence of time of the day in the multivariate analysis. Relevant PCA axes were chosen using the broken-stick model (Borcard et al., 2011).

To construct the taxonomic matrices for the statistical analyses, unidentified fish larvae (0.88% in 2004 and 1.25% in 2005) were not considered, and the unwanted influence of rare species on the analyses was avoided by including only taxa with a FO >5% and/or an NF > 0.04%.

For the initial exploration of larval fish assemblages structure, the larval fish abundance matrices were subjected to multivariate unconstrained ordination through PCA, using Hellinger's distance of centred and $\log_{10}(x+1)$-transformed values. Hellinger's distance provides a common measure allowing the combination of multivariate analyses and, in the case of biological variables, is a metric that shows similar performance to Bray-Curtis similarity (Borcard et al., 2011).

b) Modeling the environmental influences on the structure of the larval fish communities

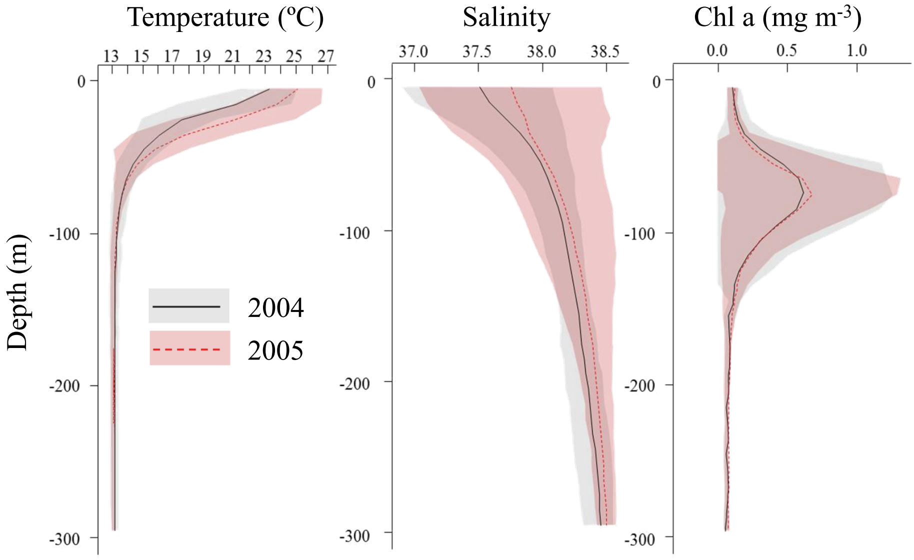
Redundancy analysis (RDA) from R package *Vegan* (Oksanen et al., 2013) was used as a constrained ordination technique to explain how much of the variability in the species structure is explained by the environmental variables, after checking for the spatial autocorrelation (Legendre and Gallagher, 2001; Borcard et al., 2011).

This technique (similar to the canonical correspondence analysis) accounts for the variance of the larval fish assemblage whose structure can be explained by an optimized linear combination of explanatory environmental variables. The best model was selected through both forward and backward modes through permutation analyses, because constrained ordination techniques cannot use the Akaike information criterion (Borcard et al., 2011). The taxon distance matrix was denoted as *spdata* and the variables to be entered in the analyses were D, ZM, DH, GV, SSS, N, SUN and MB. A maximum of five significant environmental variables were accepted to yield a reduced and relatively easy-to-interpret model.

The between-survey structure was compared separately for the environmental variables and larval fish assemblage structure through co-inertia (coIA) analysis (equivalent to covariance analysis) using the package *Ade4* (Dray and Durfour, 2007). A proxy for multivariate Pearson correlation (RV), which equals the ratio of the total co-inertia to the square root of the product of the squared total inertias from the separate analyses, was used as a comparative index (Robert and Escoufier, 1976).

5.2.4. Analysis of Diversity

The Shannon-Wiener diversity index (H’) was calculated for each station for both cruises. For consistency, we decided to use the same matrices considered in the multivariate analyses, after testing whether the diversity, calculated based on “true taxonomic categories” (in this case families), was highly correlated with diversity calculated using our taxon categories (presented in Table 5.1, reaching the species level in some cases and stopping at the family level in others) (R=0.87, p<0.0001, n=143). We conducted a minimum adequate generalised linear model (GLM) using the Akaike information criterion, employing the H’ values as a response variable and the above-mentioned environmental variables as explanatory variables. Differences in diversity between surveys and coastal (stations < 200 m depth) vs offshore regions were tested with the analysis of variance (ANOVA). In all cases, model adequacy was validated following the protocol by Zuur et al. (2010). All analyses were performed in R (R Development Core team, 2013).



mg m^{-3}) from CTD. Fluorescence data are available for 115 and 143 sampling stations for 2004 and 2005, respectively. Error bar values under 0 are not shown.

5.3. RESULTS

5.3.1. Environmental scenarios

There was a strong vertical stratification of the water column during both surveys (Fig. 5.2). Accordingly, the mean depth for the ZM was 13.45 ± 3.07 (SD) m in 2004 and 15.61 ± 5.24 m in 2005 (Fig. 5.3). The mean vertical profiles of salinity show that salinity was higher in 2005, from surface to deeper layers (Fig. 5.2). Large variability in SSS was also observed for this year (Fig. 5.2, Fig. 5.3). Vertical profiles of fluorescence showed a DCM around 80 m in both surveys, with average values of 0.5 mg m^{-3} (Fig. 5.2).

During both surveys, the sea surface temperature (SST) increased in parallel with the progress of the survey. Nevertheless, the average SST (at 10 m) in 2005 (mean 24.95 ± 0.87ºC) was much higher than in 2004 (mean 22.76 ± 0.87ºC) (Fig. 5.2). The same pattern was observed for the temperature at 25 m depth. Therefore, the surface layer was on average colder in the 2004 survey.

The horizontal distribution of integrated (0 – 100 m depth) fluorescence showed relatively similar patterns in both years, with the higher values in areas with the deeper values of ZM (Fig. 5.3c). The microzooplankton biomass (MB) ranged from 0.48 to 17.17 mg m^{-3} (mean 3.78 ± 2.49 mg m^{-3}) in 2004 and from 0.16 to 6.9 mg m^{-3} (mean 2.44 ± 1.46 mg m^{-3}) in 2005. The spatial distribution of MB was patchy, with the higher values being found in the NE part of the study area during both surveys (Fig. 5.3d). Integrated fluorescence was positively correlated to MB and negatively correlated to DH in both years (Fig. 5.4).

The exploratory analysis of the environmental variables (PCA, Fig. 5.5) yielded very similar structures for the two surveys with the main differences in the variables reflected in the third axis. In 2004, the three main axes (broken-stick model) explained 54.4% of the total variance. In 2005, slightly more variance (60.2%) was explained by three main axes.

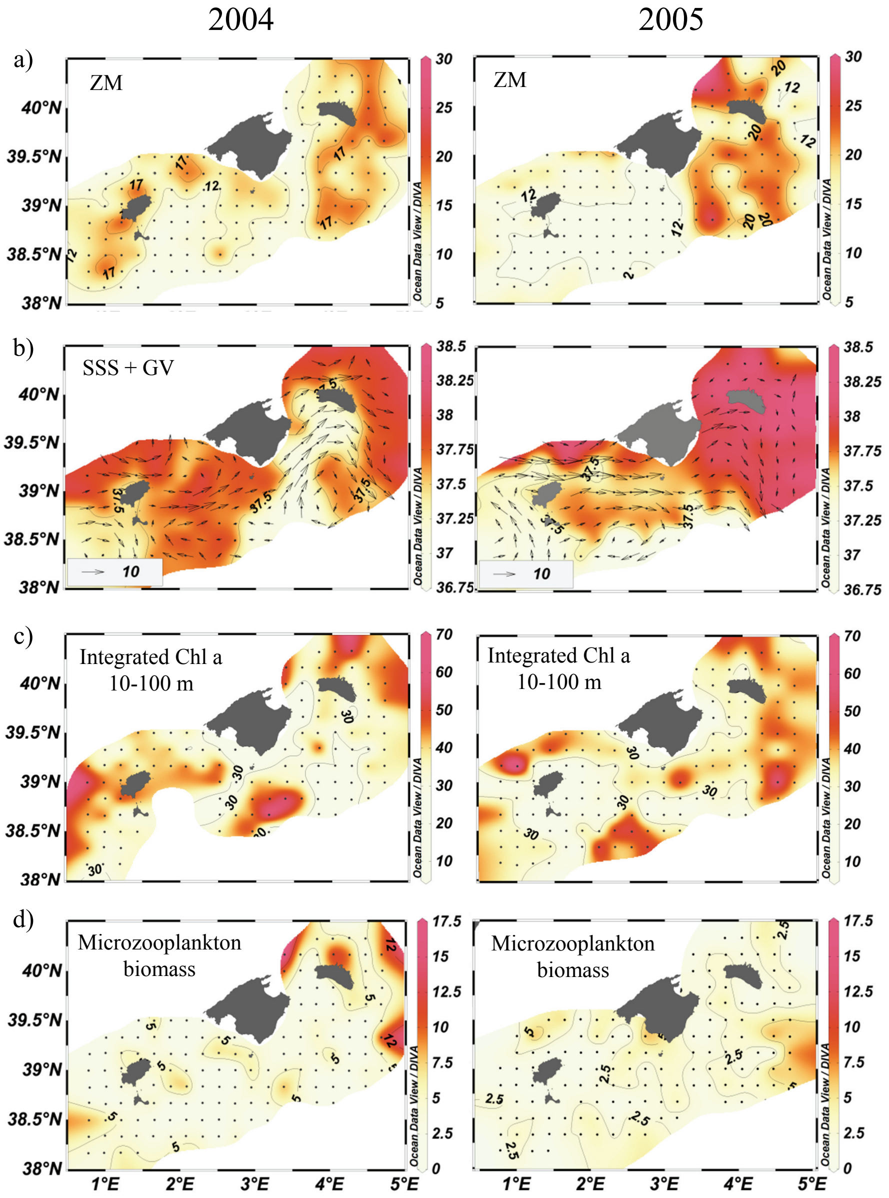


Figure 5.3. For the 2004 and 2005 sampling periods: a) Mixed layer depth (ZM, m); b) horizontal distribution of sea surface salinity (the 37.5 isohaline is considered the frontier between new and resident Atlantic Water) with superimposed derived geostrophic velocities (arrows, in cm s^{-1}); c) integrated fluorescence (Chl a, mg m^{-2}) in the first 100m of the water column; d) horizontal distribution of microzooplankton biomass (mg m^{-3}).

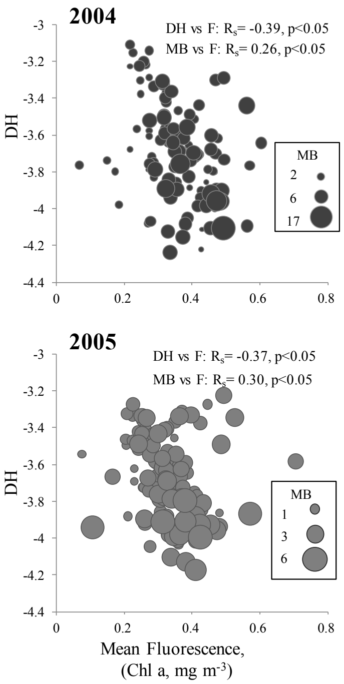
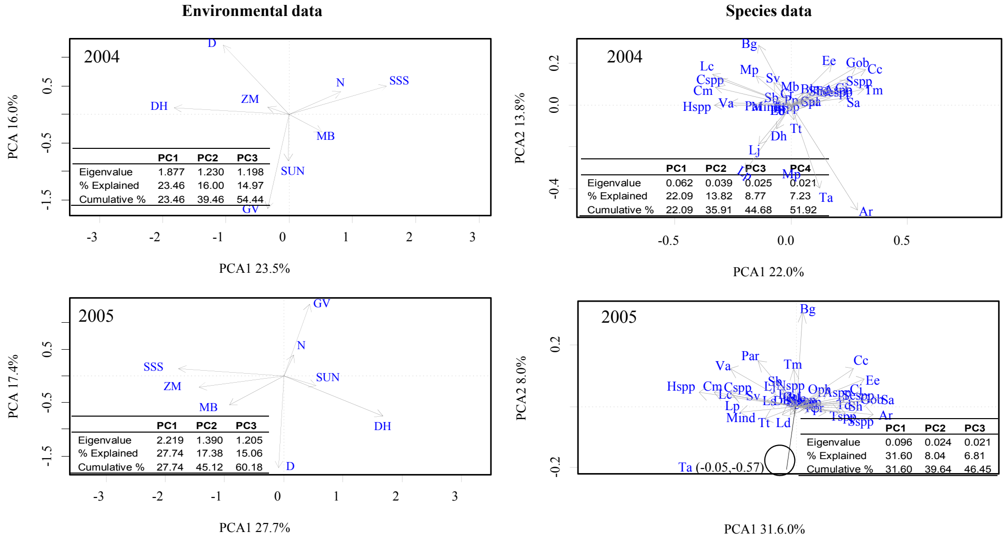


Figure 5.4. Correlations (Spearman, Rs) between mean fluorescence at 10-100m (Chl a, mg m^{-3}), dynamic height at 10 m (DH, J kg^{-1}) and Microzooplankton biomass (MB, mg m^{-3}) for both surveys. Microzooplankton is plotted as a third variable on the DH vs fluorescence graph. Note that the scales of MB are different in both years.



Environmental data, 2004:

	PC1	PC2	PC3
Eigenvalue	1.877	1.230	1.198
% Explained	23.46	16.00	14.97
Cumulative %	23.46	39.46	54.44

Species data, 2004:

	PC1	PC2	PC3	PC4
Eigenvalue	0.062	0.039	0.025	0.021
% Explained	22.09	13.82	8.77	7.23
Cumulative %	22.09	35.91	44.68	51.92

Environmental data, 2005:

	PC1	PC2	PC3
Eigenvalue	2.219	1.390	1.205
% Explained	27.74	17.38	15.06
Cumulative %	27.74	45.12	60.18

Species data, 2005:

	PC1	PC2	PC3
Eigenvalue	0.096	0.024	0.021
% Explained	31.60	8.04	6.81
Cumulative %	31.60	39.64	46.45

Figure 5.5. For each survey (2004 and 2005) and type of dataset (Environmental or species distance matrices), the PCA vectors (graphs only showing the first two axes) and PCA results (inner table) are presented for the significant axes. The codes of the vectors are explained in the text (Environmental variables) and Table 5.1 (Species data).

Table 5.1. List of taxa collected ordered by alphabetical order. Code: taxa code used in the RDA and in Figs 5.5 and Fig. 5.6. MA: mean abundance (ind m^{-2}); NF (Numerical Frequency): percentage contribution of the individuals of a species to the total number of individuals; FO (Frequency of Occurrence): percentage of stations where a species occurs. R: Rank order of abundance. Asterisks indicate taxa that were only included in the Multivariate analysis in 2004 (*) or 2005 (**).

		2004				***2005***			
Family and species	***Code***	***MA***	***NF***	***FO%***	***R***	***MA***	***NF***	***FO%***	***R***
Ammodytidae									
Gymnammodytes cicerelus	-	*0.01*	*<0.01*	*0.7*	*55*	-	-	-	-
Apogonidae									
Apogon imberbis	-	*0.01*	*0.01*	*3.5*	*47*	*0.04*	*0.04*	*3.5*	*43*
Argentinidae									
Glossanodon leioglossus	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Blennidae									
Blennidae spp	***Ble***	*0.06*	*0.04*	*9.09*	*34*	*0.03*	*0.03*	*6.99*	*46*
Bothidae									
Arnoglossus spp.	***Aspp***	*0.41*	*0.24*	*32.17*	*22*	*0.19*	*0.18*	*18.88*	*29*
Bothus podas	-	-	-	-	-	*0.02*	*0.02*	*4.9*	*50*
Bramidae									
Brama brama	***Bb****	*0.02*	*0.01*	*5.59*	*41*	*<0.01*	*<0.01*	*0.7*	*70*
Callyonimidae									
Callionymidae spp	***Cal***	*0.05*	*0.03*	*8.4*	*36*	*0.06*	*0.06*	*10.49*	*37*
Caproidae									
Capros aper	-	*0.01*	*<0.01*	*2.1*	*55*	*0.01*	*0.01*	*4.2*	*52*
Carangidae									
Caranx sp	-	*<0.01*	*<0.01*	*0.7*	*70*	-	-	-	-
Seriola dumerili	***Sd****	*0.02*	*0.01*	*3.5*	*41*	*0.05*	*0.04*	*6.29*	*41*
Trachinotus ovatus	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Trachurus mediterraneus	***Tm***	*0.93*	*0.56*	*30.07*	*12*	*0.33*	*0.33*	*17.48*	*25*
Trachurus spp.	***Tspp***	*0.08*	*0.04*	*4.9*	*33*	*1.07*	*1.01*	*11.89*	*15*
Carangidae spp	-	*<0.01*	*<0.01*	*0.7*	*70*	-	-	-	-
Carapidae									
Carapus acus	-	*<0.01*	*<0.01*	*0.7*	*70*	*<0.01*	*<0.01*	*0.7*	*70*
Centracanthidae									
Spicara spp.	***Sspp***	*1.24*	*0.8*	*12.59*	*10*	*0.58*	*0.55*	*11.19*	*20*
Centriscidae									
Macroramphosus scolopax	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Cepolidae									
Cepola rubescens	***Cr***	*0.09*	*0.06*	*9.79*	*31*	*0.34*	*0.31*	*15.38*	*26*
Chlorophthalmidae									
Chlorophthalmus agassizi	-	*<0.01*	*<0.01*	*1.4*	*63*	*<0.01*	*<0.01*	*0.7*	*70*
Clupeidae									
Sardinella aurita	***Sa***	*0.86*	*0.51*	*11.89*	*16*	*1.53*	*1.36*	*23.08*	*10*
Congridae									
Ariosoma balearicum	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Conger conger	-	*<0.01*	*<0.01*	*0.7*	*70*	-	-	-	-
Coryphaenidae									
Coryphaena hippurus	-	-	-	-	-	*0.01*	*<0.01*	*1.4*	*65*
Dactylopteridae									
Dactylopterus volitans	-	-	-	-	-	*0.01*	*0.01*	*2.1*	*57*
Engraulidae									
Engraulis encrasicolus	***Ee***	*0.92*	*0.55*	*24.48*	*13*	*1.44*	*1.4*	*32.17*	*9*
Epigonidae									
Epigonidae spp	-	*<0.01*	*<0.01*	*1.4*	*63*	-	-	-	-
Evermannellidae									
Evermannella balbo	***Eb****	*0.05*	*0.03*	*9.1*	*38*	*0.02*	*0.02*	*4.9*	*49*
Exocoetidae									
Hirundichthys rondeletii	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Gadidae									
Gadidae spp	-	*0.01*	*0.01*	*2.8*	*50*	-	-	-	-
Gobiidae									
Gobiidae spp	***Gob***	*1.04*	*0.66*	*25.87*	*11*	*1.45*	*1.34*	*21.68*	*11*
Gonostomatidae									
Cyclothone spp.	***Cspp***	*64.42*	*37.26*	*97.2*	*1*	*32.28*	*31.56*	*99.3*	*1*

Table 5.1. (*Continued)*

		2004				***2005***			
Family and species	***Code***	***MA***	***NF***	***FO%***	***R***	***MA***	***NF***	***FO%***	***R***
Labridae									
Coris julis	***Cj***	*0.62*	*0.36*	*30.07*	*20*	*0.69*	*0.67*	*32.87*	*18*
Symphodus spp.	***Sysp*****	*0.03*	*0.02*	*4.2*	*39*	*0.04*	*0.04*	*4.9*	*40*
Thalassoma pavo	-	*<0.01*	*<0.01*	*0.7*	*70*	*0.02*	*0.02*	*2.8*	*47*
Xyrichtys novacula	-	-	-	-	-	*0.01*	*0.01*	*2.1*	*52*
Labridae spp	-	*0.01*	*0.01*	*2.1*	*50*	-	-	-	-
Lophotidae									
Lophotus lacepede	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Merlucciidae									
Merluccius merluccius	-	-	-	-	-	*0.01*	*0.01*	*2.1*	*61*
Monacanthidae									
Anacanthus A	-	-	-	-	-	*0.01*	*<0.01*	*0.7*	*65*
Moronidae									
Dicentrarchus labrax	-	*0.01*	*<0.01*	*2.1*	*55*	-	-	-	-
Mugilidae									
Mugil cephalus	-	-	-	-	-	*0.01*	*0.01*	*3.5*	*52*
Mugilidae spp	-	*0.01*	*0.01*	*2.1*	*50*	-	-	-	-
Mullidae									
Mullus barbatus	***Mb****	*0.12*	*0.07*	*14.69*	*30*	*0.03*	*0.03*	*4.9*	*45*
Mullus surmuletus	-	*0.01*	*0.01*	*2.8*	*47*	*0.01*	*0.01*	*2.1*	*61*
Muraenidae									
Muraenidae spp	-	*<0.01*	*<0.01*	*1.4*	*63*	*<0.01*	*<0.01*	*0.7*	*70*
Myctophidae									
Benthosema glaciale	***Bg***	*0.81*	*0.5*	*35.66*	*17*	*2.12*	*2.01*	*60.14*	*7*
Ceratoscopelus maderensis	***Cm***	*41.02*	*24.28*	*95.8*	*2*	*15.17*	*15.08*	*97.2*	*3*
Diaphus holtii	***Dh***	*0.36*	*0.22*	*34.27*	*23*	*0.05*	*0.05*	*11.89*	*38*
Diaphus spp.	-	-	-	-	-	*<0.01*	*<0.01*	*1.4*	*65*
Hygophum spp.	***Hspp***	*35.18*	*20.07*	*95.1*	*3*	*24.94*	*24.55*	*93.71*	*2*
Lampanyctus crocodilus	***Lc***	*4.71*	*2.76*	*86.71*	*4*	*4.48*	*4.38*	*86.01*	*4*
Lampanyctus pusillus	***Lp***	*4.04*	*2.29*	*76.92*	*5*	*2.23*	*2.19*	*82.52*	*6*
Lampanyctus spp.	***Lspp*****	-	-	-	-	*0.07*	*0.06*	*1.4*	*36*
Lobianchia dofleini	***Ld***	*0.06*	*0.03*	*8.4*	*36*	*0.14*	*0.14*	*23.78*	*32*
Lobianchia gemellarii	-	-	-	-	-	*0.01*	*0.01*	*2.1*	*57*
Myctophum punctatum	***Mp***	*0.55*	*0.32*	*45.45*	*21*	*0.17*	*0.16*	*18.18*	*30*
Notoscopelus spp.	***Nspp*****	*<0.01*	*<0.01*	*0.7*	*70*	*0.07*	*0.07*	*15.38*	*34*
Symbolophorus veranyi	***Sv***	*0.2*	*0.13*	*26.57*	*28*	*0.51*	*0.49*	*46.85*	*21*
Myctophidae spp	***Mind***	*0.11*	*0.06*	*4.2*	*31*	*0.74*	*0.74*	*49.65*	*17*
Nomeidae									
Cubiceps gracilis	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Ophichthidae									
Dalophis imberbis	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Ophididae									
Ophididae spp	***Oph*****	*0.02*	*0.02*	*3.5*	*40*	*0.08*	*0.08*	*11.89*	*33*
Paralepididae									
Lestidiops jayakari	***Lj***	*0.92*	*0.53*	*60.84*	*14*	*0.57*	*0.59*	*62.24*	*19*
Lestidiops sphyrenoides	***Ls*****	*0.01*	*0.01*	*1.4*	*47*	*0.04*	*0.04*	*8.39*	*42*
Paralepididae spp	***Par***	*0.92*	*0.52*	*58.04*	*15*	*1.08*	*1.03*	*67.13*	*14*
Pleuronectidae									
Pleuronectidae spp	-	*<0.01*	*<0.01*	*1.4*	*63*	*<0.01*	*<0.01*	*0.7*	*70*
Pomacentridae									
Chromis chromis	***Cc***	*1.34*	*0.81*	*30.77*	*9*	*0.79*	*0.75*	*38.46*	*16*
Posichthyidae									
Ichthyococcus ovatus	-	*<0.01*	*<0.01*	*0.7*	*70*	-	-	-	-
Vinciguerria attenuata	***Va***	*3.2*	*1.84*	*69.93*	*6*	*1.53*	*1.48*	*75.52*	*8*

Table 5.1. (*Continued)*

Family and species	***Code***	***2004***				***2005***			
		MA	***NF***	***FO%***	***R***	***MA***	***NF***	***FO%***	***R***
Scombridae									
Auxis rochei	***Ar***	*2.75*	*1.62*	*61.54*	*7*	*2.58*	*2.4*	*45.45*	*5*
Euthynnus alletteratus	***Ea*****	*0.01*	*<0.01*	*1.4*	*55*	*0.07*	*0.06*	*5.59*	*35*
Katsuwonus pelamis	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Scomber japonicus	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Thunnus alalunga	***Ta***	*0.86*	*0.49*	*36.36*	*18*	*1.28*	*1.26*	*58.74*	*12*
Thunnus thynnus	***Tt***	*0.58*	*0.39*	*16.08*	*19*	*0.41*	*0.42*	*24.48*	*23*
Tunidae small	-	-	-	-	-	*0.01*	*0.01*	*0.7*	*55*
Serranidae									
Anthias anthias	-	*0.01*	*<0.01*	*1.4*	*55*	*0.01*	*0.01*	*2.1*	*61*
Serranus cabrilla/scriba	***Sespp***	*0.31*	*0.18*	*20.28*	*24*	*0.39*	*0.38*	*22.38*	*24*
Serranus hepatus	***Sh***	*0.26*	*0.16*	*11.19*	*25*	*0.45*	*0.43*	*16.08*	*22*
Scomberesocidae									
Scomberesox saurus	-	*<0.01*	*<0.01*	*0.7*	*70*	-	-	-	-
Scorpaenidae									
Scorpaena porcus	-	*<0.01*	*<0.01*	*0.7*	*70*	*<0.01*	*<0.01*	*1.4*	*65*
Scorpaena sp.	***Scspp*****	*0.02*	*0.01*	*3.5*	*45*	*0.02*	*0.02*	*5.59*	*48*
Sternoptychidae									
Maurolicus muelleri	-	*0.02*	*0.01*	*3.5*	*46*	*0.01*	*0.01*	*2.1*	*55*
Stomiidae									
Bathophilus nigerrimus	-	*<0.01*	*<0.01*	*0.7*	*70*	-	-	-	-
Borostomias antarcticus	-	*<0.01*	*<0.01*	*0.7*	*70*	*<0.01*	*<0.01*	*0.7*	*65*
Chauliodus sloani	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Stomias boa	***Sb***	*0.15*	*0.09*	*27.27*	*29*	*0.22*	*0.22*	*34.27*	*27*
Stomiidae spp	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Soleidae									
Buglossidium luteum	-	*0.01*	*<0.01*	*1.4*	*55*	-	-	-	-
Sparidae									
Centracanthus cirrus	-	*<0.01*	*<0.01*	*0.7*	*63*	-	-	-	-
Pagrus pagrus	***Pp***	*0.06*	*0.04*	*5.6*	*35*	*0.17*	*0.16*	*7.69*	*31*
Sparidae spp	***Spa***	*0.25*	*0.15*	*16.08*	*27*	*0.05*	*0.05*	*7.69*	*39*
Sphyraenidae									
Sphyraena sphyraena	-	*0.01*	*<0.01*	*1.4*	*55*	-	-	-	-
Syngnathidae									
Nerophis ophidion	-	-	-	-	-	*<0.01*	*<0.01*	*0.7*	*70*
Synodontidae									
Synodus saurus	-	*0.02*	*0.01*	*4.9*	*41*	*0.01*	*0.01*	*2.8*	*57*
Trachinidae									
Trachinus draco	***Td***	*0.24*	*0.15*	*11.89*	*26*	*0.21*	*0.21*	*13.29*	*28*
Trachinus spp.	-	*0.01*	*0.01*	*0.7*	*50*	*0.01*	*0.01*	*2.1*	*61*
Trichiuridae									
Trichiurus lepturus	-	-	-	-	-	*0.03*	*0.02*	*3.5*	*44*
Triglidae									
Eutrigla gurnardus	-	*0.01*	*0.01*	*1.4*	*50*	-	-	-	-
Eutrigla sp	-	*0.01*	*<0.01*	*0.7*	*55*	-	-	-	-
Lepidotrigla spp.	-	*<0.01*	*<0.01*	*0.7*	*63*	-	-	-	-
Triglidae spp	-	*0.02*	*0.01*	*4.2*	*41*	*0.01*	*0.01*	*2.8*	*57*
Uranoscopidae									
Uranoscopus scaber	-	*<0.01*	*<0.01*	*0.7*	*70*	*<0.01*	*<0.01*	*0.7*	*70*
Xiphiidae									
Xiphias gladius	-	*<0.01*	*<0.01*	*1.4*	*63*	*0.02*	*0.02*	*4.9*	*50*
Unidentified larvae		*1.45*	*0.87*	*44.06*	*8*	*1.38*	*1.25*	*34.97*	*13*

5.3.2. Composition, abundance and structure of the larval fish community

A total of 61775 and 42026 fish larvae were collected during the 2004 and 2005 surveys, respectively. For the 2004 survey, a total of 61231 larvae (99.1% of the total), belonging to 80 taxa (52 species, 13 genus and 15 families), were identified. A similar percentage of larvae, 98.7%, were identified for the 2005 survey in 88 taxa (63 species, 12 genus and 13 families). The mean larval fish abundance was higher in 2004 (172 larvae m^{-2}, range 0-876 larvae m^{-2}) than in 2005 (103 larvae m^{-2}, range 0-247 larvae m^{-2}).

The most abundant taxa for both years were the mesopelagic species *Cyclothone* spp., *Ceratoscopelus maderensis*, *Hygophum* spp. and *Lampanyctus crocodilus* (Table 5.1, Fig. 5.6). The abundance of these taxa was consistently higher in the 2004 survey (Table 5.1, Fig. 5.6). The most abundant neritic taxa were *Chromis chromis*, *Spicara* spp. and the family Gobiidae in the 2004 survey, while the epipelagic species *Engraulis encrasicolus*, *Sardinella aurita* and *Thunnus alalunga* were the most abundant in the 2005 survey. The abundance of the epipelagic species *Auxis rochei* was similar and relatively high during both surveys. The most ubiquitous species were *Cyclothone* spp, *Hygophum* spp. and the genus *Lampanyctus*. The most abundant oceanic species showed similar frequencies of occurrence in both surveys.

Excluding rare taxa, a total of 38 taxa from the 2004 and 43 from the 2005 data sets were included in the multivariate analyses. From these selected taxa, 35 were common to both surveys (Table 5.1). The exploratory analysis of the taxa (PCA, Fig. 5.5) resulted in four main axes, explaining 51.9% of the total variance in 2004 and in three axes, explaining 46.5% of the total variance in 2005. The distribution of taxa along PC1 and PC2 was similar in both years. Thus, PC1 represented a contrast between coastal and oceanic (mesopelagic) taxa, and the PC2 axis mainly separated *A. rochei* and *T. alalunga* from the other taxa in 2004 and *T. alalunga* from the other taxa in 2005.

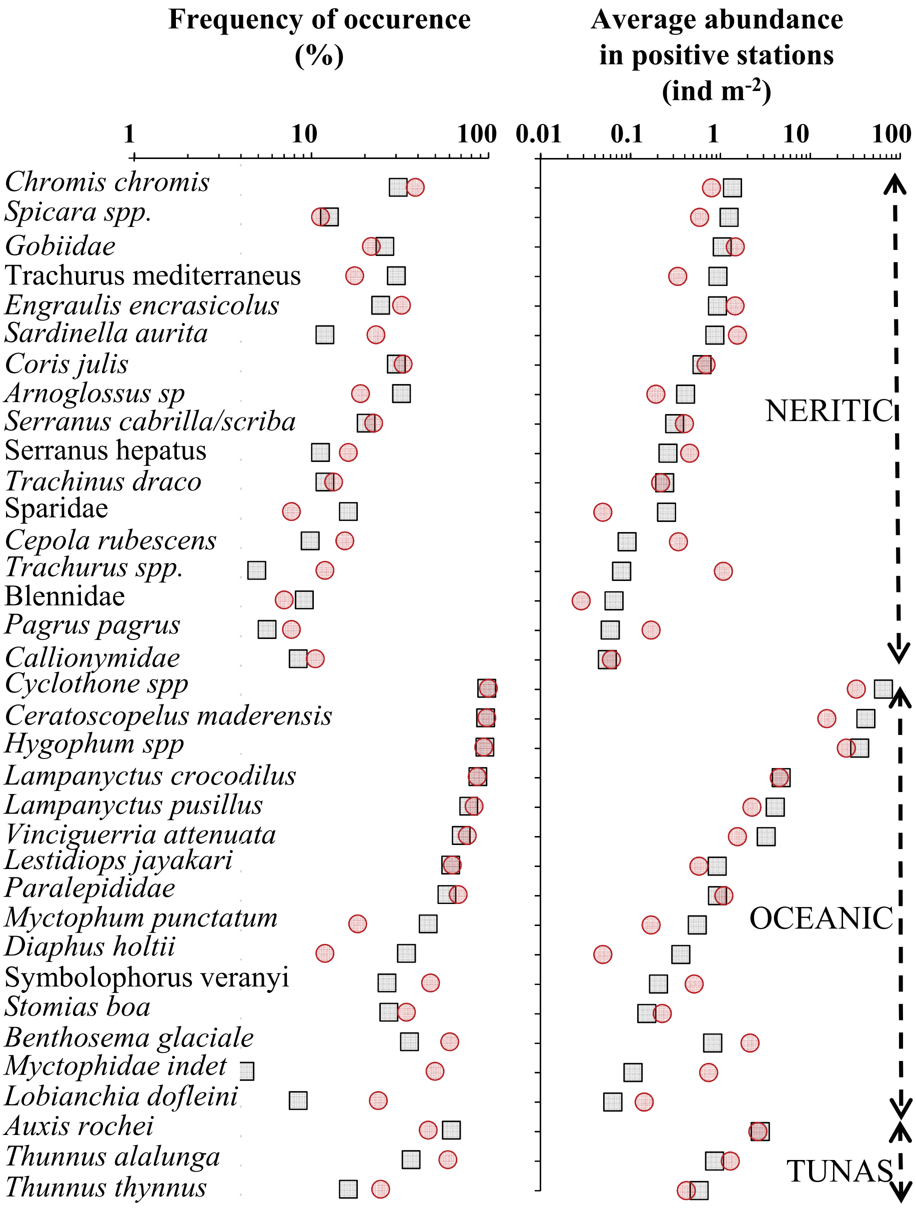


Figure 5.6. Comparison of the frequency of occurrence and average abundance of the taxa included in the multivariate analyses for (□) 2004 and (○) 2005. Note that the x axis is at a log10 scale. Three descriptive classes (neritic, oceanic and tunas) have been generated to aid in the comparison.

5.3.3. Model of the environmental influences on the structure of the larval fish community

The redundancy analysis (RDA) resulted in 3 significant axes for both years (Fig. 5.7). Also, in both surveys, the reduced models excluded SUN (time of the day-effect) and SSS.

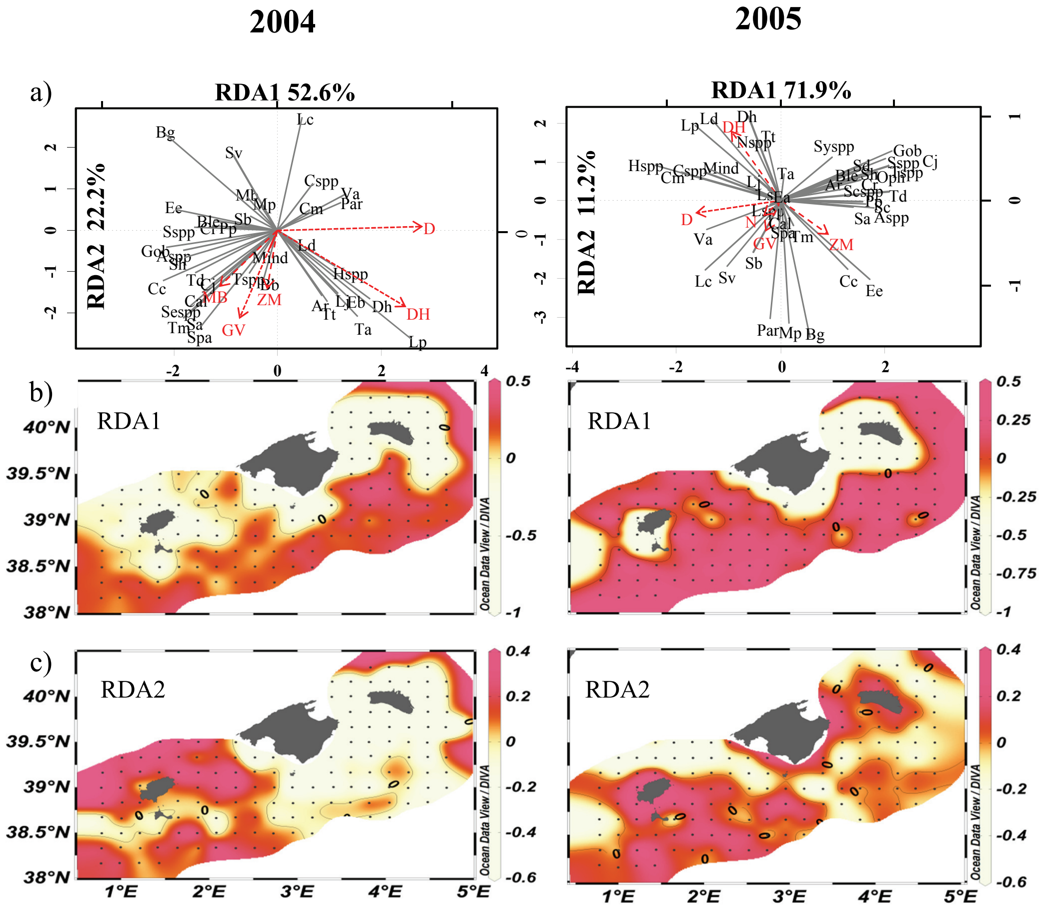


Figure 5.7. a) RDA distance triplot representing species (see Table 5.1 for taxa codes) and explanatory environmental variables: Depth (D, m), Depth of the Mixed Layer (ZM, m), Dynamic Height (DH, J kg^{-1}), Geostrophic velocity (GV, cm s^{-1}), Brunt-Väisälä Stratification Index (N, Hz) and Microzooplankton Biomass (MB, mg m^{-3}); b and c) spatial representation of the scores of the first two RDA axes.

In 2004, 9% of the variance of the larval fish community structure was explained by the significant reduced RDA model: *spdata* ~ D + DH + MB + ZM + GV, where *spdata* is the taxon distance matrix (Table 5.2). Depth and DH were clearly the main environmental drivers of RDA axis 1. A strong positive correlation of DH with mesopelagic taxa (small angles between these taxa and DH in the positive RDA1 axis) was detected. DH was highly positively correlated with *Lampanyctus pusillus* and with other Myctophids such as *Hygophum* spp. and *Symbolophorus veranyi*. However, the mesopelagic species *Benthosema glaciale* showed an opposite correlation with DH. Thunnidae species (*A. rochei*, *Thunnus thynnus* and *T. alalunga*) were also highly correlated with DH. Depth was related to neritic demersal taxa, such as *Spicara* spp., Blennidae, *Cepola rubescens* and *Pagrus pagrus*, among others, and some small neritic pelagic coastal taxa, such as *E. encrasicolus* (Figs. 5.7, 5.8). The distribution of the taxa along axis 2 responded to a combination of MB, ZM and GV, in that order (see small angles between species and explanatory variables in axis 2, Fig. 5.7). Taxa correlated with low D and high MB and ZM were those inhabiting the coastal region as adults (e.g. *Serranus* spp*., Coris julis*). An inverse response to those environmental variables on axis 2 was found for *L. crocodilus*, *Cyclothone* spp., *C. maderensis* and, again, *B. glaciale*. Some taxa showed short arrows (e.g., *Lobianchia dofleini*, unidentified Myctophidae and *Stomias boa*), which indicates a poor association with the explanatory variables (Fig. 5.7).

In 2005, the reduced model explained slightly more variance than in 2004 (11.4%, Table 5.2). The best model for this year was: *spdata* ~ D + ZM + GV + DH + N. Depth was again a key explanatory variable in RDA1 for 2005, as it was for 2004, but in this case, it operated in an inverse manner to ZM (Fig. 5.7). The large influence of RDA1 denotes D as a key variable in this survey and positive correlations with D were shown by mesopelagic taxa, whereas neritic and small pelagic species remained on the opposite side of axis 1. Furthermore, RDA2 explained half of the variance explained by the second RDA axis in the 2004 model (Fig. 5.7) and was the result of a complex combination of DH, GV and N. The strongest effect in RDA2 appeared to arise from DH, with some epipelagic species (e.g. *T. thynnus*) showing positive correlations with DH values. While in 2004, the distribution of *Myctophum punctatum* and *B. glaciale* was related to lower DH values. In this analysis*, Euthynnus alleteratus, Trachurus mediterraneus T. alalunga* and species from the *Lestidiops* genus displayed short arrows, most likely due to their low abundances (see Table 5.1).

The co-inertia (multivariate co-variability) analysis showed that the co-inertia between the larval fish assemblages in both years (RV=0.34) was slightly larger than for the environmental variables between years (RV=0.27), showing that differences between oceanographic scenarios among years (2004-2005) were higher than differences among fish assemblages (neritic-oceanic).

2004 **Overall significance of RDA**					**2005** **Overall significance of RDA**				
	DF	**Var**	**F**	**P**		**DF**	**Var**	**F**	**P**
Model	5	4.84^{c}	3.998	<0.01	Model	5	6.23^{c}	4.643	<0.001
Residual	13733.16^{u}				Residual	13736.77^{u}			
Total Var =38.00					Total Var =38.000				
% of adjusted variance explained = 9.5					% of adjusted variance explained = 11.4				
Marginal effect on species ordination	**DF**	**Var**	**F**	**P**	**Marginal effect on species ordination**	**DF**	**Var**	**F**	**P**
D	1	1.31	5.3943	<0.001	D	1	3.23	12.029	<0.001
DH	1	1.18	4.8673	<0.001	ZM	1	0.93	3.481	<0.001
BM	1	0.53	2.1829	<0.005	GV	1	0.82	3.037	<0.001
ZM	1	0.53	2.1789	<0.05	DH	1	0.60	2.234	<0.001
GV	1	0.51	2.0845	<0.05	N	1	0.60	2.222	<0.005
Residual	137					137			

Table 5.2. Results of the final RDA models for each year. The model is a linear combination of the selected variables depicted in “Marginal effect on species ordination”. Var=inertia, a proxy for multivariate variance. Permutations were 199 in all cases. c=constrained by the model, u=unconstrained. The contribution of RDA axes is referred to in the text and figure 5.6. D: Depth; ZM: Depth of the Mixed Layer; DH: Dynamic Height; GV: Geostrophic velocity; N: Brunt-Väisälä Stratification Index MB: Microzooplankton Biomass.

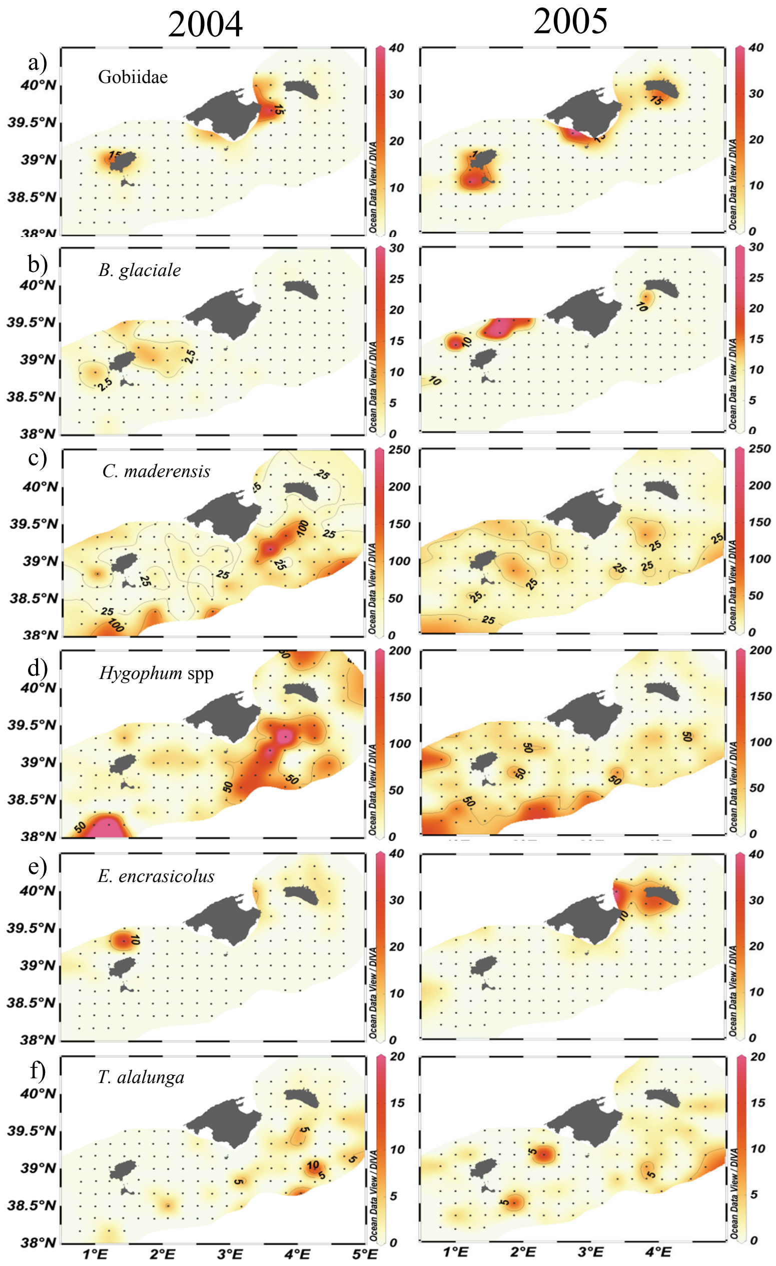


Figure 5.8. Horizontal distributions of some representative larval fish taxa (ind m^{-2}) a) Coastal species, b) Mesopelagic species inhabiting resident AW, c and d) Mesopelagic species inhabiting new AW, e) small pelagic sp. and f) big pelagic sp. Note that bars have the same length for each species.

5.3.3. Influence of the environment on larval fish diversity

The horizontal distribution of diversity visually suggested higher diversity values close to the coast (stations <200m depth; Fig. 5.9). A general linear model (GLM) revealed that the scenario in 2004 was more difficult to interpret than that in 2005. In 2004, 5 environmental variables had to be included in the GLM to explain only 8.3% of the variance in diversity (H ~ DH + GV + SUN + ZM; $Adj.R^2 = 0.08$, $F_{5,140}=3.57$, $P<0.01$). Almost three times more variance in diversity was explained in 2005 (22%), when only two significant variables were included in the model (H ~ D + ZM, $Adj. R^2=0.22$, $F_{2,140}=21.06$, $P<0.001$). As an additional analysis, an ANOVA on H' using year (2004, 2005) and a priori zonation (neritic or oceanic, based on the 200m isobath) with interaction showed no interaction effect ($F_{1,282}=0.476$, P=0.49), but significant differences in diversity were revealed between the year and zonation (Fig. 5.9). Diversity values were higher in 2005 than in 2004 (2005>2004, $F_{1,\,282}=33.86$, $P<0.001$) and for both surveys diversity was higher at the coastal stations (neritic > oceanic, $F_{1,\,282}=14.74$, $P<0.001$).

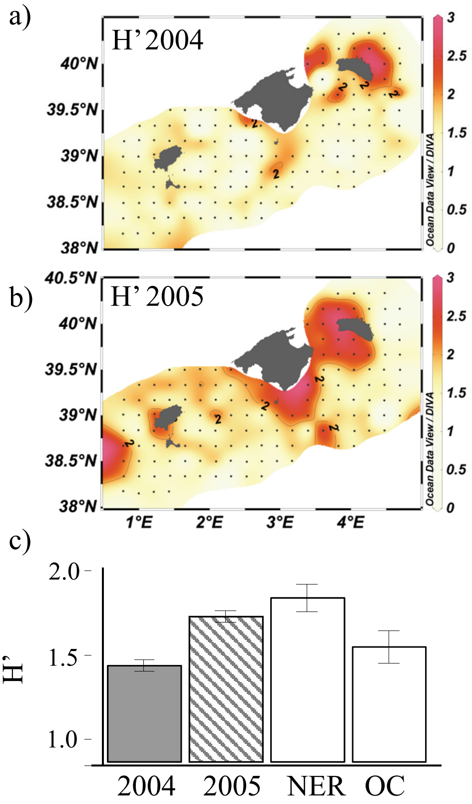


Figure 5.9. Horizontal distribution of larval fish station diversity in a) 2004 and b) 2005 surveys. c) model results (main effects) of the GLM on H'. Error bars represent one standard error. NER=neritic stations (n=35), OC=oceanic stations (n=251).

5.4. DISCUSSION

5.4.1. Oceanographic scenarios: mesoscale activity, production and microzooplankton patterns

In general, from a hydrographic point of view, 2004 can be considered to represent the high mesoscale activity summer scenario in the Balearic region showing relatively strong geostrophic currents and important inflows of new AW that reached the south of Menorca, generating a strong topographically induced gyre (Fig. 5.3b Balbín et al., 2014). On the contrary, the 2005 survey was carried out under a more stable scenario, with low mesoscale activity, since the new AW did not progress as far north as in 2004 and the mesoscale hydrographic features only occupied the southernmost part of the study area.

In terms of productivity, higher values of integrated fluorescence appeared in the areas which also presented low dynamic height values (Fig. 5.4). The higher values of microzooplankton biomass appeared to be related to higher fluorescence values and low dynamic heights. The higher values of integrated fluorescence found in 2004 are also consistent with the presence of the anticyclonic gyre. Anticyclonic gyres exhibit higher than average dynamic heights associated to downwelling processes and thus lower surface production values (Mann and Lazier, 1996). The areas associated to intrusions of new AW, which usually flow following the Emile Baudot escarpment (SE of Majorca island) and forming an anticyclonic topographically induced gyre in the area (Balbín et al., 2014), were also associated to the lowest values of microzooplankton biomass for both years (Fig. 5.3d). Jordi et al. (2009a) reported that the interannual variability and distribution of the subsurface phytoplankton biomass in the Balearic region are dominated by responses to the regional circulation rather than to biological processes, and our results support this conclusion.

5.4.2. Environmental influence on the structure of the larval fish community and diversity

Although we acknowledge that if a broader time series of data were available, a better interpretation of the results would have been possible, the analysis of data from two contrasting environmental scenarios allowed identifying the environmental key factors driving the larval fish community structure in two typical summer scenarios of our area of study. The frequency and intensity of either scenario may vary in a time-series. Also, the limitation derived from the sampling depth (70 m) has to be taken into account. Some deep distributed species might have been under-sampled or even not sampled at all, but as that limitation is common to both surveys, the comparison between them is not compromised. Moreover, the depth range of the present study includes the habitat of the vast majority of larval fish species during summer in the region (Olivar et al., 2010; Olivar et al., 2014), allowing us to draw conclusions on the larval fish community of surface waters.

Our results suggest that i) when large intrusions of new AW coming from the Alboran Sea progress to the north of the archipelago, generating high mesoscale activity in the area, the larval abundance of oceanic mesopelagic and large and medium tuna species increases. On the contrary, ii) when the density front between new and resident AW remains in the southern part of the archipelago, which results in higher general stability in the study area, the hydrographic scenario is characterized by a low general northward progression of new AW in the whole area. In this situation, the number of species inhabiting resident AW increases, probably as a result of higher dispersion of slope species to offshore waters facilitated by the absence of the density front in the middle and northern areas of the archipelago that usually forces the position of the larvae along the slope in the former scenario. In both situations, diversity remains higher in the vicinity of the islands; however, in general it is enhanced in the stable scenario. Also, high microzooplankton biomass values and neritic taxa abundance appear positively correlated in both scenarios. In the case of the stable situation (2005), this relation was hindered by the high correlation (higher than in 2004) between microzooplankton biomass and the mixed layer depth. The reduced model used to explain the assemblages structure variability through a combination of environmental variables does not select many correlated variables and the mixed layer depth was the one selected. The close relationship between mixed layer depth and neritic taxa in 2005 allow us to infer also high correlation with microzooplankton biomass.

Those results support the hypothesis that the changes in the hydrographic scenarios are reflected in the structure of the larval fish assemblages, at least in the upper layer of the water column. The effect of mesoscale activity on ichthyoplankton assemblages has been analyzed worldwide (Rodríguez et al., 2004; Lindo-Atichati et al., 2012; Asch and Checkley, 2013). In the NW Mediterranean, it has been extensively studied in the nearby Catalan Sea (e.g. Sabatés et al., 2007; Olivar et al., 2010) where the main differences in LFA between years have been explained through the effect of the strong shelf-slope front in that area and the effect of eddies. In the E Mediterranean, the structure and diversity of the LFA of the NE Aegean Sea was related to interannual environmental changes, mainly to cold and warm regimes described in the area (Somarakis et al., 2011b). In the Balearic archipelago, Hidalgo et al. (2014) related mixed assemblages of coexisting fish and crustacean larvae to the main geographic (e.g. bathymetry), hydrographic (e.g. salinity gradient) and biological (e.g. phytoplankton production) components of the seascape, concluding that year-specific biological and hydrographic gradients structure the meroplankton community in oceanic fronts.

5.4.3. Links between spawning strategies and larval fish assemblages

Larval fish assemblages result from the interaction of adult spawning strategies and environmental influences (Sabatés et al., 2007, Franco-Gordo et al., 2008). From the present study, some further clues about critical habitats for the spawning of different species can be extracted. Apart from the suitable habitat for fishes, the spawning requirements and larval tolerances play an important role in determining if a specific species will be able to adapt or redistribute.

Under a future scenario of increasing sea surface temperatures and water acidification (Hoegh-Guldberg and Bruno, 2010; Mora et al., 2013), local and regional species richness is expected to change through: i) the extinction of species that are unable to redistribute or adapt to new conditions; ii) the re-distribution of species in northern latitudes, depending on the dispersal abilities of the species and the existence of connectivity between suitable habitats; and iii) changes in spawning periods (Hiddink and Hofstede, 2008; Ben Rais et al., 2010; Calvo et al., 2011; Poloczanska et al., 2013).

The interpretation of the horizontal distribution of small fish larvae and its relationship with environmental variables has been previously used as an approach to the definition of spawning strategies. The origin of the spawning signal was used by Reglero et al. (2012) to describe the spawning strategies of tunas as environmentally or geographically driven. The term "spawning strategy" rather than "larval habitat" has been chosen based on the assumption that the small-sized larvae were spawned in the water mass where they were collected in. As it has been repeatedly shown also by other authors (Sabatés et al., 2007, 2008; Olivar et al., 2012), depth was the main variable involved in the separation between coastal and oceanic larval fish species (Fig. 5.7, First RDA axis for both years). Species showing depth as the main variable influencing their distribution might well be classified as "geographical spawners". Some purely geographical spawners (e.g., Gobiidae, *C. rubescens*, Blennidae) appear to be only related to depth in the present study, which has also been observed elsewhere (Alemany et al., 2006; Somarakis et al., 2011b; Basterretxea et al., 2013, Chapter 2).

In contrast, other fish species depend on mesoscale or large-scale oceanographic structures to ensure successful match between their offspring and their prey (Peck et al., 2012). These "environmental spawners" may have adapted to detect changes in the environmental parameters, such as salinity, sometimes in a highly species-specific manner. The species to be included in this group are those that, in the present study (Fig. 5.7), consistently (under both hydrographic scenarios) appear closely related to the environmental variables included in the RDA (e.g., *T. thynnus*, *B. glaciale*). Large and medium tuna species (e.g., *T. thynnus*), which recurrently select frontal zones and anticyclonic eddies to the south of the archipelago for spawning during a very short period of time, would be typical environmental spawners (Alemany et al., 2006, 2010; Reglero et al., 2012; Basterretxea et al., 2013, Chapter 2). Another larval group to be included in the environmental spawners is made of mesopelagic species (*Cyclothone* spp and myctophids in general), whose abundances change depending on "environmental signals". Some of these mesopelagic species are largely ubiquitous within "oceanic" (new AW) waters (see Fig. 5.8), whereas others are more restricted to resident AW (e.g. *B. glaciale*; Alemany et al., 2006; Torres et al., 2011).

Intermediate cases which follow coastal cues (e.g., depth, and possibly also factors such as benthic production or river plumes) and are highly mobile, thus being able to exploit spatially and temporally variable scenarios (e.g., shifting spawning grounds, unlike true geographical spawners) encompass small (*E. encrasicolus, S. aurita*) to medium-sized pelagic species (e.g., *Trachurus trachurus*, *A. rochei*). The variables or combination of variables driving the signals that these species follow to spawn were probably not included in the RDA. Also, the short-time scale of fluctuations of some variables usually related to the spawning of these species (e.g. position of fronts, associated production and zooplankton biomass, Sabatés et al., 2007) could not be covered by the mesoscale sampling design. Recently, Bonanno et al. (2014), analysing habitat selection responses of *E. encrasicolus* and *S. aurita* in the Mediterranean found, as a common trend in both species that the selectivity for shallower depths was mainly associated to specific environmental processes that locally increased productivity.

Our results suggest that summer larval fish communities in the Balearic archipelago are associated to mesoscale features, which in turn are related to the dynamics of the northward progression of new AW in the Balearic region, in part conditioned by the presence or absence of WIW in the channels between the islands. A prevalence of one or the other hydrographic scenarios (involving the dominance of new or resident AW and the position of the density front between them) might result in unforeseen changes in the system. A long-term knowledge on how the community and individual species react under each hydrographic scenario may be useful for management, in the frame of anticipating climate change effects on both fished populations and the whole fish community.

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IV

GENERAL DISCUSSION

In this last section we put in context the main results of this thesis and explore shortcomings and future directions. Detailed discussion of each main finding can be found at the corresponding chapters 1 to 5 in Section III.

IV.1. Environment-LFA relationships in the Balearic Sea

General mechanisms explaining the formation, maintenance and disruption of LFAs in the Balearic Sea (see Table 2 in the Introduction Section as a summary) have been, to several degrees, shown within this thesis. Although the primary driver of LFA formation is the spawning behaviour (neritic-oceanic assemblages) in most of LFA around the world (Alpine and Hobday, 2007) and also in our area (Chapter 4, 5), it is the particular regional configuration of the Balearic archipelago what spatially modulates the LFAs, and has deserved a lot of attention in the present thesis. The macroscale (regional) circulation patterns around the Balearic Sea favours the formation of LFA by promoting high mesoscale activity, in particular the summer location of the density front related to the interaction between resident surface AW and recent AW inflowing from the southern Algerian Basin, as anticyclonic gyres or current filaments, that vary in latitude depending on the year (Balbín et al., 2014). This front had already been postulated as a spawning trigger for some tunid species (Reglero et al., 2012) and thought to be responsible for modifying the LFA spatial pattern resulting from the initial distribution of spawners (Torres et al., 2011). The advantages of mesoscale features for sustaining LFAs through increasing the trophic energy available for marine organisms and enhancing retention has been extensively explained in the past (e.g. Bakun, 2006). These features may be of major importance in the case of an oligotrophic area such as the Balearic Sea. In studies on this area, frontal meso-scale events between resident and newly arrived Atlantic waters (Pinot et al., 1995) and inputs of colder northern waters into the channels (Fernández de Puelles et al., 2004; Jordi et al., 2009a), have been postulated to act as external fertilization mechanisms that enhance productivity off the Balearic Islands. The summer LFAs around the archipelago take advantage from these mechanisms (Chapters 4 & 5). Previous studies indicated that mesoscale and sub-mesoscale circulations may minimize long-distance dispersal by retaining larvae for a portion of or throughout their pelagic stage (e.g. Black et al., 1991; Boehlert et al., 1992; Werner et al., 1993; Cowen and Castro 1994).

The effects of these density fronts on the coastal LFAs diminish as distance to coast does. In general, for neritic environments, the influence of local hydrological processes on LFAs is more pronounced. Nevertheless, the influence of the density front has found to be also responsible of the formation of the summer LFAs around Cabrera archipelago (Chapter 2). This is partly explained by the peculiar bottom topography of the Archipelago, where a steep depth gradient is located at the South of Cabrera (Fig.IV.1).The scale of the sampled area in the study described in the Chapter 2 did not allow characterizing the front in all its magnitude, but its effects appear clear (Figures 2.4, 2.5 and 2.8). The currents at the slope and the oscillatory wind-induced currents interacting with the small archipelago of Cabrera are major drivers of retention (thus self-recruitment) in that area, acting like as those described in some well-studied tropical reef areas (Swearer et al., 1999; Cowen et al., 2000, 2006). In the case of Palma Bay, the other studied coastal scenario, neritic and oceanic species formed different LFAs but neither salinity nor temperatures were directly related to these differences. Instead, the local hydrology, characterized by wind-driven gyres, acts as a retention mechanism for resident larvae and restricts the entrance of foreign fish larvae to some areas of the Bay. These results confirm the role of Palma Bay (a situation that may be extended to similar coastal configurations in temperate areas) as a retention area as already predicted by models developed by Basterretxea et al. (2012).

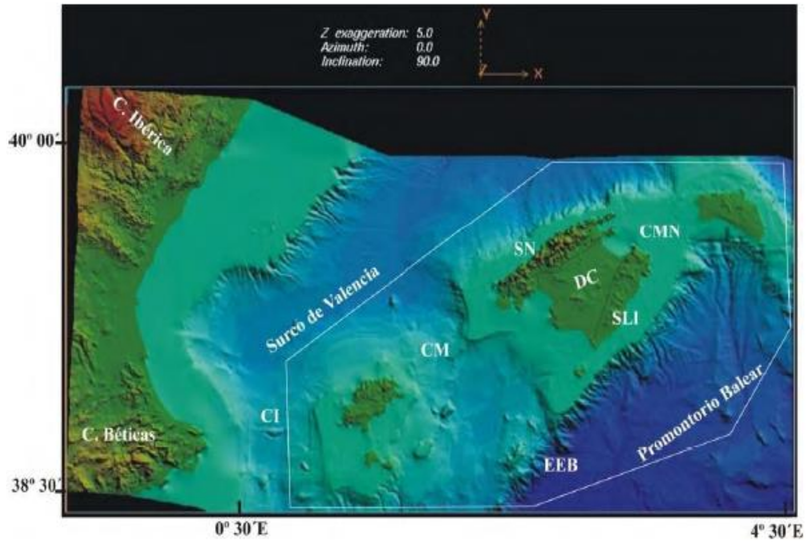

Figure IV.1. 3D Map of the main geologic and geomorphologic elements on the Balearic Promontory (PB). CI: Ibiza Channel, CM: Mallorca Channel, CMN: Menorca Channel, EEB: Emile Baudot Escarpment, SN: Northern Mountains, DC: Central Depression, SLI: Eastern Mountains. From Acosta et al. (2003).

The introduction into the analyses of a good descriptor of the local hydrography, such as the vorticity values, made the difference for being able to statistically relate physical and biological processes. It is usual in near-coast studies that the "environmental" variables introduced into the analysis do not adequately represent the associated physical processes. That disagreement makes the potential relationships impossible to determine in a statistical way. That is the case, for example, of the study performed by Swearer et al. (1999) where the influence of wind on retention in coral reefs is mentioned but not demonstrated. Also, in Pérez-Ruzafa et al. (2005) the authors relate spatial distribution of larvae to hydrographical circulation patterns in a Mediterranean coastal lagoon only by means of visual map comparisons. Admittedly, some other variables such as fluorescence or microzooplankton were not included in the present study, but the clear relationship of both zooplankton and ichthyoplankton with physics suggests that we were capturing a key phenomenon.

Finally, the seasonal formation of the coastal LFA reflects the seasonal patterns already described for production and for some fish larvae (Estrada et al., 1996; Fernández de Puelles et al., 2007). The fine-scale monitoring of the thermocline formation together with other variables enabled a more accurate description of the system dynamics, suggesting that the change in the sources of production may trigger the spawning of many species, which explained the generally higher diversity of larval fish in the summer in both the NW Mediterranean (Sabatés et al., 2007) and E Mediterranean (Somarakis et al., 2011).

IV.2. Further information gained from LFA studies

Co-occurrence of individual species in an ichthyoplankton assemblage suggests that they share common requirements during their early life histories, which may be independent of the adult's requirements. A change in the ecosystem that affects negatively one species will likely affect in the same way all the species in the assemblage. One obvious example of such a change is that induced by global climate trends. The broad scale changes in the productivity, hydrography or temperature that global climate change might bring about will impact the entire assemblage and not just individual species (Miller et al., 2002, Llopiz et al., 2014). The impact on the assemblage may not be to reduce the abundance of all or any of the species of which it is composed, but to shift its geographic location or seasonal timing.

On the other hand, the ongoing shift in the focus of fisheries management is from a single species approach to multispecies and ecosystem approaches. Obviously, these approaches require an understanding of the interrelationships among species and therefore of ichthyoplankton assemblages, and a sufficiently long time series. Identification of which species interact during early life history and the nature of these interactions may be important to understanding the response of the system to changes in patterns of commercial removals (Miller, 2002). Understanding species distributions in a variable and changing environment is critical to accurately assess and successfully manage fisheries and for marine conservation purposes (Hare, 2014). The general description of the species (and their abundances) forming LFAs in the Balearic Sea, at different scales, represent a baseline for future research on ecosystem changes. For example, the presence of the skipjack *Katsuwonus pelamis*, considered as a tropical fish, reveals a possible shift in the geographic location of the species. The data on spatial distribution and abundances of fish larvae from Chapters 4 and 5, have been combined with data on decapod crustaceans and paralarvae (cephalopods) to investigate the spatio-temporal distribution of the summer meroplankton (i.e. organisms with planktonic egg and/or larval stages) community in the Balearic Sea (Hidalgo et al., 2014, not included as a formal part of this thesis). As a result, the dynamics of the specific biological and hydrographic gradients that structure the meroplankton in mixed assemblages were identified: being the most significant ones the salinity seascape and the vertical structure of the phytoplankton rich water masses arriving from the north. Combination of both drivers results in an alternating influence (depending on the scenario) of the retention-dispersal pathways associated to hydrology and the coupling of larvae on productive conditions.

Modification of local assemblages including changes in biomass, species composition, and ratios of species or feeding groups, species diversity and recruitment success can be used as biotic indicators of habitat degradation, fishing pressure, environmental contamination and changes in the overall ecosystem productivity. Recent works in the area have demonstrated the increasing concentration of trace metals in the seawater from groundwater discharge (Rodellas et al., 2014; Tovar-Sánchez et al., 2014), from aerosols (Jordi et al., 2012) and even from direct sunscreen products from bathers (Sánchez-Quiles and Tovar-Sánchez, 2014). In the case of the aerosols deposition, the copper related to anthropogenic emissions was demonstrated to be responsible of the inhibition of phytoplankton growth in the area. The effects of these stressors and many others onto the individual species and LFAs, or the potential of LFAs to trace these external factors are an interesting avenue of research.

In terms of biodiversity, it has been emphasized in Subsection I.6 that data from the Balearic Islands were not used for the description of the biodiversity of the Mediterranean Sea (Coll et al., 2010). The acquired knowledge on LFA in the Balearic Sea derived from the present works (Chapters 1 to 5) allows comparing diversity with other areas (in terms of fish communities). It has also been said in the Introduction section that the Mediterranean Sea is considered an oligotrophic Sea. Nevertheless, the number of species found at all scales in the Balearic Sea was higher and the mean abundance values of the most abundant species comparable, to those reported in the productive Benguela current (Olivar and Shelton 1993). The number of species and mean abundances in our studies are also comparable to those reported for the central and northern California Current in the northeast Pacific Ocean during May 2004, 2005, and 2006 by Auth (2008). In relation to other areas in the Mediterranean, the number of taxa collected around the Cabrera archipelago National park (Chapter 2, 60 taxa) was similar to the 63 taxa collected in summer in the Medes Island Marine Protected area in the Catalan sea (NW Mediterranean) (López-sanz et al., 2009). The number on fish larvae nevertheless was twofold in the Medes study (16545 individuals vs the 7023 collected around Cabrera) even though in Cabrera 63 stations were sampled and in the Medes islands only 31. The high abundances of *E. encrasicolus* in the Medes study might be one of the reasons of the differences. In a summer study off the Catalan coast (NW Mediterranean) over the Blanes submarine canyon (Olivar et al., 1998) again the number of taxa reported is smaller than any of the number of taxa found at all scales in the Balearic Sea and the abundance values comparable. The main factors affecting the spatiotemporal distrubution pattern of LFAs along the Catalan coast include shelf topography and bottom type, adult habirtat and behaviour, spawning locality and spawning period, (Sabatés, 1990) . Also. as in the Balearic Sea, mesoscale hydrodinamic factors play an important rol and, in general, the number of species found at all months in the Catalan coasti is smaller than those reported in the present study and the abundances slightly higher. In the neritic waters of central Greece and northeastern Aegean Sea, relatively more eutrophic than the central Aegean and Ionian Seas, the number of summer taxa reported and the mean abundances are in the same order of magnitude than our results (Somarakis et al., 2011 a, b).

The relationships between circulation patterns and LFAs in coastal areas and between the density front and LFAs at a regional scale might be a starting point to disentangle the dynamics of the Balearic Sea pelagic system, and how coastal and pelagic domains interact. Our data have shown that pelagic species such as tuna can and do use coastal areas in some instances to spawn (e.g. close to Cabrera or at the entrance of Palma Bay), and have confirmed that commercial species such as *Sardinella aurita* do take advantage of very shallow coastal areas to spawn, which has potential implications in the face of rising temperatures. The results on coastal dynamics and inferences on seasonal larval production may help to better conceptualize the real phenomena rising to retention/dispersal mechanisms, and may be useful to validate dispersion models, such as in Basterretxea et al. (2012).

IV.3. Importance of the scales in LFA studies

The key to understanding and prediction lies in the elucidation of mechanisms underlying observed patterns. Typically, these mechanisms operate at different scales than those on which the patterns are observed. Thus, in some cases, the patterns must be understood as emerging from the collective behaviors of large ensembles of smaller scale units. In other cases, the pattern is imposed by larger scale constraints (Levin, 1992). As a consequence, spatial scale and survey resolution and duration might have an impact on the precision of population estimates (Pepin and Helbig, 2012).

Helbig and Pepin (1998 a, b) argued that the sampling resolution used in a survey relative to physical and biological scales of variability in the ocean as well as the manner in which a survey is carried out, can significantly affect both the accuracy and the precision of abundance estimates. They concluded that a sampling plan that fails to adequately resolve the energetic space and time scales of the plankton distribution will generate population estimates (i.e., estimates of mean abundance over the survey area) whose variance is greater than natural levels (Helbig and Pepin, 1998a) and thereby affect our ability to answer biological questions about the early life history of fish.

In large-scale studies, different locations are usually sampled at different times of the day and/or on different days throughout a sampling cruise (e.g. Young et al., 1986; Olivar, 1990; Sabatés, 1990; Gray, 1993). Consequently, any description of spatial pattern, or any inferences of differences in assemblages between locations, is potentially confounded with time induced variations (e.g. Morrisey et al., 1992; Thrush et al., 1994). Specifically, any differences between locations may solely be due to the fact that the different locations were sampled at different times, for purely logistic reasons. Hence, a description of how assemblages at each site vary over short time intervals, i.e. within and between consecutive days, is essential to overcome this problem and interpret the results accurately. Gray (1996) explored short-term changes in the assemblages of larval fishes in waters over the inner continental shelf off Sydney, Australia. This was done to examine the potential confounding effect of spatial pattern with small-scale temporal variability. The assemblages and densities of larval fishes at each of the sampled locations (sampled twice in two consecutive days) and depth varied throughout the 2 day sampling period. The results presented in such study illustrate how caution must be exercised when interpreting large-scale comparisons whenever sampling occurs over a number of days. Despite the variations depicted above, there were no major changes in the taxonomic composition of the ichthyofauna at either location over the two sampling days. The authors concluded that this result indicated that no new assemblage was transported into the study area over this time, which suggests that the patch size of this assemblage was relatively large and the spawning output of adults was temporally concordant, or that the fish larvae were being retained in the study area (e.g. Smith and Morse, 1985). In the case of the selected sampling scale for chapters 4 and 5 (mesoscale), the sampling took around a month, and is evident that the small-scale temporal variability in the assemblages might have been underestimated and confounded under the large scale effect of oceanographic processes. Under the impossibility of sampling all stations in the area at the same time, the repeated sampling in two consecutive years and under contrasting scenarios was considered a useful tool to at least identify the major processes (density front and spawning behaviour) affecting LFAs. For the sampling in Chapter 1 (temporal scales) the fortnightly sampling of the three different stations at different depths instead of a single one prevent from the overestimation of small-scale variability that could have hindered the broader seasonal pattern.

At smaller spatial scales (in our case coastal studies), regional topography, bathymetry and stratification can influence the effect of variations in wind forcing on the circulation in coastal areas and thereby the drift of ichthyoplankton, in a more important way than in mesoscale open-ocean surveys. Like all plankton, fish eggs and larvae drift is mainly driven by ocean currents. Ichthyoplankton have been shown to demonstrate high degree of small scale spatial patchiness (Hewitt, 1981; Matsuura and Hewitt, 1995). This may lead to a scale-dependency with greater amounts of variability at small spatial scales in contrast to the characteristic red spectrum of phytoplankton and some zooplankton which has greater variability at large spatial scale. In contrast to phytoplankton and zooplankton (Mackas et al., 1985), the spatial patterns of ichthyoplankton are governed by the balance between advection, convergence and divergence, mortality and ontogenetic changes in behaviour (e.g., directed swimming, schooling) (Bradbury et al., 2003; Leis et al., 2007). After the initial release of gametes which depends on the distribution of adults, the effect of local reproduction, important in the case of most other planktonic organisms, does not play a role. As a consequence of the high degree of small scale patchiness, the precision of population estimates for ichthyoplankton may be less scale-dependent than in other zooplankton, as long as surveys do not cross major distributional boundaries or enter into different oceanographic systems (Pepin and Helbig, 2012). No different oceanographic systems were covered by the study in Palma Bay (Chapter 3) and, in Chapter 2 (Archipelago of Cabrera) the distances between stations and the area covered by the sampling scheme allowed to easily distinguish the boundary represented by the density front.

Not only the scales chosen for sampling the environment have influence on the processes that can be detected, but also the way in which resulting data are analyzed can underestimate or hinder the effect of some of the processes. Hidalgo et al. (2015), with data from Chapters 4 and 5, performed an exercise to investigate the effect of data analysis in the different interpretation of the processes related to interannual meroplankton diversity changes in the highly dynamic ecosystem that the Balearic Sea represents in summer oceanographic conditions (due to the confluence of oceanographic and biological processes from different origin in the frontal system described in Chapters 4 and 5). The main hypothesis was that key seascape drivers shaping the regional diversity in frontal ecosystems in years with contrasting environmental scenarios may differ from those observed in common integrated analyses. To test their hypothesis, they contrasted a set of drivers (i.e. significant covariates) that affect diversity, combining information of the two years to that obtained when each year is analysed separately. The main drivers of the pooled-data analyses contrasted with those for each year-specific scenario. They concluded that primary and temporally persistent drivers can only be observed applying non-stationary methodological approaches. They also evidenced that the regional biodiversity of the pelagic realm in a highly dynamic ecosystem can be summarized attending to both static (bathymetric) and ephemeral (biological and hydrographical) environmental axes, which form changes between years. The data set in Chapter 5 for the 2004 and 2005 surveys were not pooled and the separated analysis allowed the identification of the main drivers of the LFA formation.

IV.4. Existing gaps on the knowledge of LFA in the area and future directions.

Some recent reviews on fisheries oceanography (Houde, 2008; Peck et al., 2012; Hare, 2014), point out the existence of a new wave of early life history research that has led to the development of several other hypotheses than those from Hjort (See section I.1). These new hypotheses on the mechanisms governing early life survival (Houde, 2008; Hare, 2014), yielded important discoveries in fish biology (e.g., daily increments in fish otoliths, or "ear stones"), drove advances in technology and techniques (e.g., coupled biological physical models), and underpinned large-scale interdisciplinary programs (e.g., California Cooperative Oceanic Fisheries Investigations [CalCOFI], Fisheries Oceanography Coordinated Investigations [FOCI], Global Ocean Ecosystem Dynamics [GLOBEC]), that all contributed greatly to our ability to ask and answer interesting questions about survivorship in the early life stages of fishes. Some of the most important findings have elucidated the ways in which larval growth rates interact with overall mortality rates (growth-mortality hypothesis), largely due to reduced susceptibility to predation for a larva growing more quickly through its vulnerable planktonic period (Cushing, 1975; Houde, 1987, 1997; Anderson, 1988).

Long-standing monitoring programs may provide unique opportunities to investigate changes in survey effectiveness by providing a comprehensive evaluation of the impacts that physical processes have on estimates of population abundance and change. Such an understanding may prove to be essential if researchers are to effectively couple biophysical models to yield predictive skills of sufficient accuracy and precision to infer the impacts of environmental change on fish populations (Hannah, 2007; Miller, 2007, Pepin and Helbig, 2012). Taking into account the difficulties of getting permanent funding for stablishing long standing monitoring programs, the strategy proposed by Juniper and Tunnicliffe (1997) of describing new systems by consecutive phases (determining the composition of the system, determining its structure and finally the dynamics of the system) might be a good approach. The whole puzzle will have to be constructed from small pieces, at any rate. Hare's (2014) proposal of broadening our view and integrating among multiple hypotheses and processes seems to be a good starting point.

The contribution of the present thesis to the description of the LFAs in the Balearic Sea under different configurations, although representing an advance in the description of the system and a small advance in its dynamics (relationships LFA-environment), represents only a small part of what is needed to have some basic tools to generalize the dynamics of the system around the archipelago.

In terms of determining the composition of the system, many advances and efforts in taxonomy need to be done, which on the other hand are extensive to the Mediterranean. Specially in the coastal area, identification of coastal resident larvae to the species level (e.g. Gobiids, Sparids) would shed some light in the processes involved in returning to the juvenile habitat. Extensive knowledge of taxonomy, time and experience are required to achieve reliable identifications. For new descriptions, experimental fish culture will be needed in the future and also genetic techniques.

Some parts of the system have still to be investigated to reach a complete description of its structure. In the description of the LFAs at the mesoscale level (Chapters 4 and 5), the complete water column was not sampled. The limit to the 70 m upper layer, although covering the depths were most of the fish larvae have been found in the area (Olivar et al., 2014), underestimates the presence of larvae from bathypelagic species and of some deep-distributed mesopelagics. Also, only the summer and spring-summer LFAs have been investigated. The processes shaping the maintenance of autumn and winter-reproducing populations are poorly known.

When attending to the determination of the dynamics of the system (the third of Juniper and Tunnicliffe (1997) phases), the present work has been mainly focused on physical processes affecting LFAs. In this thesis fish larvae have been considered as passive particles (except in the dispersion exercise performed in Chapter 2 around Cabrera), and apart from the spawning behaviour of adults, no other consideration on behavior has been taken. Llopiz et al. (2014) described the three major challenges that fish larvae face in the plankton: finding food, reaching juvenile habitat and avoiding predators. One of the basic gaps in the knowledge of the structure and dynamics of LFAs in the Balearic Sea, linked to larval behaviour, feeding and predator-avoidance, concerns vertical distribution of LFA through time. Different assemblages in the vertical have been identified in small areas in the outer shelf and slope of Mallorca Island (Olivar et al., 2014) but key processes such as the influence of the density front and the existing types of eddies on the vertical distribution of LFAs and the recruitment of their larvae remain unknown. At the littoral area, vertical migrations by larvae may be coupled with vertically stratified flows induced by wind and density clines (Leis, 1991; Cowen and Castro, 1994). Neither the influence of the establishment of the summer stratified water column conditions in coastal and offshore waters on the vertical position of the LFAs nor the factors affecting the returning success of the fish larvae to their nurseries have been investigated.

Trophic ecology has been described for some larvae of tuna species in the area (Catalán et al., 2007, 2011; Laíz-Carrion et al., 2013; Reglero et al., 2014), but the trophic relationships of the rest of the species have not been investigated yet. In a century where trophic-based models have occupied a prominent role in the literature, trophism of early stages has not formed part of those models. That information results very interesting in terms of relating larval survival with primary and secondary production in the area. The emphasis might be on the physiological interaction between the environment and the organism (ecophysiology, Tanaka et al., 1998; Peck et al., 2013), rather than the organism obtaining resources from the environment. To do so, the allocation of energy among basal metabolism, growth, reproduction, daily activity and seasonal activity needs to be understood and quantified (Hare, 2014). Also the effect of temperature and other environmental variables on physiology and energy allocation needs to be examined. The fact that most mortality in marine fishes takes place during the pelagic planktonic stage (e.g. Cushing 1990) makes the evaluation of the natural and predation mortality rates in the area similarly interesting. The combined role of prey, predators, physical environment and physiology needs to be investigated. All this information is useful to parametrize process-oriented models (e.g. Okunishi et al., 2012; Peck and Hufnagl, 2012).

The importance of understanding where larvae are going and whence they are coming has led to dozens of models of dispersal as a purely physical process. There is enough knowledge about the behavioral capabilities of fish larvae that we should expect them to influence dispersal outcomes, and must, therefore, be included in the dispersal models. Predictive, individually based dispersal models provide a productive way to address the challenge of quantifying both the spatial and temporal scales of connectivity and the factors that contribute to them (Leis, 2007). The results of the present work do help understanding key processes that the model has to be able to deal with. To this respect, current modelling capabilities still do not enable to depict correctly the mesoscale features (strength and position) in systems where boundary conditions are open, such as the Balearic Sea. In other areas in the Mediterranean where strong quasi-permanent currents occur these models are easier to implement in a more realistic way (e.g. Catalán et al., 2013, Ospina Álvarez et al., in press). Nevertheless, in the coastal area of the Balearic Archipelago it is becoming feasible to reproduce coastal currents, forced by winds (e.g.

Basterretxea et al., 2012), which opens another promising avenue of interaction between physics and biology in this area. To this respect, it is foreseen that information on LFAs and species-level information on behaviour and ecophysiology will have to be integrated within modeling and experimental frames to answer both particular and general questions on fisheries oceanography.

Llopiz et al., (2014) describe the actual situation of early life history researchers as charged with an additional task: elucidating how gradual, long-term changes to marine ecosystem will impact recruitment. Obviously, research on early life history of fish in the Balearic Sea will increase with time, and will be overcharged by the new topics on climate-related research (rising temperatures, ocean acidification…). As Houde (2008) defined the fisheries research during a period of time as been under Hjort's shadow, Llopiz et al., (2014) aware researchers about the danger of being under the new shadow of global-change-related early life history research. The maintenance of a balance between "classical studies" and global change-studies represent an interesting challenge that the author of this work gladly accepts for future research.

V

GENERAL CONCLUSIONS

1. - Coastal larval Fish Assemblages exhibit a rapid change in their composition at the onset of the thermocline formation in the Coastal waters of the Archipelago. The winter-spring assemblage is characterized by only a few species with relatively high abundance. In contrast, a significantly higher number of taxa coexist in the summer ichthyoplanktonic assemblage.

2. - The diversion of energy flow from pelagic to benthic ecosystems during the spring-summer transition in the Balearic Sea waters could partly explain the observed differences in the spawning strategies of coastal resident fish species. While the spring spawning species present a certain degree of coupling to plankton dynamics, coastal resident species most commonly funnel energy through coupling to the benthic seasonality in which seagrass habitats are key contributors to fish maintenance.

3. - At scales smaller than mesoscale, around the Marine Protected Area (MPA) of Cabrera Archipelago, two distinct larval fish assemblages were clearly identified (coastal and oceanic). Frontal zones play an important role in the confinement of larvae in the shelf, and the seasonal and interannual variations in self-recruitment to the MPA could be related to the presence and variability of these boundary fronts, which are ultimately driven by basin-scale processes.

4. - The present study provides further evidence of another source of hydrodynamic regulation of larval distribution around the Archipelago of Cabrera. Boundary circulation at the slope and oscillatory wind-induced currents interacting with the islands are major drivers of recruitment to the small archipelago over which specific larval behavior may operate. With some variations, this provides a stable yet dynamically regulated system that efficiently favors self-recruitment to the Marine Protected Area.

5. - Also at submesoscale, in Palma Bay, a high number of local summer-spawners species and some epipelagic taxa take advantage of the role of the Bay as a retention area for fish larvae. A central small gyre acts as the retention mechanism for local species with most of those species distributed in the middle of the gyre rather than closer to the coast (nearer to their adult distribution).

6. - A multivariate predictive approach based on Redundancy Analysis (RDA) revealed differences between the LFA in the bay, constituted by small pelagic and benthopelagic families (Gobiidae, *Chromis chromis* and *Serranus hepatus*) and offshore LFA, mostly constituted from meso and large pelagic fish larvae. These larval fish assemblages were structured according to depth variations and zooplankton abundance, and remained relatively unmixed because of the circulation patterns in the mouth of the bay that uncouple its dynamics from alongshelf circulation

7. - At the mesoscale scales, in summer, the Balearic Sea harbors a relatively abundant and diverse larval fish community despite being considered an oligotrophic region.

8. - Depth and consequently, the spawning location of adult fishes are the main factors in shaping the horizontal structure of the LFA in the Balearic Sea.

9. - An enlarged analysis using contrasting scenarios of mesoscale activity, features such as the position of the density front between New and Resident Atlantic waters that usually occupies the archipelago waters in summer, are drivers that influence the distribution of the summer LFA in the area. This opens questions on the potential changes in the system under altered frequencies in the position of the front.

10. -The diversity of habitats (coastal, oceanic, inter-islands, topographic accidents), the position of the Balearic Sea between the most diverse areas in the Mediterranean and the active regional circulation makes the archipelago a hotspot for marine diversity studies. The results from the present thesis stablish a baseline for future comparisons on the effects of future environmental variations (anthropogenic or not) in the area on the LFA.

VI

CONCLUSIONES GENERALES

1.- En aguas costeras del archipiélago de Cabrera la composición de las comunidades de larvas de peces cambia drásticamente coincidiendo con el final de la formación de la termoclina. La comunidad de invierno-primavera se caracteriza por un numero bajo de especies con abundancias relativamente altas. En contraposición, en la comunidad estival de larvas de peces coexiste un número de taxones significativamente mayor.

2. - El cambio del flujo de energía desde ecosistemas pelágicos hacia bentónicos que tiene lugar en la transición primavera-verano en las aguas del mar Balear explican en parte las diferencias observadas en los patrones de reproducción de las especies costeras residentes. Mientras las especies de puesta primaveral se ven en cierto grado acopladas a la dinámica planctónica, las especies costeras residentes podrían canalizar la energía acoplándose a la estacionalidad bentónica en la que las fanerógamas marinas representan una contribución clave para el mantenimiento de las comunidades de peces.

3. - A escalas horizontales inferiores a mesoescala, alrededor del área marina protegida del Parque Nacional de Cabrera se identificaron claramente dos comunidades de larvas de peces diferentes (costero y oceánico). Las zonas de frente intervienen activamente en el confinamiento de larvas en la plataforma; podrían relacionarse las variaciones estacionales e interanuales del auto reclutamiento al área con la presencia y variabilidad de esas zonas de frente con origen en procesos a escala regional.

4. - Este trabajo presenta evidencias sobre otra forma de regulación de la distribución de la larvas de peces alrededor del archipiélago de Cabrera debida a la hidrodinámica. La circulación en el talud y corrientes oscilatorias inducidas por el viento que interactúan con las islas son los factores más influyentes en el reclutamiento al pequeño archipiélago. Sobre esos factores opera el comportamiento larvario. Con alguna variación, estos factores constituyen un sistema estable regulado por la dinámica marina que de manera efectiva favorece el auto reclutamiento al área marina protegida.

5. - También a submesoescala, un número alto de especies locales de puesta estival en la bahía de Palma se aprovechan del papel de la bahía como área de retención para larvas de peces. Un giro central actúa como mecanismo de retención para especies locales. La mayoría de esas especies se distribuyen más cerca del giro central que en zonas muy cercanas a costa (próximo al hábitat de sus adultos).

6. - Mediante una aproximación predictiva multivariante basada en el análisis de redundancias (RDA), se encontraron diferencias entre la comunidad de larvas de peces de la bahía, constituida principalmente por pequeños pelágicos y familias bentopelágicas (Gobiidae, *Chromis chromis* y *Serranus hepatus*) y la comunidad de aguas adentro, en su mayoría compuesta por larvas de mesopelágicos y grandes pelágicos. Esas comunidades estaban estructuradas de acuerdo a las variaciones de la profundidad y la abundancia de zooplancton y además permanecían separadas por los patrones de circulación a la entrada de la bahía, que desacopla la dinámica interna de la circulación a lo largo de la plataforma.

7. - A nivel de mesoescala, en verano, el mar Balear cobija una comunidad de larvas de peces relativamente abundante y diversa pese a ser considerada una zona oligotrófica.

8. - La profundidad y, consecuentemente el lugar de puesta de los peces adultos, son los factores principales que afectan en la distribución horizontal de las comunidades de larvas de peces en el mar Balear.

9. - Aun así, tras un análisis más completo utilizando escenarios contrastados de actividad de mesoescala en la zona, la posición del frente de densidad entre aguas recientes y residentes atlánticas que normalmente está presente en verano también tiene influencia sobre la distribución de las comunidades estivales de larvas de peces en el área. Este resultado abre nuevas incógnitas sobre los cambios potenciales que puede sufrir el sistema bajo frecuencias alteradas en la posición del frente.

10.- La diversidad de hábitats (costero, oceánico, inter-isla, accidentes topográficos etc…). La posición del archipiélago balear entre las áreas de mayor diversidad en el Mediterráneo y la elevada actividad que presenta la circulación regional hacen del Mar Balear un punto de interés para los estudios de biodiversidad. Los resultados de esta tesis suponen una línea de base con la que comparar los efectos de futuras variaciones ambientales (antropogénicas o no) sobre las comunidades de larvas de peces del área.

VII

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