1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Dynamic modulators of larval fish self-recruitment in an insular marine protected area (MPA).

GOTZON BASTERRETXEA¹, IGNACIO A. CATALÁN¹, ANTONI JORDI ¹, ITZIAR ÁLVAREZ¹, MIQUEL PALMER¹, ANA SABATÉS ².

¹ *Instituto Mediterráneo de Estudios Avanzados, IMEDEA (UIB-CSIC). Miquel Marqués 21, 07190 Esporles, Mallorca, Spain*

² *Institut de Ciències del Mar, CSIC. Pg. Marítim de la Barceloneta, 37-49, 08003 Barcelona, Spain.*

For submission to: *Fisheries oceanography*

Running head: Modulators of larval fish self-recruitment

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 modulation of larval arrival to the MPA to a combination of three processes: (1) retention by topographically generated circulation patterns around the island, (2) shelf break frontal dynamics, and (3) larval behavior/survival. Specifically, within the 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 modulator 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-track model simulations suggested the relevance of behavioral processes in recruitment. 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.

Key words: larval fish, dispersal, recruitment, island, MPA, Western Mediterranean

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 since they are modulated by the degree of coupling between ocean dynamics and the species-specific biological characteristics of the regional fish populations, such as larval phase duration, larval physiology and behavior, and adult behavior. According to the classical theory guiding fisheries, 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; Sabates *et al.*, 2007) but the probability of dispersal to the open sea by enhanced physical forcing episodes is reduced (Álvarez *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 suggests 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; Jones *et al.*, 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 regarding the regional changes in ichthyoplankton assemblages can be obtained based on the identification of distinct water masses provides (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 recirculation patterns associated with coastal topographic features and sea-bottom irregularities are of primary importance for coastal spawning species (Sabates *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 such as marine banks and canyons (BolzLough, 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 vs. abiotic processes in larval distributions may be markedly different. For instance, while in highly dynamic systems larval dispersion is generally assumed to be passive

(e.g. Rooper *et al.*, 2006), under weaker flows active habitat selection by late-stage larvae becomes effective (PattrickStrydom, 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 (39.15 °N 2.96 °E; Fig. 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 mild and mainly wind forced. (Álvarez *et al.*, 2012) 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 (Sabates *et al.*, 2007). In the absence of remarkable processes that stimulate primary productivity during this season (i.e., coastal upwelling), topographically steered flows promoting plankton accumulation could favor larval retention and survival (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 modulate 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 deepens our knowledge of fish larval dispersal in CNP and therefore also on fish population dynamics in this MPA, their biogeography and their possible response to external stressors, including fisheries.

METHODS

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. 1). The passage between Mallorca and CNP is relatively shallow and narrow (~ 9 km), with depths of less than 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 (Álvarez *et al.*, 2012). This offshore water penetration is determined by shelf-break flows resultant 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.

General circulation and shelf currents

General circulation patterns were depicted from sea-level 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 the survey, the shelf circulation in southern Mallorca was monitored using a bottom-mounted acoustic Doppler current profiler (ADCP, 1 MHz Nortek Aquadopp) placed at a depth of 25 m (Fig. 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).

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. 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 in order to calibrate the fluorometer. The measured sea water variables were interpolated using the objective analysis from the CTD stations and a regular grid of 30 × 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. 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 opening, a mesh size of 53 μm , and equipped with a flowmeter. Although the net was intended for microzooplankton, size-selection not was 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} .

Ichthyoplankton was sampled using oblique Bongo net tows at each biological station (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 seafloor 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 highest 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 random individuals from each station by examination under a binocular microscope (precision = 0.01 mm).

Statistical analyses

Two multivariable descriptive analyses were performed with the aim of describing the main environmental and larval assemblage features. First, a PCA and a cluster analysis (UPGMA) were carried out considering only the environmental data, which included depth (DEPTH, m), distance to coast (DIST, m), temperature ($^{\circ}\text{C}$) at 10 m (T10), salinity at 10 m (S10), $\sigma\text{-t}$ (kg m^{-3}) at 10 m (D10), Simpson's stratification index (STR), integrated chlorophyll-a (CHLINT, mg m^{-2}), and total zooplankton abundance (ZOO, ind m^{-3}). The Simpson's stratification index was calculated every 2 m in order to characterize the strength of the thermocline (SimpsonBowers, 1981). Second, 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 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 (ClarkeWarwick, 1994).

Larval dispersal estimations

To analyze the effect of ITWs on larval trajectories, estimates of current velocity and direction were obtained using the Princeton Ocean Model (POM). POM 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 seabed.

ITWs were generated by forcing the model with a constant wind of 10 m s^{-1} blowing during one day. After this day, the model was run over 10 days without any forcing, to allow the propagation of the ITWs. The resultant three-dimensional currents of this 10-day simulation were stored at hourly intervals and then used in a post-processing mode to drive a separate particle-tracking model for the transport of fish larvae (Basterretxea *et al.*, 2012; Casabianca *et al.*, 2012). In addition, a behavioral term was included in the particle-tracking model to test the effect of larvae swimming at modest speeds. Three cases were simulated: (1) no swimming capability, (2)

sustained shoreward swimming at a speed of 5 cm s^{-1} , and (3) shoreward swimming at 5 cm s^{-1} only when currents were offshore-directed.

For Peer Review

RESULTS

Environmental setting

Figure 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 ($< 6 \text{ cm s}^{-1}$); 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. 2a), following a notable intensification in response to winds of $\sim 9 \text{ m s}^{-1}$ from the northeast. It is noteworthy that 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 near-shore environment.

The oscillatory dynamic over the shelf notably contrasts with current patterns further offshore. Figure 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.

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 near-shore upwelling along the eastern coast of Mallorca responding to the northeasterly winds (Fig. 4a). Contrastingly, near-surface salinity showed a pronounced front between the eddy and the waters around Mallorca (Fig. 4b). As seen in the temperature-entropy (TS) diagram (Fig. 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 (mode 2).

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. 4c). Phytoplankton biomass displayed a characteristic non-uniform distribution in the water column, i.e., low ($< 0.1 \text{ mg m}^{-3}$) surface values and a deep chlorophyll maximum located well beneath the pycnocline, at depths of some 75 m. Mixed-layer fields were modestly enhanced ($\sim 0.02 \text{ mg m}^{-3}$) 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. 4d). The mean zooplankton abundance was $4425 \pm 1490 \text{ ind m}^{-3}$. Copepods comprised the dominant group, representing $21 \pm 11\%$ 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, whereas 65% was explained by the first two (Fig. 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. 5b1). The environmental cluster-derived station grouping corroborated that mean zooplankton abundance was significantly higher at inshore stations (see below).

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 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. 5a2). The resulting cluster discriminated three groups of stations: oceanic (O), mainly including stations within the eddy characterized by mode 1 waters; coastal (C), comprising most of the stations within the shelf, characterized by mode 2 waters; and 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). 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: $F = 44.1$ $DF = 2$, $P < 0.001$; ANOVA for number of species: $F = 10.35$, $DF = 2$, $P < 0.001$; 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 , vs. 3468 ± 1154 ind m^{-3} , $df = 41$).

The SIMPER analysis (Table 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). Noticeably, *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. 6a, 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, at the 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, *Chromis chromis* and *Serranus hepatus* markedly differed in their distributions (Fig. 6c, e). Likewise, differences were observed in oceanic taxa (Fig. 6d, f).

Observed and modeled larval dispersion

Two of the most frequent species that spawn in the shelf, *Serranus cabrilla* and *Coris julis*, were selected for dispersion analysis (simulations experiments). The sizes, expressed as the standard length (SL) structure, of these two species are displayed in Fig. 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 with 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. 8) and at a station in the slope front (St 31).

Current measurements (Fig. 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. 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.

1
2
3 In addition, the effect on advanced developmental stage larvae of a modest (5
4 cm s⁻¹), sustained swimming ability in the shoreward, direction was tested. These
5 examples assumed orientated swimming, although despite the obvious importance of
6 orientation it is in most cases an unproven factor. As shown in Fig. 9b, dispersion was
7 notably reduced and the majority of larvae returned to the settling region in the MPA
8 (41% of the particles remained close, i.e., < 10 km from CNP). Given the oscillatory
9 nature of the currents, the simulation indicated that sustained swimming is not
10 necessary for recruitment. The dispersal resulting from a swimming behavior that is
11 activated only when currents are offshore directed was also simulated. As shown in
12 Fig. 9c, this behavior, which involves swimming 46% of the time, produced similar
13 results (37% of the particles remained close, i.e., < 10 km, to CNP), but with a highly
14 reduced energetic cost.
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

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 modulated by: (1) different, albeit interacting, forcings, (2) retention by topographically generated circulation patterns, and (3) shelf-break frontal dynamics, over which larval behavior may operate. 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 identified. 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. 6). This was not only due to the spawning behavior of the adults, but also 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. 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), 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 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, that 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 that, although they could not be spatially resolved by the present sampling, produce a bulk effect on larval retention. Consistent with our data (Fig. 2), the most efficient generators of trapped waves are transient along-shore 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 fish-larval 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 three months (Tsikliras *et al.*, 2010; Álvarez *et al.*, 2012). 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. 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.

1
2
3 A second modulator of environmental variability is the presence of boundary or
4 upper-slope circulation. The position of the Balearic Islands, i.e., in a transition zone
5 between different water masses, favors the persistence of slope currents and
6 associated mesoscale instabilities, both of which are important in driving the exchange
7 of water and organisms between the shelf and ocean (Sabates *et al.*, 2004). Also, open-
8 sea eddies in this basin are associated with the Algerian current instability (Millot,
9 1985; Millot *et al.*, 1990). These features are relatively frequent in southern Mallorca
10 and they exert significant effects on the cross-shore distribution of shelf taxa (Alemany
11 *et al.*, 2006) in addition to being relevant for typically oceanic species, including tuna,
12 as reported by (Torres *et al.*, 2011). The effect of these eddies may also differ in
13 accordance with their origin and age. While mesoscale anticyclonic eddies that
14 develop in the vicinity of continental margins may transport large quantities of shelf
15 water and larvae to the open ocean (e.g., Holliday *et al.*, 2011), the role of long-lived
16 oceanic eddies interacting with the shelf, as in our case, has yet to be clearly defined.
17 There is evidence that, although their trajectories can be altered, warm core oceanic
18 eddies remain remarkably robust when interacting with shelf-slope walls (Wei and
19 Wang, 2009). The frontal zones derived from this interaction could play an important
20 role in the confinement of larvae in the shelf, and the seasonal and interannual
21 variations in self-recruitment to the MPA could be related to the presence and
22 variability of these boundary fronts, which are ultimately driven by basin-scale
23 processes.
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42

43 Since the flux along the southeastern coast of the Balearics is rather instable,
44 boundary currents may be characterized by marked intensity variations and even
45 reversals, produced by meridional large-scale water-mass adjustments in the Western
46 Mediterranean. These changes in boundary flows may even be the main drivers of the
47 anticyclonic eddies in the Algerian basin, as proposed by (Testor *et al.*, 2005), which in
48 turn would modify their effectiveness in shelf retention. However, the time scale of
49 these variations is comparatively long-lived such that their overall effect on fish larval
50 dispersal would be expected to be dependent on the relationship between their spatial
51 persistence and the length of the fish spawning period. When the slope front is
52 intensified, larval dispersal to offshore, unfavorable waters is dramatically reduced, as
53
54
55
56
57
58
59
60

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., Sabates 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 modulator of larval distribution and abundance is larval survival and the associated behavioral responses. Predation and, secondarily, starvation are considered to be the main agents of larval mortality (Bailey and Houde, 1989; Leggett and Deblois, 1994; Fiksen and Jorgensen, 2011). 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 (ParisCowen, 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 hydrodynamism 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 adaption to beneficial larval transport. This is due, among other reasons, to the variable nature of the shelf currents. Also, the response to food may well be a driver of larval behavior, but 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 (e.g., Sabates *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). Nevertheless, the ability of the different species and developmental stages to exploit food reservoirs requiring important vertical migration will vary (Sabates *et al.*, 2008). Indeed, a horizontal swimming behavior may be more rewarding at smaller spatial scales, in particular when flows are weak and directionally varying. Larval size distribution may in fact reflect this necessity. Differences in the distribution between recently hatched larvae and postflexion larvae could be a function of a better swimming capacity. (Werner *et al.*, 1993) showed that, in a study of cod and haddock, the inclusion of directional swimming to recruitment area resulted in a better match between their model and field observations. In reef areas late-stage fish larvae were shown to be strong swimmers able to maintain a speed of tenths of cm s^{-1} 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, while 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. Settlement-stage fish likely use cues to locate their target settlement habitat (Kingsford *et al.*, 2002). Assuming that larvae orient themselves towards the coast, this could partially explain the observed distributions of larger (> 6 mm) larvae around CNP. Orientation abilities develop in larvae with a size of 7–8 mm (Leis, 2007); this SL marks the increase in swimming endurance for some fish species (Clark *et al.*, 2005). It is plausible that 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. There is evidence suggesting that some pre-settling larvae are able to detect coastal noise at distances of many kilometers (Wright *et al.*, 2005). Likewise, other sensorial cues, such as olfaction, can be considered for some species (Baird *et al.*, 1996; Gerlach *et al.*, 2007). In the case of wrasses, the olfactory organ is well developed prior to settlement and is comparable to that of adult fish (Lara, 2008), which would provide this family with a competitive advantage for habitat selection.

In conclusion, the present study provides evidence for the interaction of three main processes: oscillatory wind-induced currents on the shelf, boundary circulation at the slope, and larval behavior drive recruitment to CNP. These, with some variations, provide a stable yet dynamically modulated system that efficiently favors self-recruitment to the MPA.

ACKNOWLEDGEMENTS.

This work was supported by a MARM (Parques Nacionales) grant TALACA (PN 38/2005) and MINECO REC-2 (CTM2011-23835). A. Jordi's work was supported by a Ramón y Cajal grant from the Spanish Ministry of Economy and Competitiveness. We are grateful to Sílvia Pérez, David Roque, Benjamín Casas and Federico Cardona for assistance during the cruise. We also acknowledge the cooperation of the crew of *R/V Regina Maris* during the survey. Wind records from Palma Airport were provided by Agencia Estatal de Meteorología (AEMET).

REFERENCES

- Alemany, F., Deudero, S., Morales-Nin, B., Lopez-Jurado, J.L., Jansa, J., Palmer, M., Palomera, I., 2006. Influence of physical environmental factors on the composition and horizontal distribution of summer larval fish assemblages off Mallorca island (Balearic archipelago, western Mediterranean). *Journal of Plankton Research* 28 (5), 473-487.
- Almany, G.R., Berumen, M.L., Thorrold, S.R., Planes, S., Jones, G.P., 2007. Local replenishment of coral reef fish populations in a marine reserve. *Science* 316, 742-744.
- Álvarez, I., Catalán, I.A., 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.
- Antoine, D., Morel, A., Andre, J.M., 1995. Algal pigment distribution and primary production in the Eastern Mediterranean as derived from coastal zone color scanner observations. *Journal of Geophysical Research-Oceans* 100 (C8), 16193-16209.
- Bailey, K.M., Houde, E.D., 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* 25, 1-83.
- Baird, R.C., Johari, H., Jumper, G.Y., 1996. Numerical simulation of environmental modulation of chemical signal structure and odor dispersal in the open ocean. *Chemical Senses* 21 (2), 121-134.
- Banas, N.S., McDonald, P.S., Armstrong, D.A., 2009. Green Crab Larval Retention in Willapa Bay, Washington: An Intensive Lagrangian Modeling Approach. *Estuaries and Coasts* 32 (5), 893-905.
- Basterretxea, G., Garcés, E., Jordi, A., Maso, M., Tintore, J., 2005. Breeze conditions as a favoring mechanism of *Alexandrium taylori* blooms at a Mediterranean beach. *Estuarine Coastal and Shelf Science* 62 (1-2), 1-12.
- Basterretxea, G., Jordi, A., Catalán, I.A., Sabatés, A., 2012. Model-based assessment of local-scale fish larval connectivity in a network of marine protected areas. *Fisheries Oceanography* 10.1111/j.1365-2419.2012.00625.x.
- Bertolini, F., D'Ancona, U., Padoa Montalenti, E., Ranzi, S., Sanzo, L., Sparta, A., Tortonese, E., Viali, M., 1956. Uova, larve e stadi giovanili di Teleostei. *Stazione Zoologica di Napoli*.
- Boehlert, G.W., Watson, W., Sun, L.C., 1992. Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the Tropical Pacific. *Deep-Sea Research Part a-Oceanographic Research Papers* 39 (3-4A), 439-466.
- Bolz, G.R., Lough, R.G., 1984. Retention of ichthyoplankton in the Georges Bank region during the autumn-winter seasons, 1971-1977. *Journal of Northwest Atlantic Fishery Science* 5, 33-45.
- Borcard, D., Gillet, F., Legendre, P., 2011. *Numerical Ecology* with R. Springer.
- Bradbury, I.R., Laurel, B.J., Robichaud, D., Rose, G.A., Snelgrove, P.V.R., Gregory, R.S., Cote, D., Windle, M.J.S., 2008. Discrete spatial dynamics in a marine broadcast spawner: Re-evaluating scales of connectivity and habitat associations in Atlantic cod (*Gadus morhua* L.) in coastal Newfoundland. *Fisheries Research* 91 (2-3), 299-309.
- Casabianca, S., Penna, A., Pecchioli, E., Jordi, A., Basterretxea, G., Vernesi, C., 2012. Population genetic structure and connectivity of the harmful dinoflagellate *Alexandrium minutum* in the Mediterranean Sea. *Proceedings of the Royal Society B-Biological Sciences* 279 (1726), 129-138.
- Clark, D.L., Leis, J.M., Hay, A.C., Trnski, T., 2005. Swimming ontogeny of larvae of four temperate marine fishes. *Marine Ecology-Progress Series* 292, 287-300.
- Clarke, K.R., Warwick, M., 1994. Change in marine communities: an approach to statistical analysis and interpretation. *Natural environmental Research Council*, Plymouth,

- Cowen, R.K., Hare, J.A., Fahay, M.P., 1993. Beyond hydrography: can physical processes explain larval fish assemblages within the middle atlantic Bight? *Bulletin of Marine Science* 53 (2), 567-587.
- Cowen, R.K., Paris, C.B., Olson, D.B., Fortuna, J., 2003. The role of long distance dispersal versus local retention in replenishing marine populations. *Gulf and caribbean Research Supplement* 14, 129-137.
- Crec'hriou, R., Alemany, F., Roussel, E., Chassanite, A., Marinaro, J.Y., Mader, J., Rochel, E., Planes, S., 2010. Fisheries replenishment of early life taxa: potential export of fish eggs and larvae from a temperate marine protected area. *Fisheries Oceanography* 19 (2), 135-150.
- Csanady, G.T., 1997. On the theories that underlie our understanding of continental shelf circulation. *Journal of Oceanography* 53, 207-229.
- Cushing, D.H., 1990. Recent studies on long-term changes in the sea. *Freshwater Biology* 23 (1), 71-84.
- Dudley, B., Tolimieri, N., Montgomery, J., 2000. Swimming ability of the larvae of some reef fishes from New Zealand waters. *Marine and Freshwater Research* 51 (8), 783-787.
- Fiksen, O., Jorgensen, C., 2011. Model of optimal behaviour in fish larvae predicts that food availability determines survival, but not growth. *Marine Ecology-Progress Series* 432, 207-219.
- Gerlach, G., Atema, J., Kingsford, M.J., Black, K.P., Miller-Sims, V., 2007. Smelling home can prevent dispersal of reef fish larvae. *Proceedings of the National Academy of Sciences of the United States of America* 104 (3), 858-863.
- Govoni, J.J., 2005. Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. *Scientia Marina* 69, 125-137.
- Holliday, D., Beckley, L.E., Olivar, M.P., 2011. Incorporation of larval fishes into a developing anti-cyclonic eddy of the Leeuwin Current off south-western Australia. *Journal of Plankton Research* 33 (11), 1696-1708.
- Huggett, J., Freon, P., Mullon, C., Penven, P., 2003. Modelling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: the effect of spatio-temporal spawning patterns. *Marine Ecology-Progress Series* 250, 247-262.
- James, M.K., Armsworth, P.R., Mason, L.B., Bode, L., 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269 (1505), 2079-2086.
- Jones, G.P., Milicich, M.J., Emslie, M.J., Lunow, C., 1999. Self-recruitment in a coral reef fish population. *Nature* 402, 802-804.
- Jones, G.P., Planes, S., Thorrold, S.R., 2005. Coral reef fish larvae settle close to home. *Current Biology* 15, 1314-1318.
- Jordi, A., Basterretxea, G., Angles, S., 2009a. Influence of ocean circulation on phytoplankton biomass distribution in the Balearic Sea: Study based on Sea-viewing Wide Field-of-view Sensor and altimetry satellite data. *Journal of Geophysical Research-Oceans* 114.
- Jordi, A., Basterretxea, G., Wang, D.P., 2009b. Evidence of sediment resuspension by island trapped waves. *Geophysical Research Letters* 36.
- Jordi, A., Basterretxea, G., Wang, D.P., 2011. Local versus remote wind effects on the coastal circulation of a microtidal bay in the Mediterranean Sea. *Journal of Marine Systems* 88 (2), 312-322.
- Jordi, A., Wang, D.P., 2008. Near-inertial motions in and around the Palamos submarine canyon (NW Mediterranean) generated by a severe storm. *Continental Shelf Research* 28 (17), 2523-2534.
- Jordi, A., Wang, D.P., 2009. Mean dynamic topography and eddy kinetic energy in the Mediterranean Sea: Comparison between altimetry and a 1/16 degree ocean circulation model. *Ocean Modelling* 29 (2), 137-146.

- Kingsford, M.J., Leis, J.M., Shanks, A., Lindeman, K.C., Morgan, S.G., Pineda, J., 2002. Sensory environments, larval abilities and local self-recruitment. *Bulletin of Marine Science* 70 (1), 309-340.
- Lara, M.R., 2008. Development of the nasal olfactory organs in the larvae, settlement-stages and some adults of 14 species of Caribbean reef fishes (Labridae, Scaridae, Pomacentridae). *Marine Biology* 154 (1), 51-64.
- Largier, J.L., 2003. Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications* 13 (1), S71-S89.
- Leggett, W.C., Deblois, E., 1994. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research* 32 (2), 119-134.
- Leis, J.M., 2007. Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Marine Ecology-Progress Series* 347, 185-193.
- Leis, J.M., Carson-Ewart, B.M., 1997. In situ swimming speeds of the late pelagic larvae of some Indo-Pacific coral-reef fishes. *Marine Ecology-Progress Series* 159, 165-174.
- Leon-Chavez, C.A., Sanchez-Velasco, L., Beier, E., Lavin, M.F., Godinez, V.M., Farber-Lorda, J., 2010. Larval fish assemblages and circulation in the Eastern Tropical Pacific in Autumn and Winter. *Journal of Plankton Research* 32 (4), 397-410.
- Lopez-Sanz, A., Vert, N., Zabala, M., Sabates, A., 2009. Small-scale distribution of fish larvae around the Medes Islands marine protected area (NW Mediterranean). *Journal of Plankton Research* 31 (7), 763-775.
- MacPherson, E., Becerro, M., Coma, R., Palacin, C., Turon, X., Uriz, I., 2009. Biodiversidad genética de organismos marinos en el Parque nacional de cabrera: Aplicaciones para la conservación. In: L. Ramirez and B. Asensio (Ed.) (Eds), *Proyectos de investigación en Parques Nacionales. Naturaleza y Parques Nacionales*. Madrid. pp.
- Maso, M., Sabates, A., Olivar, M.P., 1998. Short-term physical and biological variability in the shelf-slope region of the NW Mediterranean during the spring transition period. *Continental Shelf Research* 18 (6), 661-675.
- Mellor, G. (1993) Users guide for a three-dimensional, primitive equation, numerical ocean model. <http://www.aos.princeton.edu/WWWPUBLIC/htdocs.pom>.
- Millot, C., 1985. Some features of the Algerian current. *Journal of Geophysical Research-Oceans* 90 (NC4), 7169-7176.
- Millot, C., 1991. Mesoscale and seasonal variabilities of the circulation in the Western Mediterranean. *Dynamics of Atmospheres and Oceans* 15 (3-5), 179-214.
- Millot, C., 1999. Circulation in the Western Mediterranean Sea. *Journal of Marine Systems* 20 (1-4), 423-442.
- Millot, C., Taupierletage, I., Benzohra, M., 1990. The Algerian eddies. *Earth-Science Reviews* 27 (3), 203-219.
- Montgomery, J.C., Tolimieri, N., Haine, O.S., 2001. Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries* 2 (3), 261-277.
- Muhling, B.A., Beckley, L.E., Koslow, J.A., Pearce, A.F., 2008. Larval fish assemblages and water mass structure off the oligotrophic south-western Australian coast. *Fisheries Oceanography* 17 (1), 16-31.
- Neill, W.H., Miller, J.M., Vanderveer, H.W., Winemiller, K.O., 1994. Ecophysiology of marine fish recruitment: A framework for understanding interannual variability. *Netherlands Journal of Sea Research* 32 (2), 135-152.
- Nishimoto, M.M., Washburn, L., 2002. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. *Marine Ecology-Progress Series* 241, 183-199.

- Olivar, M.P., Emelianov, M., Villate, F., Uriarte, I., Maynou, F., Alvarez, I., Morote, E., 2010. The role of oceanographic conditions and plankton availability in larval fish assemblages off the Catalan coast (NW Mediterranean). *Fisheries Oceanography* 19 (3), 209-229.
- Paris, C.B., Cowen, R.K., 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography* 49 (6), 1964-1979.
- Parrish, R.H., Nelson, C.S., Bakun, A., 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography* 1, 175-203.
- Pascual, A., Gomis, D., 2003. Use of surface data to estimate geostrophic transport. *Journal of Atmospheric and Oceanic Technology* 20 (6), 912-926.
- Patrick, P., Strydom, N.A., 2009. Swimming abilities of wild-caught, late-stage larvae of *Diplodus capensis* and *Sarpa salpa* (Pisces: Sparidae) from temperate South Africa. *Estuarine Coastal and Shelf Science* 85 (4), 547-554.
- Perkins, H., Pistek, P., 1990. Circulation in the Algerian basin during June 1986. *Journal of Geophysical Research-Oceans* 95 (C2), 1577-1585.
- Puillat, L., Taupier-Letage, L., Millot, C., 2002. Algerian Eddies lifetime can near 3 years. *Journal of Marine Systems* 31 (4), 245-259.
- Rooper, C.N., Gunderson, D.R., Hickey, B.M., 2006. An examination of the feasibility of passive transport from coastal spawning grounds to estuarine nursery areas for English sole. *Estuarine Coastal and Shelf Science* 68 (3-4), 609-618.
- Roughan, M., Mace, A.J., Largier, J.L., Morgan, S.G., Fisher, J.L., Carter, M.L., 2005. Subsurface recirculation and larval retention in the lee of a small headland: A variation on the upwelling shadow theme. *Journal of Geophysical Research-Oceans* 110 (C10).
- Sabates, A., Olivar, M.P., 1996. Variation of larval fish distributions associated with variability in the location of a shelf-slope front. *Marine Ecology-Progress Series* 135 (1-3), 11-20.
- Sabates, A., Olivar, M.P., Salat, J., Palomera, I., Alemany, F., 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography* 74 (2-3), 355-376.
- Sabates, A., Salat, J., Maso, M., 2004. Spatial heterogeneity of fish larvae across a meandering current in the northwestern Mediterranean. *Deep-Sea Research Part I-Oceanographic Research Papers* 51 (4), 545-557.
- Sabates, A., Zaragoza, N., Grau, C., Salat, J., 2008. Vertical distribution of early developmental stages in two coexisting clupeoid species, *Sardinella aurita* and *Engraulis encrasicolus*. *Marine Ecology-Progress Series* 364, 169-180.
- Shepherd, S.A., Lowe, D., Partington, D., 1992. Studies on southern Australian abalone (genus *Haliotis*) XIII: Larval dispersal and recruitment. *Journal of Experimental Marine Biology and Ecology* 164 (2), 247-260.
- Simpson, J.H., Bowers, D., 1981. Models of Stratification and Frontal Movement in Shelf Seas. *Deep-Sea Research Part a-Oceanographic Research Papers* 28 (7), 727-738.
- Somarakis, S., Drakopoulos, P., Filippou, V., 2002. Distribution and abundance of larval fish in the northern Aegean Sea – eastern Mediterranean – in relation to early summer oceanographic conditions. *Journal of Plankton Research* 24, 339-357.
- Somarakis, S., Nikolioudakis, N., 2010. What makes a late anchovy larva? The development of the caudal fin seen as a milestone in fish ontogeny. *Journal of Plankton Research* 32 (3), 317-326.
- Sotka, E.E., Wares, J.P., Barth, J.A., Grosberg, R.K., Palumbi, S.R., 2004. Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Molecular Ecology* 13 (8), 2143-2156.
- Sponaugle, S., Lee, T., Kourafalou, V., Pinkard, D., 2005. Florida current frontal eddies and the settlement of coral reef fishes. *Limnology and Oceanography* 50 (4), 1033-1048.
- Stobutzki, I.C., Bellwood, D.R., 1998. Nocturnal orientation to reefs by late pelagic stage coral reef fishes. *Coral Reefs* 17, 103-110.

Testor, P., Send, U., Gascard, J.C., Millot, C., Taupier-Letage, I., Beranger, K., 2005. The mean circulation of the southwestern Mediterranean Sea: Algerian Gyres. *Journal of Geophysical Research-Oceans* 110 (C11).

Torres, A.P., Reglero, P., Balbin, R., Urtizberea, A., Alemany, F., 2011. Coexistence of larvae of tuna species and other fish in the surface mixed layer in the NW Mediterranean. *Journal of Plankton Research* 33 (12), 1793-1812.

Tsikliras, A.C., Antonopoulou, E., Stergiou, K.I., 2010. Spawning period of Mediterranean marine fishes. *Reviews in Fish Biology and Fisheries* 20 (4), 499-538.

Wei, J., Wang, D.P., 2009. A three dimensional model study of warm core ring interaction with continental shelf and slope. *Continental Shelf Research* 29 (13), 1635-1642.

Werner, F.E., Page, F.H., Lynch, D.R., Loder, J.W., Lough, R.G., Perry, R.I., Greenberg, D.A., Sinclair, M.M., 1993. Influences of mean advection and simple behavior on the distribution of cod and haddock early life stages on Georges Bank. *Fisheries Oceanography* 2 (2), 43-64.

Wright, K.J., Higgs, D.M., Belanger, A.J., Leis, J.M., 2005. Auditory and olfactory abilities of pre-settlement larvae and post-settlement juveniles of a coral reef damselfish (Pisces : Pomacentridae). *Marine Biology* 147 (6), 1425-1434.

TABLES

Table 1. Descriptors of the main taxa of fish larvae in Cabrera National Park during summer. C, constancy. (*) species selected for the multivariate analysis. In parentheses, the abbreviated name used in the multivariate analyses.

Family	N.	Abundance	C (%)	Range of	Family	N. larvae	Abundance	C (%)	Range of
Anguilliformes* (ANG)	10	0.16	13.95	3-7	Ophidiidae *(OPH)	73	1.15	67.44	2-42
Apogonidae	28	0.44	27.91	2-21	Paralepididae	17	0.27	20.93	2-29
Argentinidae	1	0.02	2.33	6	<i>Notolepis rissoi</i>	22	0.35	13.95	4-64
Blenniidae *(BLE)	48	0.76	46.51	2-20	<i>Paralepis</i> sp *	6	0.09	11.63	5-7
Bothidae	217	3.41	67.44	2-157	Phosychthyidae	4	0.06	6.98	4-10
Bramidae	4	0.06	9.30	3-4	Pomacentridae	608	9.56	79.07	5-179
Callyonimidae	6	0.09	11.63	3-9	Serranidae	3	0.05	6.98	2-5
Caproidae	2	0.03	4.65	2-3	<i>Serranus cabrilla</i> *(SCA)	66	1.04	46.51	3-24
Carangidae	6	0.09	9.30	2-7	<i>Serranus hepatus</i> *(SHE)	198	3.11	48.84	2-95
<i>Trachurus mediterraneus</i> *(TRA)	54	0.85	44.19	2-22	Scomberesocidae	33	0.52	37.21	2-14
<i>Trachurus</i> spp	2	0.03	4.65	4-5	Scombridae	330	5.19	37.21	2-254
Cepolidae	82	1.29	44.19	2-67	<i>Thunnus alalunga</i> *(THA)	35	0.55	20.93	3-30
Clupeidae	199	3.13	41.86	2-189	<i>Auxis rochei</i> *(ARO)	46	0.72	25.58	3-111
Cygnoglossidae	15	0.24	23.26	2-17	Other Scombridae	9	0.14	9.30	2-13
Engraulidae	89	1.40	60.47	2-57	Scorpaenidae	3	0.05	4.65	2-5
Gobiidae*(GOB)	629	9.89	72.09	2-236	<i>Scorpaena</i> sp.	2	0.03	2.33	5
Gobiesocidae	3	0.05	4.65	2-5	Soleidae	2	0.03	4.65	2-6
Gonostomatidae	1800	28.32	100.00	2-758	Other soleidae	2	0.03	2.33	4
Labridae	407	6.40	69.77	2-124	Sparidae	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
Merlucciidae	6	0.09	11.63	3-6	Sphyrnaidae	1	0.02	2.33	2

Mullidae	57	0.90	51.16	2-48	Sternoptychidae	11	0.17	18.60	4-17
Myctophidae	262	4.12	65.12	2-132	Stomiidae	4	0.06	9.30	2-5
<i>Hygophum hygomii</i> *(HHY)	371	5.84	55.81	2-277	Sygnathidae	2	0.03	4.65	2-3
<i>Benthoosema glaciale</i> * (BGL)	37	0.58	34.88	2-52	Trachinidae				
<i>Lampanyctus pusillus</i> *(LPU)	140	2.20	51.16	2-106	Triglidae	26	0.41	27.91	2-17
<i>Lampanyctus crocodilus</i> * (LCR)	32	0.50	39.53	2-27	<i>Trigla</i> spp *(TRI)	15	0.24	18.60	2-17
<i>Lobianchia dofleini</i> * (LDO)	53	0.83	37.21	2-26	Uranoscopidae	3	0.05	6.98	2-3
<i>Myctophum punctatum</i> * (MYC)	16	0.25	23.26	2-28	Xiphiidae	1	0.02	2.33	3
<i>Symbolophorus veranyi</i>	11	0.17	16.28	2-13					
Other Myctophidae*(MY_NI)	24	0.38	32.56	2-23					

Table 2. Description of the community structure of each predefined cluster group, and SIMPER analysis using Bray-Curtis similarity (similar to Hellinger's distance, Borcard et al. 2011). Only taxa contributing >2% to the within-station similarity in standardized abundance were 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 (%); $r = s \cdot SD-1$ (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.

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

FIGURE LEGENDS

Figure 1. Location of the survey area in the NW Mediterranean Sea. The inset shows the 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) are used for convenience in the following figures to display the results.

Figure 2. (a) Alongshore (u, black line) and cross-shore (v, gray line) components of the near-surface alongshore flow speeds (m/s) at the mooring site. Vectors have been rotated 8° counter-clockwise towards the direction of maximum variance. Gray arrows indicate oscillatory intensification episodes corresponding to island-trapped waves associated with the increases in local wind stress (black arrows) shown in the lower panel (b). The gray band indicates the dates of the cruise.

Figure 3. (a) Sea surface height (SSH, cm) and derived oceanic circulation patterns (cm/s). Note the NE-SW transition area across the Balearic Islands and the 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 derived from the CTD data obtained 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); the dotted line corresponds to the water mass on the shelf (mode 2). Gray shading shows 1 S.D. of each water mass.

Figure 4. a) Near-surface (20 m) temperature (°C), (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 × 1000). The white line in the maps indicates the position of the 200-m isobath.

Figure 5. PCA, cluster and distribution map for environmental variables (a1, b1, and c1) and for larval fish taxa (a2, b2, and c2).

Figure 6. Distribution of (a) coastal and (b) oceanic fish larval species (ind. 10 m^{-2}) as clustered in Table 2 (groups O and C) and the abundances of two coastal (*C. chromis* and *S. hepatus*) and two oceanic (*B. glaciale* and *L. pusillus*) taxa. The thick gray line marks the approximate position of the front between the two water masses.

Figure 7. Comparison of the length-frequency (bars) and cumulative frequency (line, right axis) distributions of *Serranus cabrilla* and *Coris julis*.

Figure 8. Larval abundances for < 6-mm and > 6-mm size classes of *Serranus cabrilla* and *Coris julis*. The gray line marks the approximate position of the front between the two water masses.

Figure 9. Modeled distribution of passive particles released around CNP (a). Distribution assuming one week of continuous shoreward larval swimming at speeds of 5 cm/s (b). Pattern assuming one week of larval swimming only when advected in the offshore direction (c). Units are in particles per unit.

Figure 1. Location of the survey area in the NW Mediterranean Sea. The inset shows the 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) are used for convenience in the following figures to display the results.

88x61mm (300 x 300 DPI)

Figure 2. (a) Alongshore (u , black line) and cross-shore (v , gray line) components of the near-surface alongshore flow speeds (m/s) at the mooring site. Vectors have been rotated 80 counter-clockwise towards the direction of maximum variance. Gray arrows indicate oscillatory intensification episodes corresponding to island-trapped waves associated with the increases in local wind stress (black arrows) shown in the lower panel (b). The gray band indicates the dates of the cruise.

91x63mm (300 x 300 DPI)

Figure 3. (a) Sea surface height (SSH, cm) and derived oceanic circulation patterns (cm/s). Note the NE-SW transition area across the Balearic Islands and the 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 derived from the CTD data obtained 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); the dotted line corresponds to the water mass on the shelf (mode 2). Gray shading shows 1 S.D. of each water mass.
59x25mm (300 x 300 DPI)

Figure 4. a) Near-surface (20 m) temperature (°C), (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 × 1000). The white line in the maps indicates the position of the 200-m isobath.
 171x237mm (300 x 300 DPI)

Figure 5. PCA, cluster and distribution map for environmental variables (a1, b1, and c1) and for larval fish taxa (a2, b2, and c2).
222x323mm (300 x 300 DPI)

Figure 6. Distribution of (a) coastal and (b) oceanic fish larval species (ind. 10 m⁻²) as clustered in Table 2 (groups O and C) and the abundances of two coastal (*C. chromis* and *S. hepatus*) and two oceanic (*B. glaciale* and *L. pusillus*) taxa. The thick gray line marks the approximate position of the front between the two water masses.

243x278mm (300 x 300 DPI)

Figure 7. Comparison of the length-frequency (bars) and cumulative frequency (line, right axis) distributions of *Serranus cabrilla* and *Coris julis*.
77x73mm (300 x 300 DPI)

Figure 8. Larval abundances for < 6-mm and > 6-mm size classes of *Serranus cabrilla* and *Coris julis*. The gray line marks the approximate position of the front between the two water masses.
161x221mm (300 x 300 DPI)

Figure 9. Modeled distribution of passive particles released around CNP (a). Distribution assuming one week of continuous shoreward larval swimming at speeds of 5 cm/s (b). Pattern assuming one week of larval swimming only when advected in the offshore direction (c). Units are in particles per unit. 86x42mm (300 x 300 DPI)