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3 **Model-based assessment of local-scale fish larval connectivity in a**
4 **network of marine protected areas (MPAs)**
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ABSTRACT

We assessed by numerical modeling the coastal fish larval dispersion along the southern coast of Mallorca (Balearic Islands, NW Mediterranean) with the objective of determining the factors that contribute to successful recruitment. We assumed that fish larvae dispersal is mainly regulated by physical transport. Currents are mainly wind driven in this area; therefore, changes in wind forcing have a first-order impact on larval transport. The synoptic wind patterns were systematically analyzed based on self-organizing map analysis. The wind fields were clustered using a neural network pattern recognition approach into two modes, producing opposite along-shelf flow. The seasonal changes between spring and summer in the dominance of either mode modulate the along-shelf circulation, producing flow shifts under some circumstances. This variability in the wind regime was consistent throughout the 10 years analyzed (2000-2009). Using the Princeton Ocean Model (POM) and a particle-tracking algorithm, we analyzed the effect of wind-forced currents in the connectivity among near-shore habitats. We show that, at the spatial scale considered, the coastal morphology and stochastic wind forcing favor local recruitment (mean of 30% self-recruitment). Maximum transport distances of 20-30 km were typically associated with particles left to drift for 21 days. The implications for the performance of the four marine protected areas near SW Mallorca Island are discussed. Our results suggest that, although wind episodes determine the fate of short-time spawning events, on a seasonal basis, regular larval supply to coastal zones is ensured by wind stochasticity.

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Key words: dispersal, larvae, connectivity, coastal, marine protected area, Mediterranean

For Peer Review

INTRODUCTION

Many marine fishes have a planktonic larval phase that occurs in the water column away from the adult habitat. During this pelagic stage, the larvae are capable of broad dispersal, and their return to the adult populations is often variable, resulting in substantial fluctuations in the population size (e.g., Roberts, 1997; Pedersen et al., 2003; but see Leggett and Frank, 2008). The flow-induced pelagic dispersal patterns of fish eggs and larvae from their spawning grounds are crucial for determining the survival of reef and coastal fishes that require reaching a suitable settlement site at the end of a relatively short larval stage (weeks to months). Thus, the supply of larvae is the determinant of the stability of the open populations of fishes that depend upon the return and settlement of the planktonic larvae to balance the adult mortality losses (Cowen, 1985; Sinclair, 1988; Sponaugle and Cowen, 1996). Furthermore, knowledge of the patterns of larval dispersal between benthic habitat patches is critical to understanding the connectivity and persistence of marine metapopulations (Hastings and Botsford, 2006; Sale et al., 2006, Pineda et al., 2007).

The traditional view of the potentially high dispersal for marine propagules (e.g., Roughgarden et al., 1988; Siegel et al., 2003) has been tempered by the growing evidence of restricted dispersal, which would imply that local recruitment is more important than previously thought (Jones et al., 1999; Jones et al., 2005; Knutsen et al., 2007). The interaction of different biophysical mechanisms may fully or partially counter dispersion and enable the retention of larvae near their natal source. The relative importance of passive

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3 versus active larval behavior mechanisms in coastal recruitment is still unclear because,
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5 among other reasons, these relationships vary among species and larval developmental
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7 stages (Leis, 2007). Fish larvae are able to perform vertical diel migrations that
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9 significantly affect their final location (Leis, 2007; Vikebø et al., 2007). Furthermore, they
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11 may follow ambient cues at the horizontal scale to successfully reach nursery areas or
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13 survive (e.g., Bradbury and Snelgrove, 2001; Leis, 2010; Vermeij et al., 2010). The extent
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15 to which the larval behavior affects recruitment is still under discussion. In addition to the
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17 behavioral aspects, many of which are still unresolved for several fish species, different
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19 studies show that physical and biological processes that promote the retention and
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21 aggregation of larvae in the appropriate environmental conditions for their development
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23 and growth probably determine their survival and increase recruitment. These results
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25 suggest an important role of physics in the persistence and distribution of many fish
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27 populations (Kingsford and Suthers, 1994; Hinckley et al., 1996; Agostini and Bakun,
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29 2002).

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36 The inner shelf circulation is of particular importance in the dispersal processes of
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38 coastal fish species that exhibit a strong relationship to particular littoral habitats, such as
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40 seagrass beds, sandy seabeds or rocky shores, from which they rarely migrate. Among the
41
42 physical processes determining recruitment success in the inner-shelf (i.e. where
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44 bathymetry is < 50 m), wind-driven flow plays a major role in transporting eggs and larvae
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46 towards or away from coastal nursery grounds (Norcross and Shaw, 1984). This
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48 phenomenon is because most marine fish eggs are buoyant and therefore are affected by
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50 wind-induced surface layer transport. Variations in wind fields have been associated with
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52 the variability in the initial dispersal of larvae (Appeldoorn et al., 1994; Hinrichsen et al.,
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3 2003), recruitment (Cury and Roy, 1989; Kingsford and Finn, 1997) and the abundance of
4 adult stocks (Bailey 1981; Myers and Drinkwater 1988; Shenker et al.1993). This physical
5 variability acts at different temporal scales. For example, although shifts in prevailing
6 currents induce seasonal and interannual variability, episodic events and local scale
7 oceanographic structures are related to intra-seasonal variability (Sponaugle and Cowen,
8 1996).

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17 Understanding how fish populations are interconnected by larval dispersal is
18 essential to the successful management of living marine resources, especially when
19 considering spatial management measures, such as marine protected areas (MPAs)
20 (Almany et al., 2009). For MPAs to be successful in protecting marine populations, an
21 individual MPA must be self-sustaining or adequately connected to other MPAs via larval
22 dispersal. Information on larval dispersal is critical in practical terms because the degree of
23 connectivity among geographic areas sets the scale at which management strategies for
24 exploited marine species need to be applied. Understanding larval dispersal mechanisms,
25 rates, and distances can help to determine the optimal size and location of MPAs and
26 adequately protect connectivity (Sala et al., 2002; Sale et al., 2005; Laurel and Bradbury,
27 2006). Studies of fish larvae connectivity have revealed a high range of variability, from
28 high levels of self-recruitment within a specific area to a significant dispersal among areas,
29 at scales of tens of km (Planes et al. 2009). Relevant levels of larval connectivity may be
30 modified by the availability of recruitment habitat (Jones et al., 2007) and a suite of post-
31 recruitment processes (Hamilton et al., 2008).

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53 The inner shelf circulation around Mallorca is considered to be relatively uncoupled
54 from regional oceanographic features because of the low tidal forcing in the Mediterranean;
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3 therefore, wind-induced processes are particularly important (Jordi et al., 2011). Seagrass
4 meadows, which extend down to depths of 40m, have long been argued to be important
5 nursery areas because their high productivity and structural complexity provide both
6 enhanced foraging opportunities and refugia from predators for larvae and juvenile fishes;
7 therefore, they are important for sustaining the biodiversity of fish assemblages (e.g.,
8 Howard et al., 1989). Despite the increasing concern for and economic valuation of littoral
9 fish species associated with recreational and artisanal fisheries in temperate areas (Cooke
10 and Cowx, 2004; Morales-Nin et al., 2005), little is known about the scale of their
11 connectivity patterns and how MPAs can be efficiently used for conservation or fishery-
12 management purposes (Morales-Nin et al., 2010). With some overlaps, species such as
13 *Coris julis*, *Symphodus ocellatus*, *Diplodus annularis*, *Sarpa salpa*, *Serranus scriba* and
14 *Spondylisoma cantharus* typically inhabit the *Posidonia oceanica* seagrass beds, whereas
15 species such as *Symphodus roissali*, *Symphodus tinca* or *Diplodus sargus* are associated
16 with the rocky–algal reef habitats. Other conspicuous species, such as *Gymnammodytes*
17 *cicerellus*, *Lithognathus mormyrus*, *Gobius geniporus*, *Mullus barbatus* or *Uranoscopus*
18 *scaber*, are observed over sandy areas. The adults of some of the littoral species associated
19 with seagrass beds have narrow home ranges of less than 1 km² (March et al., 2010), which
20 may imply that the adult populations are highly sensitive to local management actions,
21 including the establishment of MPAs. This high preference for some habitats, and in some
22 cases the scarcity of some of these habitat types, means that some species settle in
23 practically the same sheltered sites year after year (Macpherson, 1998; Vigliola et al.,
24 1998). Furthermore, these protected areas have been reported as important spawning areas
25 for targeted fishery species (Crec'hriou et al., 2010).
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3 Because of the importance of the artisanal and recreational fishery to the economy
4 of many islands of the Mediterranean Sea and the ongoing efforts towards stock
5 management through the development of MPAs (Goñi et al., 2000; Gell and Roberts,
6 2003), the larval dispersal patterns of coastal fish species in temperate areas, where
7 research is rather limited in comparison with coral reef zones, merit further attention.
8 Evidence from hydrodynamic models and genetic data indicate that the scales of dispersal
9 can vary widely at different locations in space and time (e.g., Cowen et al., 2003; Sotka et
10 al., 2004). The purpose of this study was to analyze, at scales of kilometers, the
11 connectivity patterns of the inner-shelf larval fish species of Mallorca Island and how they
12 are affected by wind-driven circulation. In particular, we focus our study on the dispersal
13 patterns produced by dominant wind regimes clustered in two wind modes, their seasonal
14 and inter-annual variations. The southern coast of the island extends for approximately 140
15 km, including five coastal MPAs (two of them are considered to be a single MPA for the
16 purposes of this paper). In formulating management decisions to protect the coastal
17 ecosystems contained within these MPAs, it is important to understand the drivers of
18 coastal recruitment and the level of exchange in networked MPAs; however, this issue
19 remains unresolved to date.
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METHODS

Study area

For the purposes of this study, we assume that the southern Mallorca shelf is divided into an inner- and outer-shelf region. Although the outer shelf is influenced by ocean dynamics, the inner shelf is affected primarily by wind-induced processes. The sea bottom in this area is primarily covered by seagrasses (*Posidonia oceanica*) that can extend to a depth of 40 m with different extents of coverage (Duarte, 1991) and with interspersed sandy and rocky areas. Bays and coastal inlets provide refuge for juvenile fishes. Because of the ecological value of the island shelf, five marine protected areas have been established, including the National Park of Cabrera (Fig. 1). Two of these areas, Malgrats and Toro, are small and close together and, for the purpose of this paper, have been considered to be a single MPA. Further offshore, the bottom habitats are mainly sandy or mud.. During summer, the vertical motions are restricted by a strong seasonal thermocline that occurs at depths ranging from 30-40 m in the inshore and neritic waters.

One of the most conspicuous climatic features of Mallorca is wind seasonality. As is true over much of the western Mediterranean Sea, the most consistent winds during the winter-spring transition are derived from synoptic scale depressions that sweep west to east causing southwesterly winds. This situation continues to early May but diminishes in frequency and intensity as the influence of the Azores anticyclone extends to this region as summer approaches. The warmer days of spring result in a sea breeze regime that becomes gradually established by the end of May, although it can occur on warm days during winter.

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3 The sea breeze usually develops under anticyclonic situations, weak surface pressure
4 gradients, intense solar radiation and clear skies (Ramis and Alonso, 1988). The wind
5 vector direction varies around Mallorca with the topography of the island and the time of
6 day; it generally presents midday southeasterly to southwesterly direction in the studied
7 area (see Ramis et al., 1990).
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15 Although the main patterns of regional scale circulation are well described (Millot,
16 1994; Garcia-Lafuente et al., 1995; López-Jurado et al., 1995, 1996; García-Ladona et al.,
17 1996; Pinot et al., 2002) and the local circulation in some bays has been analyzed in detail
18 (Basterretxea et al., 2004; Orfila et al., 2005; Basterretxea et al., 2007), less is known about
19 the shelf-scale circulation, which is assumed to be weak and highly variable. Werner et al.
20 (1993) identified the shelf circulation patterns off of southern Mallorca under idealized
21 wind forcing. They described southeastward shelf circulation during winter storm
22 conditions from WSW and locally variable currents under sea breeze forcing. Recently,
23 Jordi et al. (2011) showed that the oscillatory motions associated with the presence of
24 island trapped waves (ITWs) are a major feature of the coastal dynamics of Mallorca,
25 accounting for approximately 70% of the low frequency variance on the shelf. Along linear
26 coastlines, ITWs produce coast-parallel oscillatory motions with low net transport;
27 however, non-linear interactions with topography can produce residual flows affecting the
28 distribution of contaminants, particles and planktonic organisms. Because tidal forcing is
29 low (spring range <0.25 m), both locally wind-forced transport and wind-generated ITWs
30 are considered to be important contributors to fish larval dispersal patterns.
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55 *Meteorological data and wind pattern classification*
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3 For analyzing wind patterns, 12-hourly wind maps were constructed by optimal
4 interpolation of wind data that was recorded by two coastal meteorological stations (Palma
5 Airport and Cape Salines) and the QuikSCAT satellite for the study period (2000-2009).
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7 The resultant synoptic wind maps were classified using a self-organizing map (SOM)
8 algorithm. The SOM is a non-linear cluster analysis tool based on a self-organizing
9 mapping neural network, which has no supervision on its learning. It is designed for pattern
10 recognition and classification (Kohonen, 1984, 1997) and identifies patterns in the input
11 data, based on their underlying variance structure. The SOM algorithm computes the
12 patterns or modes so that they optimally describe the domain of the observations. In recent
13 years, SOMs have been widely used as pattern recognition tools in synoptic meteorology
14 (Richardson et al., 2003; Liu and Weisberg, 2005; Mau et al., 2007). We used the
15 MATLAB SOM toolbox developed by Vesanto et al. (2000). Compared with other
16 common neural networks, SOMs demonstrate more powerful capabilities in classifying,
17 recognizing and clustering wind patterns.
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40 *Model implementation*

41 The hydrodynamics of southern Mallorca were simulated using a three-dimensional
42 density-resolving model, based on the Princeton Ocean Model (POM). The resolution of
43 the hydrodynamic model was 200 m in the horizontal, and its 25 non-equidistant (sigma)
44 vertical layers were organized to enhance the resolution near the surface and the seabed.
45 The flow fields produced by surface wind forcing were obtained from the 12-hourly wind
46 maps for ten years (2000-2009). The results of the hydrodynamic computation were stored
47 at hourly intervals and then used in a post-processing mode to drive a separate behavioral
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3 and particle-tracking model for the development and transport of fish eggs and larvae. A
4 random walk term was used to approximate the effects of the sub-grid scale processes on
5 particle trajectories (Xue et al., 2008). This random movement has a mean of zero and a
6 variance of $2K_h\Delta t$, where K_h is a horizontal diffusivity constant set at $500 \text{ m}^2\text{s}^{-1}$.
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8 Comparative tests were performed using a K_h of $50 \text{ m}^2\text{s}^{-1}$
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15 We based our dispersal analysis on 10-year simulations (2000-2009) of 19,325
16 passive tracers that were released at weekly intervals from seagrass/rocky bottoms (<40 m
17 depth) for a 6-month season (March to August) each year. This period covers the spawning
18 season of most Mediterranean coastal fish species (Tsikliras et al., 2010). Considering that
19 the pelagic larval duration of Mediterranean coastal fish species typically ranges from 2
20 weeks (e.g. *Oblada melanura*, *Boops boops*) to 4 weeks (e.g. *Coris julis*) before settlement
21 (Raventós and Macpherson, 2001), the tracers were released assuming a pelagic larval
22 duration (PLD) of 3 weeks. Comparisons with 2- and 4-week releases were also performed.
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24 The particles were homogeneously distributed in the release areas (the seagrass-covered
25 bottoms in Fig. 1) and were left to drift for the abovementioned time periods. The
26 connectivity estimates were obtained by subdividing the inner-shelf into 25 ~6 km wide
27 sectors following the coastline. Consistent with observations that the eggs and larvae of
28 coastal species mainly occur near the surface (e.g., Olivar and Sabatés, 1997; Olivar et al.,
29 2001), the depth of the release of the particles was random within the first 10 m of the
30 water column. No patchiness was considered within each quadrant.
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50 A reflective boundary condition was used to prevent particles from moving onto
51 land. The eggs and larvae were treated as passive, neutrally buoyant particles, flowing near
52 the surface. We assumed that during the first 3 weeks of age, transport of fish propagules is
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3 mainly driven by physical forces. Furthermore, as no information on individual behavior or
4 mortality is available for the vast majority of species in the area, biological traits were not
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6 considered. We assumed individual larvae to have been recruited to a particular coastal area
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8 if they were found in the inner-shore habitat (defined by each the box area) at the end of the
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10 pelagic larval period. For the purpose of this paper, connectivity (C) is defined as the
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12 number of particles arriving into box i from box j by the end of the prescribed PLD period
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14 divided by the number of particles initially released in zone j . We also defined retention
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16 capacity (RC) as the number of particles remaining in box j at the end of the prescribed
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18 PLD period divided by the number of particles initially released in box j .
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24 To evaluate the model performance, we compared the results with current data
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26 obtained at 3 moorings, two in Palma Bay and one in Cape Salines (refer to Fig. 4 for
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28 mooring locations). In the three cases, bottom-mounted Nortek 1MHz Aquadopp profilers
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30 were deployed for 6-month periods at an approximate depth of 26 m. ADCP 1 was moored
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32 from March to October 2007, and ADCP 2 and 3 were deployed from March 2009 to
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34 October 2009. Details of the model performance can be found in Jordi et al. (2011). The
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36 matching of the model-derived particle distributions with the observed fish larvae
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38 distribution, with particular emphasis on retention, was performed by analyzing the larval
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40 spatial patterns of a coastal resident species, *Chromis chromis*, obtained from field research
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42 cruises. This species is a coastal spawner with benthic eggs and pelagic larvae. Larval
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44 distribution maps were obtained for surveys conducted in Cabrera NP (July 2007, boxes 10
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46 to 17) and Palma Bay (July 2010, boxes 4 to 8). Samples were gathered from hauls from
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48 standard bongo-nets with 335 μm mesh equipped with flowmeters (General Oceanics
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50 model 230) and preserved in 2% sodium borate-buffered formalin. Standard length (SL,
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3 mm) was measured from up to 30 random individuals from each station under a binocular
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6 microscope (precision=0.01 mm). We analyzed the abundance of large larvae (size above
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8 population median value) for the two surveys. Based on the larval size at hatching and at
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10 four days of development provided by Padoa (1956) and the size at the age of newly settled
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12 individuals (Raventós and Macpherson, 2001), these larvae are at least a week in age. The
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14 assumption underlying this analysis is that larger larvae will accumulate in areas of higher
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16 retention. Despite these data only providing a general view of one of the wind situations
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18 analyzed (summer conditions), the high environmental stability during the surveys, which
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20 was typical for that period, and the abundance of the selected species suggest that the
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22 observed distributions may be a good proxy for an average summer distribution.
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RESULTS

Wind patterns

Only the first two patterns or modes derived from the application of the SOM algorithm to the wind maps were considered. These modes captured 79% of the total wind variability around Mallorca and allowed a simple interpretation of the seasonal variation. The frequency of occurrence of the other wind patterns is relatively low. The resulting averaged features of the synoptic field characterizing each mode are shown in Fig. 2. Mode 1 comprised north to northeasterly winds that were typically characteristic of the anticyclonic circulation that prevail in the summer. Mediterranean summers are warm and mostly dry due to the influence of a high-pressure ridge extending from the Azores subtropical high (Xoplaki et al., 2003). Although the effect of the local sea breeze was not captured in the QuickSCAT data, comparisons with the wind records at Palma Airport and Cape Salines revealed that it was associated with the situations of high atmospheric pressure included in mode 1. Mode 2 mainly corresponded to the passage of low-pressure systems through the Iberian Peninsula, generating westerly and southwesterly winds.

As displayed in Fig. 3a (only the year 2007 is represented), both wind modes alternated throughout spring, and mode 1 became prevalent on summer. This seasonal shift in atmospheric conditions most frequently occurred in mid-June, but, in some years, summer conditions settled earlier (e.g., years 2000 and 2006). Although summer conditions were very similar among the years, the most noticeable interannual variability occurred during spring (Fig. 3 b and c). In particular, in the years 2001 and 2008, mode 2 winds were

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3 remarkably prevalent. Large scale weather patterns are known to have an impact on the
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5 intensity and frequency of Mediterranean cyclones.
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10 *Wind-induced coastal circulation*

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12 Coastal circulation obtained from the ADCP records reflected weak currents (mean
13 vector velocity $\sim 1.4 \text{ cm s}^{-1}$) with notable change in the drift direction between the spring
14 and summer. This mean value was variable depending on the events included in the
15 averaging period. Enhancement of the current intensity by $\sim 500\%$ was observed in Cape
16 Salines where ADCP1 is located (Fig. 4a). South and westward circulation was prevalent
17 under mode 1 winds, whereas eastward drift was promoted under mode 2 forcing. These
18 observations were in qualitative agreement with the model results, although somewhat
19 more intense flow was obtained in the simulations (average difference of 0.7 cm s^{-1}).
20 Although we used the wind modes as depicted by the SOM for easy interpretation, the
21 model was forced by real winds. Numerical comparisons of the averaged spatial patterns
22 for both modes revealed significant changes on both sides of Cape Salines and generally
23 weaker circulation under mode 1 forcing. Coastal drift flushed the water parallel to the
24 coast in a clockwise direction under this mode and in the opposite direction for mode 2
25 (Fig. 4b and c). The model solution generated a cyclonic gyre to the east of Cabrera and an
26 area of weakened flow towards the northwest of Cabrera under mode 1 forcing.
27 Conversely, sheltering and recirculation occurred to the lee of Cape Salines under mode 2
28 winds. Obviously, these mean patterns should not be considered to be stationary because
29 the development and size of these gyres were dependent on the strength of the coastal
30 forcing.
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Simulated larval dispersal for modal winds

To determine the effect of the two wind modes obtained by the SOM classification in the connectivity patterns of the study area, we analyzed the transport of particles during 3 week periods for episodes when the wind consistently corresponded to each wind mode, i.e., the occurrence of a specific mode is greater than the mean occurrence of this mode plus two times the standard deviation. The pattern obtained by this classification method is summarized in Fig. 5a and b. Under both wind-forcing scenarios, limited dispersal from spawning grounds was observed (low dispersion from the main diagonal of the matrix). Coherently with the current patterns, mode 1 produced westward dispersal along the western coast (sectors 1-13) and southward transport along the eastern coast, whereas dispersal in the opposite direction occurred under mode 2 winds. This reversal was particularly notable along the western coast, where differences of up to 6% were achieved. The generally lower energy of the mode 1 conditions also favored higher (2-3%) self-recruitment. This phenomenon had notable effects in the exchange among the MPAs, which was increased by the more dispersive mode 2.

As shown in Fig. 5c, a slightly smeared version of the connectivity obtained for the two wind modes was obtained for the mean pattern of the 10 years analyzed. Self-recruitment values indicated that between 13 and 66% (mean $30\pm 14\%$) of the particles remained in the original zone 3 weeks after being released and that $30\pm 10\%$ were lost to unfavorable areas (boundary sectors excluded). The alternation of the wind forcing produced an isotropic diffusion with a low preferential direction of transport. The exceptions were primarily caused by the topographical features of the coast (e.g., between

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3 sectors 9 and 16). Moderate transport (i.e., >10%) occurred primarily among contiguous
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5 cells, and the transport success to more distant areas was modest. Indeed, the significant
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7 connectivity (>1%) oscillated between 20 and 30 km from the spawning areas.
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10 The area with the highest retention corresponded to the inner part of Palma Bay
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12 (sectors 6 and 7), where currents were weakened by the coastal topography. Cabrera
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14 National Park also retained a significant percentage of particles ($46 \pm 4\%$, MPA-4), which
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16 was attributed to the recirculation patterns produced in the coastal flow by the islands.
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18 However, low export was expected from this area. Conversely, the lowest retention (i.e.,
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20 <20%) occurred in cells situated in the vicinity of capes (sectors 1, 4, 5, 8 and 17). MPAs 1
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22 and 2, located within the boundaries of Palma Bay, primarily dispersed particles to other
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24 areas. In contrast, MPA-3 was a receptor of larvae that originated in other zones,
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26 particularly under mode 1 winds when sectors 17 and 18 contributed with up 43% of the
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28 particles arriving to this MPA. This is caused by the weakening of the coastal flow to the
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30 west of Cape Salines (see Fig. 4). As shown in Fig. 5d, the importance of this role as source
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32 or sink for larvae varied seasonally in all cases, except for MPA-4, for which seasonal
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34 differences are low.
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43 *Inter-annual variations*

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45 The inter-annual variations in wind forcing produced changes in the recruitment success,
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47 but the rank of importance in the connectivity with other areas rarely varied; the few times
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49 this occurred, the variations were among neighboring areas. Comparison of the spring
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51 dispersal among years, with the predominance of mode 2 winds in 2008 and mode 1 in
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53 2003, revealed an increase in the east- and northward-directed connectivity, with the most
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3 notable differences along the eastern coast (sector 17 and above, Fig. 6a). Because mode 1
4 conditions typically prevailed in summer, when most of the littoral species spawned, the
5 inter-annual variations between two years with either a high or low percentage of mode 1
6 winds (2005 and 2001) were explored. For those years, as expected, transport south and
7 westward was emphasized, but a remarkable increase in the self-connectivity of MPA-4
8 was observed. Inter-annual variations had a significant effect on the self-recruitment of the
9 system. The mean range of variation for the 10 years simulated was $10.8 \pm 4.1\%$, but some
10 areas, like sector 17 in the south of Cabrera, experienced variations of up to 18%.
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24 *Sensitivity analysis and comparison with field data*

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27 A comparative test conducted using PLDs of 2 and 4 weeks yielded very low (not
28 significant) but site-specific differences in long-distance connectivity and negligible
29 variations in self-recruitment, which was mainly dictated by the diffusivity values.
30 Conversely, variations in diffusivity had a major impact in the connectivity estimates, while
31 maintaining the same connectivity pattern, as shown in Fig. 7. Retention was significantly
32 higher and dispersal to nearby areas was lower, when a diffusivity value of $50 \text{ m}^2 \text{ s}^{-1}$ was
33 used. This suggests that in nearshore environments where K_h is notably reduced larval
34 retention would be above our estimated values.
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46 The retention capacity estimates showed increased retention in Palma Bay (sectors 6 and 7)
47 and in areas where topographically generated retention patterns were expected (13, 14, and
48 to a lesser extent 15, 16 and 21; Fig. 8a). In general, the larval distribution maps agreed
49 with model results, yet some differences were observed (Fig. 8b and c). It should be noted
50 that, although the model results indicated the average patterns, the field data corresponded
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3 with the episodic scenarios. The larval distribution maps confirmed that Palma Bay was a
4 retentive area, although, unlike the model results, the larvae aggregated in the approximate
5 center of the Bay and not along the inner coast. The accumulation at either side (southeast-
6 northwest) of Cabrera (MPA-4) was consistent with the alternation of the different wind
7 modes along Cabrera. Nevertheless, this effect was not evident west from Cape Salines
8 (sector 13), where the model results indicated a highly retentive area.
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22 DISCUSSION

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27 Our connectivity analysis revealed that weak and variable flow dynamics, together
28 with topographically driven differences in the response of currents to wind changes, were
29 the main determinants of high retention rates in southern Mallorca. The presence of
30 topographic hot spots for larval retention emphasized the importance of small spatial scales
31 (i.e., 20-30 km) to the demography of inner-shelf fish species. We estimated that an average
32 of 30% of the spawned larvae remained in the source areas, allowing for their full
33 development within the proximity of adult habitat. To understand the importance of this
34 value to larval potential survival, several points must be considered. First, our model does
35 not include larval mortality. Natural larval mortality before metamorphosis varies widely
36 with temperature, growth, species, and/or patchiness, with values ranging from 1 to 50%
37 day⁻¹ (Houde, 1989; McGurk, 1986). High egg mortality also occurs, although egg
38 development lasts only for a few days (McGurk, 1986). Stage-duration depends mainly on
39 the species and temperature, and the stage mortality will vary with the instantaneous
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3 mortality over the duration of the stage. Second, the size of the compartments used can
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5 influence the connectivity and self-recruitment results. This size depends on the species
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7 considered, its home range and spawning habits. Our interpretation is based on the fact that
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9 several key Mediterranean littoral species have a small home range (~ 1 km, March et al.,
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11 2010; Alós et al., 2011; Palmer et al., 2011), at least in their adult phase, which is within
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13 the order of magnitude of our selected compartments. The self-recruitment values of up to
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15 70% observed herein are not particularly high considering the topography of the coast and
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17 the stability of the water mass. High self-recruitment values for a littoral Mediterranean
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19 species whose adults exhibit a small home range (*Trypterigion delaisi*) have been
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21 confirmed genetically (Carreras-Carbonell et al., 2007), and our results expand upon the
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23 hypotheses of strong larval self-recruitment patterns for littoral species. In tropical areas,
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25 high self-recruitment of coral-reef fish has been documented even in extremely small areas
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27 (Jones et al., 2005).

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34 Growing evidence indicates the importance of self-recruitment in the early life stage
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36 success of coastal (Carreras-Carbonell et al., 2007), reef (Jones et al., 2005) and neritic
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38 populations (Churchill et al., 2011; see also reviews by Levin 2006 and Cowan and
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40 Sponaugle 2009). Although post-recruitment mortality may modify recruitment patterns,
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42 increased survival caused by self-replenishment may in turn influence survivorship to
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44 adulthood and self-maintenance of the population (Bradbury et al., 2008), particularly in
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46 oligotrophic systems, in which the export of larvae to the outer shelf would likely result in
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48 poor feeding conditions. Indeed, unlike open systems in which recruitment success may
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50 vary with changes in ocean dynamics, relying on local replenishment confers notable
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52 interannual adult population stability to inner-shelf species. This stability appears to be a
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3 common feature of coastal spawning organisms for which self-recruitment is high, as
4 revealed by genetic and numerical dispersal studies (e.g., Lefebvre et al., 2003; Planes et
5 al., 2008).
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10 Self-recruitment along the inner shelf is enhanced by cross-shore shear and in the
11 lees of topographic features such as capes and islands where increased primary and
12 secondary productivity may create favorable foraging habitats (Rissik et al., 1997; Hamne
13 and Hauri, 1981). Our simulations indicate that most inshore larval trapping is due to the
14 rugged coastline that attenuates the flow near the coast, allowing larvae to remain within
15 the original area. As expected, we obtained higher self-recruitment (more leptokurtic
16 dispersal shape) than that predicted by Gaussian dispersal kernels for straight coastlines and
17 uniform alongshore flows (Siegel et al., 2003). Advection to other areas is controlled by
18 release from source environments due to diffusive motions. Therefore, increased dispersal
19 to nearby areas is obtained at higher K_h values while maintaining a similar connectivity
20 pattern. Largier (2003) thoroughly reviewed the effect of diffusivity and its inshore-
21 offshore variations. He discussed the relevance of the exponential increase in K_y (cross-
22 shore diffusivity) from near the shore (1–10 m²/s) to approximately 100 m²/s over the
23 wind-driven shelf. Assuming similar values for our system, our estimates of dispersal
24 would be conservative, and higher self-recruitment would be expected, as suggested by Fig.
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7. Moreover, we have not considered the influence of larval behavior (i.e., swimming and sensory abilities), which depending on the species could either reduce dispersal and consequently favor self-recruitment (Cowen, 2002), or increase the exchange among fish populations.

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3 Arguably (see e.g., Farmer and Berg, 1990), the presence of eddies and other
4 recirculating structures enhance larval retention, a well-known phenomenon observed in
5 coastal flows (Signell and Geyer, 1991; Swearer et al., 1999) that may also thereby
6 influence the productivity of the waters. Significant eddy formation was predicted in the
7 model simulations in the vicinity of Cape Salines, to the west of Cabrera and, less
8 prominently, in other coastal topographic irregularities. Eddies lasting for some hours have
9 also been described in Palma Bay, affecting sectors 6 and 7 (Jordi et al. 2011). Although in
10 some areas eddy formation may be caused by variations in Ekman drift, they are
11 particularly associated with interactions between ITWs and the coast. In contrast to oceanic
12 areas where eddies are weakly influenced by the dissipation of vorticity, in shallow water,
13 the lifetime of eddies is relatively short because of the strong influence of bottom friction
14 and the variability of wind forcing. Therefore, these eddies are not necessarily permanent,
15 although they are common enough to be statistically significant, in particular under mode 1
16 winds. This phenomenon is consistent with the RC estimates shown in Fig. 8 (see also Fig.
17 4), where the areas affected by recurrent eddy presence suggested net larval retention,
18 which is compatible with the results from the larval surveys. The topographically generated
19 eddies with timescales of the same order as those of the PLDs could be effective in
20 retaining fish larvae. Thus, the relatively reduced PLDs of summer spawners (Macpherson
21 and Raventós, 2006) due to high water temperatures in that period, together with persistent
22 mode 1 winds, would favor eddy trapping.

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Ayata et al. (2010) compared the dispersal kernels and connectivity matrices among
16 populations of marine invertebrates and demonstrated a significant impact of PLD on
the dispersal kernels. For all spawning months and the spawning populations, a shorter

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3 PLD resulted in shorter mean dispersal distances. On average, they found that a decrease of
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5 50% in PLD (from 4 to 2 weeks) caused a decrease of 45% in mean dispersal distance. In
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7 addition, O'Connor et al. (2007) demonstrated a negative relationship between temperature
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9 and pelagic larval durations (PLDs) for a wide range of marine species. Reduced PLDs
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11 induced by temperature increases could lead to substantial modifications of dispersal and
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13 connectivity patterns. At first look, our results seem to contradict this relationship because
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15 in the time range considered (2-4 weeks), PLD seemed not to be critical for the dispersal
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17 range of these species in a variable forced system. However, this result is caused by the
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19 different timescales considered.
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25 As Mitarai et al. (2008) stated, connectivity matrices are a function of several time
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27 scales, such as planktonic larval duration, the frequency and duration of larval release, and
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29 the inherent time scale of coastal circulation processes. We based our connectivity
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31 estimations on mean patterns rather than on specific wind episodes because, for larvae with
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33 relatively long PLDs, the importance of episodic events tends to diminish (Salomon, 1990;
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35 Thiébaud et al., 1994) and therefore larval dispersal is more related to mean meteorological
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37 conditions. In temperate areas with slow and unpredictable current conditions, spawning
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39 timing is not critical. Conversely, if the focus switches to areas with notable current shifts
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41 (e.g. Carson et al 2010) or to species with short spawning periods or to specific spawning
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43 pulses with scales close to atmospheric synopticity, the variations in PLD become critical.
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45 The association between settlement pulses and intense weather events is documented for a
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47 wide range of crustaceans (Johnson and Hester, 1989; Epifanio, 1995; Briones-Fourzan et
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49 al., 2008). Short and synchronous spawning events are typical for coral reef species (e.g.,
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51 Tucker 1998), where advection is critical.
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3 On a seasonal basis, the variability in wind direction, together with oscillatory
4 motions produced by ITWs, retained inner-shelf fish larvae close to the spawning grounds,
5 favoring self-recruitment. Seasonality did not notably vary the connectivity pattern, but it
6 does affect dispersion to other areas. Our data show that dispersive losses were reduced
7 during the summer, when mode 1 winds consistently blew. Reduced wind variability
8 (alternation between mode 1 and 2) also decreased in this season. Seasonal winds may
9 directly influence the settlement success, either by reducing spawning success during
10 periods of high winds and turbulent conditions or by enhancing the likelihood of coastal
11 retention during periods of minimal wind (Johannes, 1978; Lobel, 1989; Colin, 1992).
12 Changes in the wind regime affected transport and have also been related to the onset of
13 spawning. For example, Thomson and Hourston (2011) related the initiation of sockeye
14 salmon spawning to the weakening of wind forcing.
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31 Despite the evidence that dispersal was often limited to small scales, our simulations
32 suggest that a notable proportion (~30%) of larvae could be advected offshore. The fate of
33 these larvae was unknown and, because of dilution, their contribution to the sustainment of
34 the adult population was likely to be negligible. However, the potential recruitment of some
35 of these individuals to remote areas was regulated by episodic processes rather than by
36 mean flow and could episodically become significant. These successful events could be
37 ecologically important because they could contribute to the replenishment of populations in
38 remote areas and to the large-scale genetic exchange.
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55 *Implications for the existing MPAs*
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6 For MPAs to be successful in the protection of marine populations, individual MPAs must
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8 either be self-sustaining or adequately connected to other MPAs via dispersal (Planes et al.,
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10 2009). The spatial scale over which populations are connected by larval dispersal is critical
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12 to the efficiency of MPA networks because protection usually increases with increasing
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14 MPA size or when MPA spacing is close enough to allow species persistence via network
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16 connectivity rather than self-replenishment (Moffit et al., 2011). If open populations do not
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18 buffer against local extinction, there is likely to be increased susceptibility to disturbance
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20 and localized fishing effort (Bradbury et al., 2008). Consequently, spatial management
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22 strategies that are based on networked no-take areas may be successful in enhancing and
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24 protecting local recruitment. However, a growing body of research highlights the evidence
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26 of restricted dispersal, questioning the paradigm that marine populations are
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28 demographically open at the spatial scales therein addressed (e.g., Jones et al., 1999;
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30 Swearer et al., 1999; Sotka et al., 2004; Leggett and Frank 2008). Considering that many
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32 coastal resident fish populations are characterized by localized population structure with
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34 limited dispersal and high self-recruitment, the networking of MPAs carried out in
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36 Southern Mallorca seems to be a reasonable approach for tackling conservation issues.
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46 The size of individual reserves and the placement and distance between the reserves within
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48 the network will depend on the patterns of larval dispersal and the connectivity among the
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50 populations (Stobutzki, 2001). Apostolaki et al. (2002) stated that the greatest success in
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52 MPAs is observed for species that occupy discrete habitats in which the required habitats
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54 are in close proximity, such as when spawning habitats overlap larval/juvenile nursery
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3 areas. Coastal fishery management for Majorca Island is an example of a complex system
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5 in which the combined use of MPAs with other measures operating on the recreational and
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7 commercial fleet may be the only way of sustaining both conservation and marine use by
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9 multiple users (Morales-Nin et al., 2010). However, too often the implementation of these
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11 measures has not been coordinated (nor evaluated) under single or multiple objective
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13 schemes.
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20 In our case, the four MPAs considered can be essentially grouped in two clusters with
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22 different characteristics based on coastal hydrography. MPA-1 and 2 are characterized by
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24 higher dispersal rates because of their locations in areas of enhanced flow (next to
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26 prominent capes). In contrast, MPA-3 and 4 are high-retention areas, favoring the
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28 recruitment of larvae from other zones. From a conservation perspective, both roles present
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30 interest, but the premises for their effective design are different. Populations in MPAs
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32 located in retention areas display a strong self-recruitment component. Assuming that
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34 coastal resident species present a small home range (proven only for adults of some
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36 species) and the low mean dispersal herein reported, population persistence would be
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38 guaranteed at these sites. The Area of Cabrera National Park harbors high species richness
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40 and abundance/biomass of fishes (Reñones et al., 1997; Harmelin-Vivien et al., 2008) being
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42 a potential important spawning area for targeted fishery species (Crec'hriou et al., 2010).
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44 Some vulnerable species in the area, like dusky grouper (*Epinephelus marginatus*), appear
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46 to be very sensitive to protection levels and show high biomass and broad size structure
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48 suggesting that the population is self-recruiting (Reñones et al., 1999). The geographical
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50 location of this MPA provides the adequate environmental setting to generate retention
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3 areas (thus favoring larval development and acquisition of behavioural properties that
4 promote survival). One notable difference between these two MPAs (3 and 4) is that
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6 alongshore exchange is expected in MPA-3, whereas because of its relatively isolated
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8 nature, MPA-4 is less likely to seed other areas. This low dispersal from islands to the
9
10 mainland has been previously observed in other areas and suggests that islands are less
11
12 effective in enhancing fisheries (the other objective of MPAs) through larval export
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14 (Williamson et al., 2004; Bell, 2008). For MPAs promoting high dispersion, their
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16 effectiveness relies on networking with other MPAs or with unprotected zones that offer
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18 suitable nursery habitats. In Mallorca, our estimates show that the required distance for
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20 those connections is 20-30 km. This requirement is met by MPA-1 and 2, which might
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22 effectively replenish the nearby Bay of Palma, where most of the recreational fishing effort
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24 is concentrated (Morales et al., 2005).
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34 In summary, we provide evidence of i) the relatively high rates of potential self-recruitment
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36 in the coastal areas of a Mediterranean Island and how environmental features are linked
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38 with connectivity values and ii) how established small-scale MPAs in close proximity to
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40 one another in a coastal Mediterranean zone serve different functions in either exporting or
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42 retaining capacity. This information is essential because the degree of connectivity among
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44 the MPAs sets the scale at which management strategies for exploited species need to be
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46 applied.
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10 <http://www.cis.hut.fi/projects/somtoolbox/>.
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For Peer Review

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FIGURE LEGENDS

Figure 1. Bathymetric map showing the location of the study area along the southern coast of Mallorca (see inset for location). The areas shaded in green indicate the presence of seagrass meadows or rocky bottoms that determined the particle release points. The sectors used for dispersal calculations are indicated. The four MPAs referred to in the text are colored in yellow. MPA-1, Malgrats-Toro, includes 2 nearby small protected areas that have been considered as a single MPA for the purpose of this paper.

Figure 2. Mode 1 (a) and Mode 2 (b) regional wind patterns as depicted from the self-organizing map (SOM) classification of the interpolated wind data recorded by two coastal meteorological stations (Palma Airport and Ses Salines) and the QuikSCAT satellite data for the period (2000-2009).

Figure 3. (a) The spring-summer variation in the mode winds for 2007 obtained from the mean daily pattern classification. The transition between spring and summer conditions is indicated with a dotted line. (b) The interannual variations in the frequencies of the characterized wind clusters during spring (March-May) and (c) summer (June-August).

Figure 4 (a) Mean mode 1 (black) and mode 2 (gray) currents as obtained from ADCP records and (b) mean model-generated surface currents for mode 1 and (c) mode 2 winds. Note that the vector scale in panel (a) has been enlarged for clarity.

Figure 5. The connectivity matrix expressed as the % of particles released from each of the zones on the x-axis arriving in zones on the y-axis. The color indicates the percentage of the larvae from a source location arriving at a destination location at the end of the larval development period (3 weeks). The dashed line represents self-recruitment. (a) The connectivity matrix for persistent mode 1 episodes and (b) mode 2 winds. (c) The 10-year mean connectivity for the period considered and (d) seasonal differences (summer-spring). Note that the color bar for panels a, b and c is logarithmic (upper left). Black boxes indicate the seasonal changes in the dispersal from/to the four MPAs shown in Fig. 1.

Figure 6. Variation in the connectivity matrix between years with different wind mode percentages. (a) Spring variations between 2008 and 2003 and (b) summer differences for 2005 through 2001.

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2
3 Figure 7. Box-whisker plot (median line, 25% and 75% quantiles box, 5% and 95%
4 quantiles whiskers) of the percentage of self-recruitment of the particles and those lost from
5 the habitat for different diffusivity values ($\text{m}^2 \text{s}^{-1}$).
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8 Figure 8. (a) RC (%) for spring and summer in the different sectors of the study region. The
9 sign indicates either negative or positive balance between export and recruitment. (b) The
10 distribution of large-sized larvae of *Chromis chromis* in Palma Bay and around Cabrera (c)
11 in surveys conducted in July 2010 and 2007, respectively. Units are $\text{ind. } 10 \text{ m}^{-2}$. RC is
12 defined as the number of particles remaining in box j at the end of the prescribed PLD
13 period divided by the number of particles initially released in box j .
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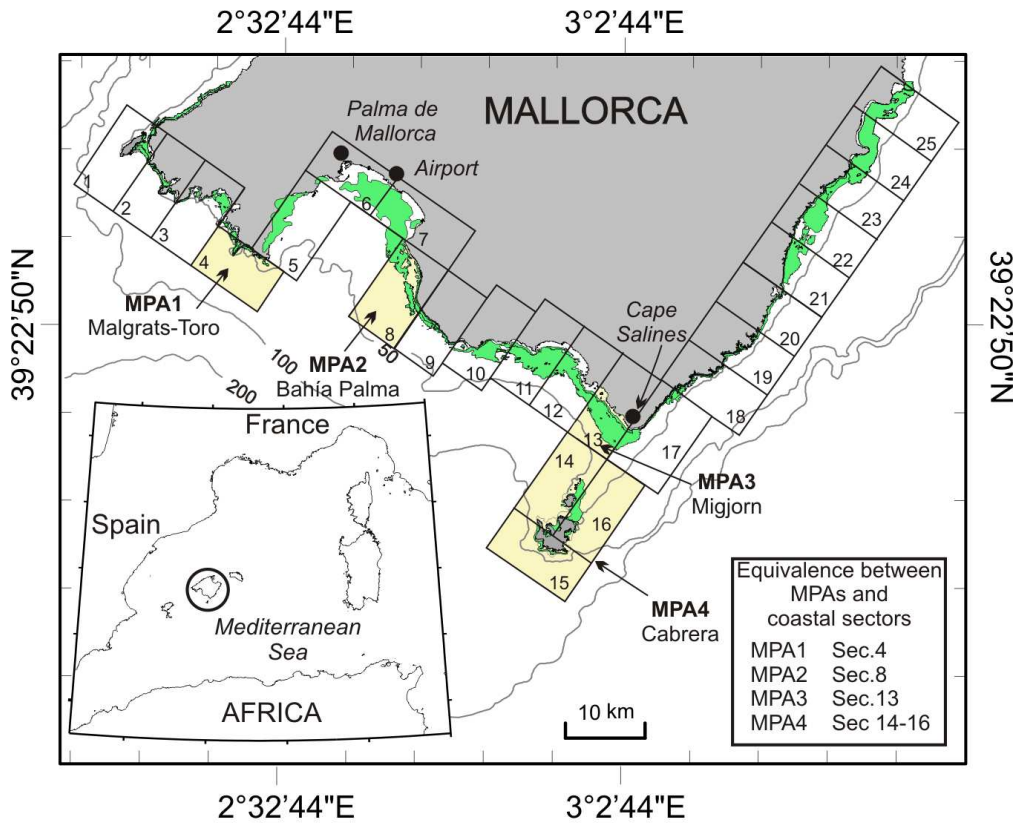


Figure 1

Figure 8. (a) RC (%) for spring and summer in the different sectors of the study region. The sign indicates either negative or positive balance between export and recruitment. (b) The distribution of large-sized larvae of *Chromis chromis* in Palma Bay and around Cabrera (c) in surveys conducted in July 2010 and 2007, respectively. Units are ind. 10 m⁻².
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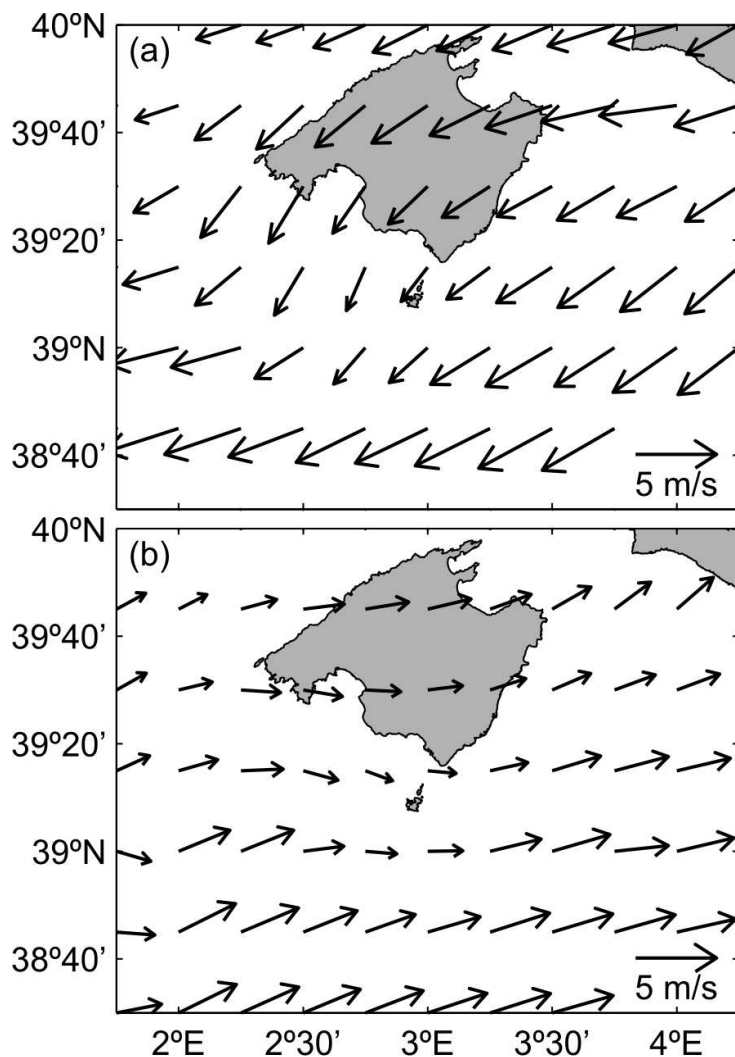


Figure 2

Figure 2. Mode 1 (a) and Mode 2 (b) regional wind patterns as depicted from the self-organizing map (SOM) classification of the interpolated wind data recorded by two coastal meteorological stations (Palma Airport and Ses Salines) and the QuikSCAT satellite data for the period (2000-2009).

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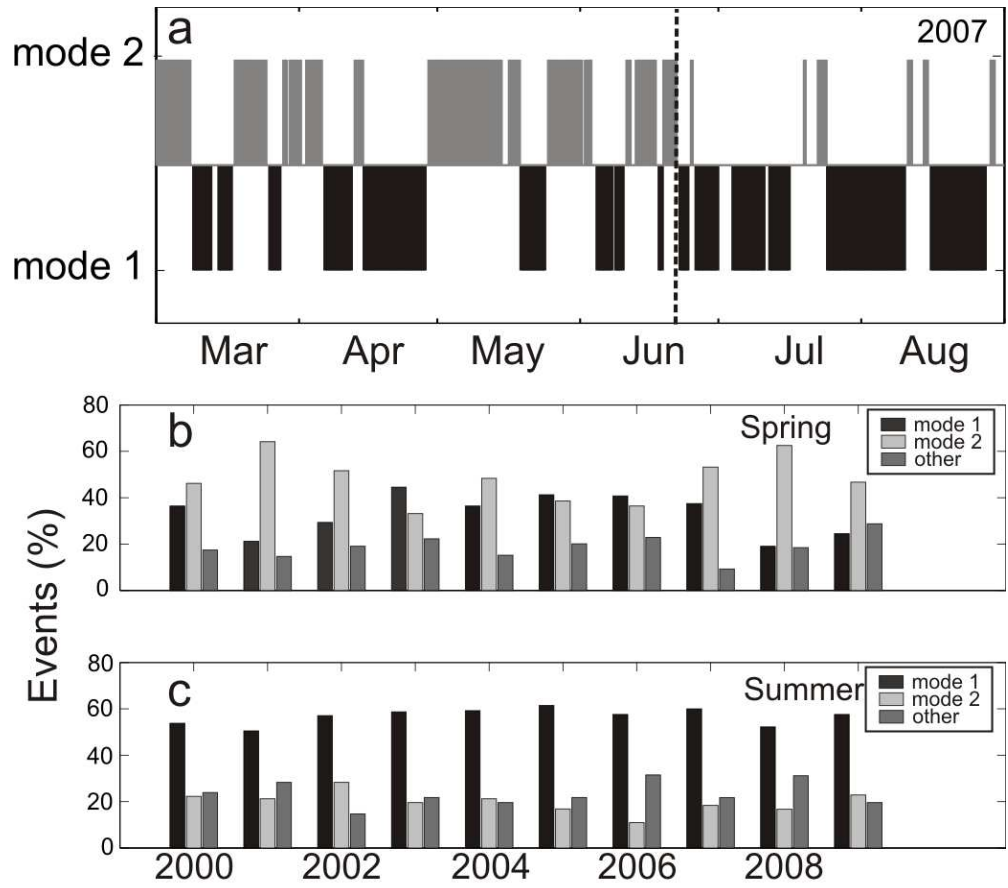


Figure 3

Figure 3. (a) The spring-summer variation in the mode winds for 2007 obtained from the mean daily pattern classification. The transition between spring and summer conditions is indicated with a dotted line. (b) The interannual variations in the frequencies of the characterized wind clusters during spring (March-May) and (c) summer (June-August).
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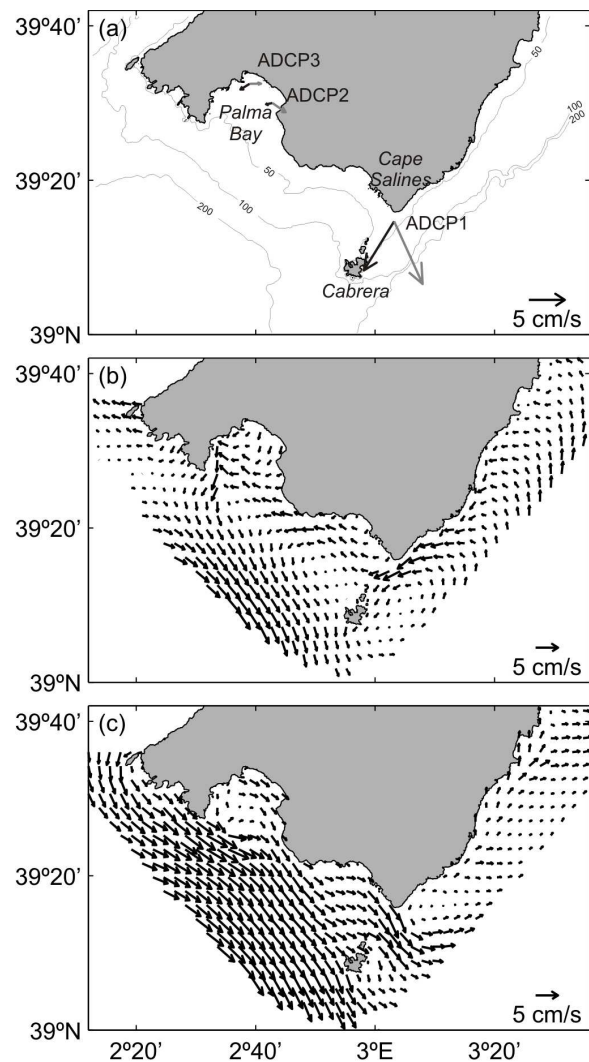


Figure 4

Figure 4 (a) Mean mode 1 (black) and mode 2 (gray) currents as obtained from ADCP records and (b) mean model-generated surface currents for mode 1 and (c) mode 2 winds. Note that the vector scale in panel (a) has been enlarged for clarity.

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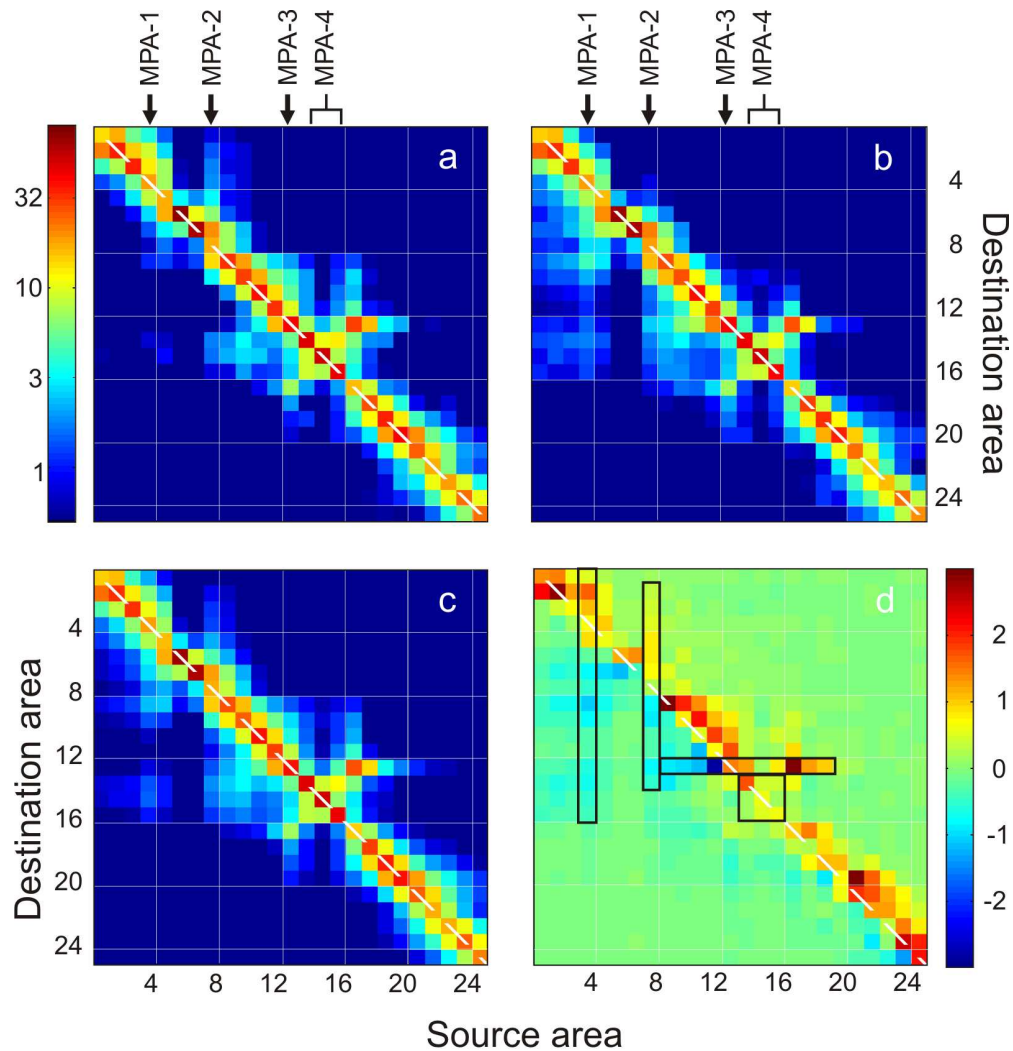


Figure 5

Figure 5. The connectivity matrix expressed as the % of particles released from each of the zones on the x-axis arriving in zones on the y-axis. The color indicates the percentage of the larvae from a source location arriving at a destination location at the end of the larval development period (3 weeks). The dashed line represents self-recruitment. (a) The connectivity matrix for persistent mode 1 episodes and (b) mode 2 winds. (c) The 10-year mean connectivity for the period considered and (c) seasonal differences (summer-spring). Note that the color bar for panels a, b and c is logarithmic (upper left). Black boxes indicate the seasonal changes in the dispersal from/to the four MPAs shown in Fig. 1.

135x163mm (300 x 300 DPI)

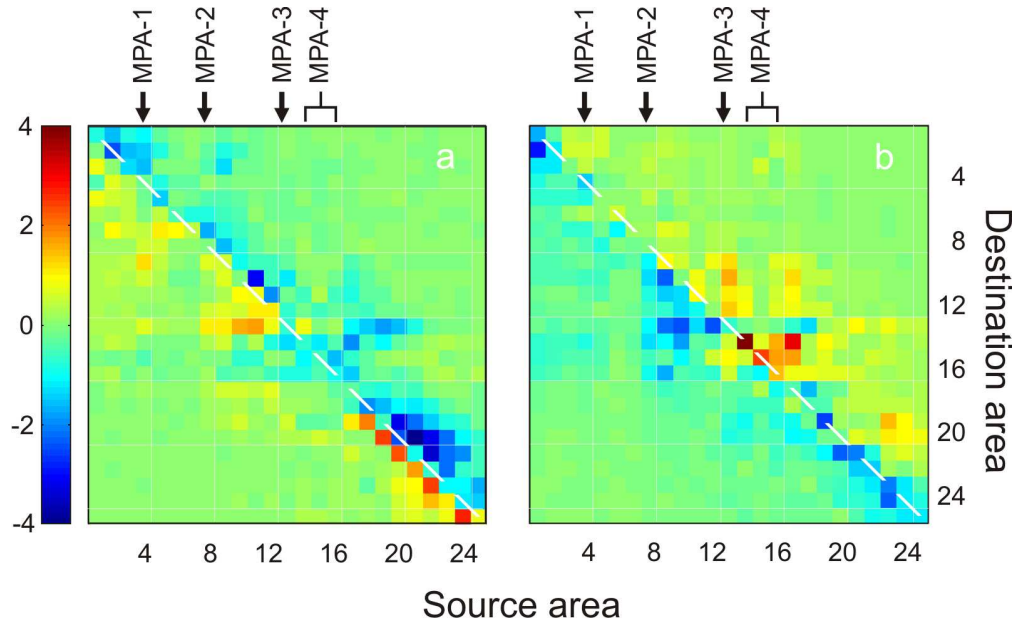


Figure 6

Figure 6. Variation in the connectivity matrix between years with different wind mode percentages. (a) Spring variations between 2008 and 2003 and (b) summer differences for 2005 through 2001. 135x112mm (300 x 300 DPI)

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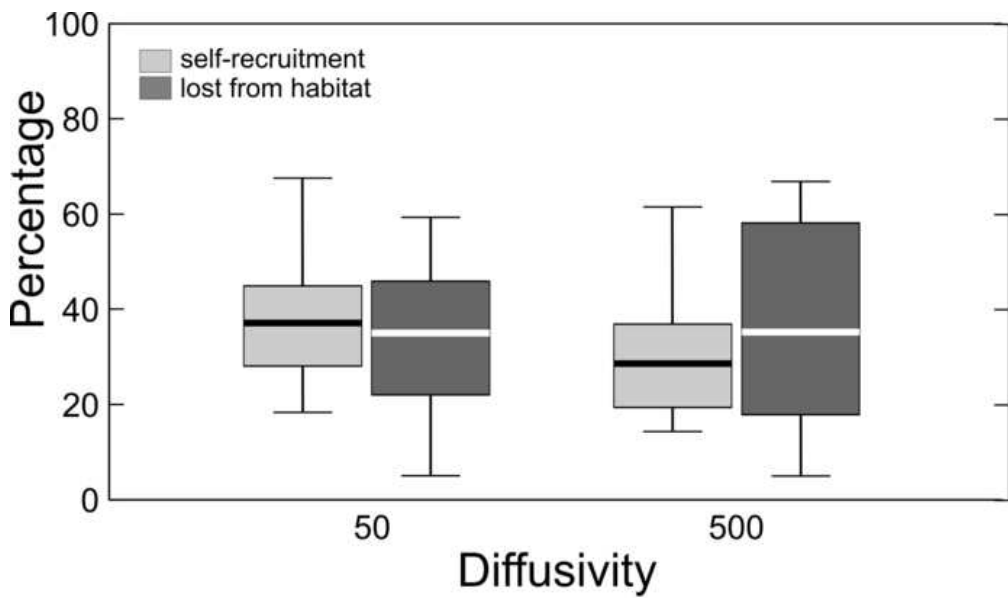


Figure 7

58x48mm (300 x 300 DPI)

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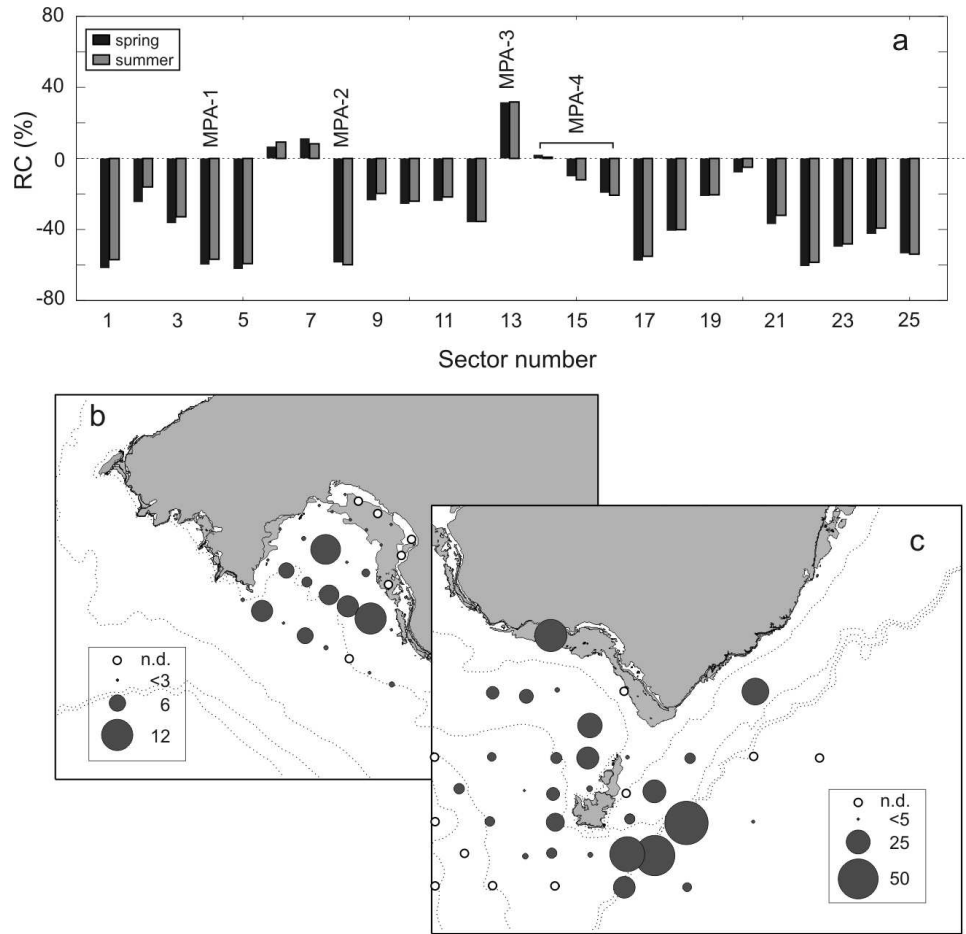


Figure 8

Figure 8. (a) RC (%) for spring and summer in the different sectors of the study region. The sign indicates either negative or positive balance between export and recruitment. (b) The distribution of large-sized larvae of *Chromis chromis* in Palma Bay and around Cabrera (c) in surveys conducted in July 2010 and 2007, respectively. Units are ind. 10 m⁻².
111x139mm (300 x 300 DPI)