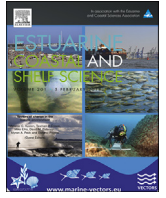




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Connectivity between coastal lagoons and sea: Asymmetrical effects on assemblages' and populations' structure

Angel Pérez-Ruzafa ^{a,*}, Francesca De Pascalis ^b, Michol Ghezzi ^b,
 Jhoni Ismael Quispe-Becerra ^a, Raquel Hernández-García ^a, Irene Muñoz ^a,
 Carlos Vergara ^a, Isabel María Pérez-Ruzafa ^c, Georg Umgieser ^{b,d}, Concepción Marcos ^a

^a Department of Ecology and Hydrology, Faculty of Biology, Regional Campus of International Excellence Mare Nostrum, University of Murcia, 30100, Spain

^b Institute of Marine Science - National Research Council (ISMAR-CNR), Venice, Italy

^c Department of Plant Biology, Faculty of Biology, Complutense University of Madrid, Spain

^d CORPI, Coastal Research and Planning Institute, Klaipeda University, Lithuania

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ABSTRACT

Connectivity among marine populations plays a fundamental role in the dynamic of metapopulations and communities. Moreover, genetic connectivity is important for the evolutionary history and adaptive capability of species while demographic connectivity is essential to maintain ecological processes. In coastal lagoons, isolation degree or confinement is considered the main factor structuring biological assemblages. These environments also function as nursery areas for many marine species that colonize the lagoons as larvae or juveniles, returning to the sea for reproduction. It is therefore essential to know the connectivity between lagoons and sea for the management of biodiversity and the exploitation of coastal living resources. This work analyses the role that connectivity between coastal lagoons and sea plays in the assemblages and subpopulations structure of the first.

To this purpose, a finite element hydrodynamic model was used coupled with a lagrangian module to simulate the potential exchange of organisms between Mar Menor lagoon (Western Mediterranean) and the adjacent sea. Connectivity parameters from 40 stations, located inside and outside the Mar Menor, have been estimated. The outcomes of the eight simulations carried out were compared with field data, including ichthyoplankton species composition and genetic fluxes in 6 species with different life stories. The results suggest that pelagic larval phases are longer than expected or the species can extend PLD within certain limits if the conditions for the settlement are not adequate. Repetition can improve the chance of self-recruitment, coupling larval duration, competency period and finding the adequate location for settlement.

The results also show that connectivity between all lagoon and Mediterranean stations is very low and is independent of geographical distance. There is a strong asymmetry in the probability of receiving particles, being lower the probability of colonization of the lagoon stations from the sea than vice versa. Despite its low values, connectivity can explain up to 65% of the similarities in species composition of the ichthyoplankton and between 30 and 96% of the variance in genetic differentiation of the studied species.

The low value of connectivity and colonization rates is enough, however, to maintain the genetic fluxes between populations and, at the same time, restricted connectivity can play an important role in maintaining high diversity and heterogeneous assemblage structure.

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1. Introduction

Marine connectivity, or exchange among marine populations through the dispersal of individuals as larvae, juveniles, or adults (Sale et al., 2005; Abesamis et al., 2016), is considered essential for understanding from the ecological flow that guarantee the genetic

* Corresponding author. Department of Ecology and Hydrology, Faculty of Biology, Regional Campus of International Excellence Mare Nostrum, University of Murcia, 30100, Spain.

E-mail address: angelpr@um.es (A. Pérez-Ruzafa).

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exchange between subpopulations, to the marine population dynamics, the management of fishery stocks, or the design of marine reserves (Cowen et al., 2000, 2006, 2007; Sale et al., 2005; Jones et al., 2009a; Olds et al., 2016) and, at ultimate extent, the ecosystem responses to changing environmental conditions (De Lucio et al., 2003; Gawarkiewicz et al., 2007). Therefore, connectivity processes are increasingly considered in a wide range of applications ranging from assessment of pollutant risk to nearshore fisheries management (Steneck et al., 2006; Mitarai et al., 2009). However, its study in the marine environment is still in a very low percentage compared to studies in terrestrial ecosystems (Ayram et al., 2016).

Connectivity depends on the habitat characteristics and its fragmentation, the distance between patches, and the species dispersal capability, being therefore scale dependent (Söndgerath and Schröder, 2002). For most benthic marine species, the exchange between populations occurs primarily during the pelagic stages (Cowen and Sponaugle, 2009). Because of this, and due to the dispersion capacity of the currents, it is usually assumed that marine environment is more likely to be functionally connected than terrestrial ecosystems (Jones, 2002). However, distribution patterns and dispersal capability are not always evident (Mora and Sale, 2002; Reisser et al., 2014) and, despite the increasing research and progresses made on this topic (Levin, 2006; Jones et al., 2009b; Lett et al., 2010; Leis et al., 2011), the difficulties to obtain direct data on larval biology and on how environmental changes (i.e. circulation patterns, temperature, prey and predator abundance, adaptive behaviour) affect dispersal patterns and the survival of larval stages still remain (Ghezzeo et al., 2015).

Coastal lagoons are among those marine habitats with highest biological productivity (Alongi, 1998), playing an important ecological role and offering a variety of goods and services to human populations, making them one of the more valuable ecosystems in the world (De Groot et al., 2012).

They are isolated and confined environments (Guelorget and Perthuisot, 1983; Kjerfve, 1994) that show a high diversity of environments, habitats and distinct communities which are suitable for different fish and invertebrate species, most of them with fishing interest (Pérez-Ruzafa et al., 2004, 2007a; Tagliapietra et al., 2009). At the same time, coastal lagoons show biological gradients in species richness, assemblage structure, abundance and productivity that are not well explained by salinity and have been related to confinement, a parameter defined by Guelorget and Perthuisot (1983) as the turnover time of marine water and the impoverishment in some oligoelements of marine origin, and redefined by Pérez-Ruzafa and Marcos (1992, 1993) as the probability of colonization of the lagoon areas by marine species. In the latter way, confinement gradients would be an expression of the decreasing colonization rates by marine species from the inlets to the inner areas of the lagoons and would depend on the number and size of the inlets and the distance to the sea. Therefore, if connectivity patterns between sources and sinks of recruits, and the scales at which they take place, result essential in understanding species composition and assemblage's structure in marine communities (Cowen et al., 2006), it is particularly true in coastal lagoons.

Furthermore, connectivity between lagoons and the sea is especially important because of the active migrations of some key fish species entering the lagoons as larvae or juveniles, growing on natural food, and returning to the sea for reproduction. This behaviour is the base of a traditional form of fishery, that takes advantage of the passage of adults through the channels, practiced in about 29,000 ha of coastal lagoons bordering the Mediterranean (FAO, 1979). However, although the role that connectivity between juveniles in estuarine/coastal environments and adult marine subpopulations plays in maintaining marine fish populations is

recognized, the extent to which different factors affect this connectivity is still uncertain (Vasconcelos et al., 2011).

It is noteworthy that while Ghezzeo et al. (2015) showed that the probability of receiving lagrangian particles (assimilating larvae to them) from the sea is very low in three representative coastal lagoons with very different water renewal rates, genetic studies show high genetic fluxes between lagoon and coastal sea populations but with more or less significant genetic differentiation in the studied species (Vergara-Chen et al., 2010a, 2010b; Gonzalez-Wanguemert and Perez-Ruzafa, 2012; Milana et al., 2012; Hegele-Drywa et al., 2015).

So, the aim of this study is to analyse and test the role that hydrodynamic connectivity can play structuring biological assemblages and promoting genetic connectivity in a Mediterranean coastal lagoon, testing the possible effects of considering different time scales, the possibility that a larva can return to the same place several times or the pelagic larval durations when computing connectivity.

2. Material and methods

We have studied the connectivity inside the Mar Menor lagoon (SW Mediterranean), and between it and the open sea, using a hydrodynamic model coupled with a particle-tracking model, driven by realistic meteorological forcing. The results have been contrasted with biological data on ichthyoplankton assemblages and genetic structure of benthic species with different life stories and reproductive strategies (Fig. 1).

2.1. Study site

The Mar Menor, with an area of 135.5 km², is a choked (sensu Kjerfve, 1994) and hypersaline coastal lagoon, located in a Spanish semi-arid region of the SW Mediterranean coastline (37°44' N, 0°47' W) (Fig. 1). Its average depth is 3.6 m, with a maximum of just over 6 m. Considering its low tidal range (0.05 m), the water level fluctuation can be contemplated almost constant. The water column is always well mixed but salinity shows heterogeneous spatial and temporal distribution depending on season, rainfall, runoff, and Mediterranean influence through the main inlets, with a minimum of 38.1 PSU and a maximum of 51 PSU (Pérez-Ruzafa et al., 2005).

The exchanges with the sea take place through three inlet complexes located in the sand bar that separates the lagoon from the Mediterranean. The northern complex, with three main channels, namely La Torre, El Ventorrillo, and El Charco, of which the first two are natural, cover an area of 1 Km wide, and less than 50 cm deep. El Estacio and Marchamalo, in the middle and south respectively of the sand bar, were built by man before the 19th century (Lillo 1981). Throughout history, the northern inlets and El Estacio were used for fishing weirs or "encañizadas" taking advantage of the migration of fish and producing high fishing yields. But Marchamalo (at present 30 m wide, 40 cm deep), at the South, never worked adequately and was abandoned due to the continuous silting of sediments that precluded the interchange of waters and the movement of fish. In 1973, El Estacio inlet was dredged and widened (70 m wide, and up to 6 m deep) to allow navigation. Then, El Estacio channel became the main connection between the lagoon and the Mediterranean, causing major changes in the environmental conditions, such as a drop in salinity, a smoothing in temperatures, and changes in biological assemblages, including the colonization of new species and the disappearance of fishing in the traditional fishing weirs "encañizadas" (Pérez-Ruzafa et al., 1991; Pérez-Ruzafa and Marcos, 2005; Marcos et al., 2015).

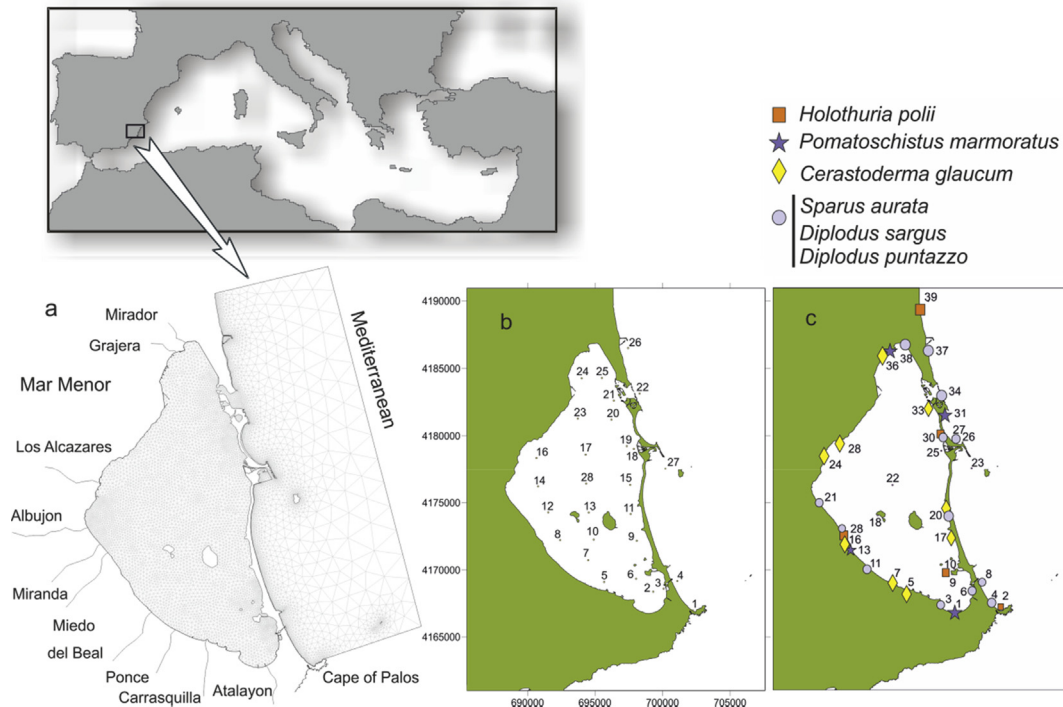


Fig. 1. Location of the sampling stations considered in this work and used for the computation of connectivity. a) numerical grid of SHYFEM model; b) off shore stations considered in the study of ichthyoplankton assemblages; c) coastal stations used for the different genetic studies. Map axes correspond to UTM coordinates expressed in metres.

2.2. Hydrodynamic model and lagrangian module

A 2D hydrodynamic model (SHYFEM) (Umgiesser et al., 2004) has been used to simulate the circulation and transport of the water masses in the lagoon and the adjacent waters. This model has been already applied successfully to other lagoons (Umgiesser et al., 2014) and to the Mar Menor basin where was calibrated and validated using independent data (De Pascalis et al., 2012). The model uses finite elements for spatial discretization of the domain and a semi-implicit algorithm for integration in time, resolving the vertically integrated shallow waters equations in their formulations with levels and transports. The 2D approach is appropriate for the Mar Menor because, due to very low river discharges and depth, no stratification can be observed.

Following Ghezzi et al. (2015), larvae dispersion has been modelled by a lagrangian module linked to the lagoon hydrodynamic model. The movement of each particle, which represents a planktonic organism, has been described by the spatial variation of its position, and the advective displacement was the result of the current speed. The turbulent fluctuations were parameterized by a stochastic method and calculated with the Random Walk method. This technique has been used to include the diffusive processes generated by the small-scale turbulence, typically parameterized by the horizontal scale diffusion.

We considered only the passive transport in horizontal direction of planktonic organisms without mortality during the pelagic larval phase and without simulating their response to environmental factors such as temperature, salinity or food availability, and we do not consider the possibility of any vertical or horizontal active movement of the organisms.

2.2.1. Grid and simulation setup

In order to simulate the particle exchange with the Mediterranean, the numerical domain has been represented by the lagoon and a portion of its sea shelf, considering as open boundary the

west off-shore border of the domain, and as closed boundaries the whole perimeter of the lagoon, islands and the sea coast line (Fig. 1a). The obtained numerical grid has 8850 nodes and 16116 triangular elements with size range from 10 to 1800 m and arrives to the 70 m depth isoline in the Mediterranean. The areas nearest to the coastline have the finest resolution, while the central part of the lagoon and the offshore Mediterranean areas has the lowest grid resolution (up to 200 m, and 1800 m respectively).

All the simulations (Table 1) have been conducted imposing an average realistic long-shore current at the sea side and adopting realistic forcing, using meteorological information measured in the San Javier meteorological station (on the lagoon coast), tides, wind and runoff discharges through the nine watercourses in the watershed (Fig. 1a). The discharge values were estimated from field data taking into account the land use, as described in De Pascalis et al. (2012). The tide time-series were calculated using the harmonic constants reported in Arévalo (1988) with TAPPY software (Tidal Analysis Program in PYthon). The numerical grid has been calibrated adopting the same method reported in De Pascalis et al. (2012).

We have estimated connectivity parameters from 40 stations, distributed inside and outside the Mar Menor, in eight simulations and in the years where we had biological and hydrological data. Of all stations, 28 had data on hydrography and ichthyoplankton assemblages and 39 had data on genetic of different species. All ichthyoplankton localities are >200 m from the coast and/or >3 depth, while all genetic stations are in coastal waters shallower than 1.5 m depth and less than 20 m from coast. Each station represents a source of particles with a constant emission rate of one particle every 500 s. The study period includes the years 1997-98 and 2009-2011.

The minimum geographical distance between stations considered in this work for computing lagrangian connectivity is 328.5 m inside the Mar Menor and 335 m in the Mediterranean, and the maximum 20.8 Km and 24.4 Km respectively. The minimum

Table 1Overview of simulations performed with SHYFEM. uPLD: unlimited pelagic larval duration; PLD_{30.5}: with a pelagic larval duration of 30.5 days.

Simulation period (years)	Ichthyoplankton stations		Genetic stations	
1997–1998	Sim1: PLD _{30.5}	Sim2: uPLD	Sim5: PLD _{30.5}	Sim7: uPLD
2009–2011	Sim3: PLD _{30.5}	Sim4: uPLD	Sim6: PLD _{30.5}	Sim8: uPLD

distance between a Mar Menor and a Mediterranean locality is 709 m and the maximum 24 Km.

2.2.2. Connectivity matrix

To study the role of hydrodynamic connectivity in ichthyoplankton assemblages and the genetic structure of lagoon populations, different aspects of connectivity computation were analysed: 1) the influence of pelagic larval duration (PLD); 2) the influence of repetition; 3) the influence of time scales in connectivity values and its temporal variability; and 4) the spatial variability, its relation with Euclidean distances and the asymmetry of connectivity.

1. To analyse the influence of PLD, we considered two cases in each simulation: with unlimited pelagic larval duration (uPLD) and with a pelagic larval duration of 30.5 days (PLD_{30.5}). The first case is an estimate of the maximum theoretical connectivity if a larva could be maintained indefinitely in the water column until it finds a suitable place for settlement. In the second case, we chose a PLD of 30.5 days because it covers the PLD of the studied species in this work (Kingston, 1974; Mazzoldi and Rasotto, 2001; Falk-Petersen, 2005; Mcpherson and Raventos, 2006; Tarnowska et al., 2012; Di Franco et al., 2013) and the average larval duration of many taxonomic groups according to the bibliography (Shanks, 2009; Selkoe and Toonen, 2011).

2. We defined repetition when a particle transits in a station already visited. The calculation without repetition means that a particle coming back in an already visited station is not counted as only the transit of new particles is considered. Computation of connectivity without repetition involves than only the probability of first arrival is considered. However, connectivity with repetition involves that maximum computed probability could be higher than one, and means that a larvae could increase their chance of settling in a place in the case that adequate conditions for doing so were not given at the first opportunity.

3. To analyse the influence of time scales in connectivity values and its temporal variability we have computed connectivity on two situations: continuous simulations throughout the study period (resulting cumulative values of connectivity), and performing independent monthly calculations (coinciding with the larval period considered).

To detect time scales of variability in connectivity we have considered the factors month, season and year.

The total number of simulations were eight: four for ichthyoplankton and four for genetic stations, performed for the 12 months period in 1997–98 and for 26 months period in 2009–2011, and considering both situation with PLD_{30.5} and uPLD.

The transitional probability or lagrangian connectivity matrix is a square matrix where columns represents the source (station *i*) and rows are destination (station *j*). It describes the transit from a source station (population *i*) to another station (population *j*). Elements along the diagonal represent the self-recruitment or self-correlation of each station with itself.

The matrix entries are related to: 1) the total number of particles released by station *i* and arriving in station *j*; 2) the total number of particles starting from station *i* and arriving in station *j* without repetition; 3) the probability of a particle produced in station *i* to arrive in station *j*; and 4) the relative frequency of a particle

produced in station *i* to arrive in station *j*, accounting for repetition.

Connectivity is defined as the probability of one particle produced in station *i*, to arrive in station *j*. It is calculated as the number of particles arriving in station *j* from station *i* (n_{ij}) per unit area (A_j), divided by the total number of particles produced by station *i* (n_i).

$$p_{ij} = \frac{(n_{ij}/A_j)}{n_i}$$

The matrix was computed with monthly frequency and a total yearly matrix was also computed at the end of the simulations. To do this, the cumulated number of particles n_{ij} was estimated for each analysed period (individual months, cumulated months and total year).

2.3. Biological data

To compare connectivity measures with biological descriptors two types of data were used: 1) species composition and structure of ichthyoplankton assemblages; and 2) population genetic structure and genetic fluxes of selected lagoon species.

2.3.1. Composition and structure of ichthyoplankton assemblages

Zooplankton was sampled during daylight hours at 28 stations in the Mar Menor and in the Mediterranean (Fig. 1b). Two monthly samplings were conducted from February to December in 1997 and from January to December from 2009 to 2011. Samples were collected by horizontal shallow tows (depth range 2–0.5 m) using a plankton net (50 cm mouth diameter and 500 μm mesh-size) equipped with a digital flowmeter (Pérez-Ruzafa et al., 2004).

To relate ichthyoplankton data with the connectivity matrix, a Bray-Curtis distance matrix between stations was generated from the abundance matrix with $\ln(x+1)$ transformation of the data.

2.3.2. Population genetics

Although detailed information on larval pelagic duration or spawning period duration is scarce, population genetic structure has been studied in six lagoon species representing different life-histories and dispersal capabilities. Except for *Sparus aurata* Linnaeus, 1758 and *Diplodus puntazzo* (Walbaum, 1792), all species data come from studies already published (González-Wangüemert et al., 2009; Vergara-Chen et al., 2010a, 2010b, 2013; Hernández-García et al., 2015).

Cerastoderma glaucum (Bruguière, 1789) is a typical lagoon inhabitant with no populations in the nearest coastal area and low dispersal capability both for larvae and adults (Tarnowska et al., 2012). This species has few large benthic eggs, its pelagic larval stage is restricted to 1–2 weeks and juveniles show low mobility (Kingston, 1974; Tarnowska et al., 2012). Sample size consisted in 231 individuals from 9 localities inside the Mar Menor (20–31 individuals per collecting site) (Fig. 1c). The sampling was carried out in a single effort during 2008, targeting the same year classes in all localities. Methods and results of their genetic study are described in González-Wangüemert et al. (2009) and Vergara-Chen et al. (2013).

Holothuria poli Delle Chiaje, 1824 and *Pomatoschistus marmoratus* (Risso, 1810), have planktonic larval phase but sedentary benthic adults with low mobility and small home-range. *H. poli* is a

recent colonizer in the Mar Menor lagoon, being its first record in 1989 (Pérez-Ruzafa, 1989). The duration of its pelagic larval stage is 2–3 weeks. 158 individuals of *H. poli* were collected in August 2007 in five sampling sites from shallow benthic habitats (26–39 individuals per collecting site), three inside the Mar Menor lagoon and two in the Mediterranean, (Fig. 1c). The genetic study of lagoon and coastal sea populations of these species is described in Vergara-Chen et al. (2010a).

P. marmoratus inhabit and reproduce in the lagoon (Pérez-Ruzafa et al., 2006b), having nesting and egg care behaviour and a pelagic larval stage of 2 weeks (Mazzoldi and Rasotto, 2001). Adults are sedentary (Gysels et al., 2004; Berrebi et al., 2005) and show moderate daily movements (Bardin and Pont, 2002). 196 individuals were collected in five sampling sites (35–43 individuals per collecting site), three inside the Mar Menor lagoon and two in the Mediterranean (Fig. 1c). The genetic study of lagoon and coastal sea populations of these species is described in Vergara-Chen et al. (2010b).

Finally, *Sparus aurata* Linnaeus, 1758, *Diplodus puntazzo* (Walbaum, 1792) and *Diplodus sargus* (Linnaeus, 1758), are typical lagoon migrant species, arriving as juveniles in spring and coming back to the sea in autumn as adults. No larvae of these species have been found in planktonic samples inside the lagoon (Pérez-Ruzafa et al., 2004). In *S. aurata*, metamorphosis into the juvenile stage takes place 23–26 days after hatch (Falk-Petersen, 2005), pelagic larval duration for *D. puntazzo* ranges between 19 and 48 days (Mcpherson and Raventos, 2006) and *D. sargus* produce eggs and larvae that develop in pelagic waters for a period ranging from 14 to 28 days (Di Franco et al., 2013). Young of Year (YOY) of these species were sampled using light traps and sein net in the shallow areas around the lagoon and in the proximity of the inlets, both at the lagoon and at seaside, in May and June of 2009 and 2011 (Fig. 1c). This sampling was designed to compare cohorts at the same stage in the critical phase of colonizing the lagoon. A total of 413 specimens of *D. sargus*, 415 of *S. aurata* and 185 of *D. puntazzo* was collected. The genetic study for *D. sargus* is described in Hernández-García et al. (2015) and the genetic methods for *Sparus aurata* and *Diplodus puntazzo* follow Brown et al. (2005) and Roques et al. (2007), respectively.

For all species, the mitochondrial and/or nuclear (microsatellite markers) DNA variation from lagoon and marine samples was estimated. Genetic distance or degree of differentiation between populations was determined utilizing F_{st} -statistics using Genepop (Raymond and Rousset, 1995) and following the method of Weir and Cockerham (1984).

2.4. Data analyses

Spatial and temporal variability in the connectivity results was tested using a three-way Anova. For temporal variability we considered the factors YEAR (with three levels, 1997–98, 2009–2010 and 2010–2011), each annual period starting in March and ending in February of the next year; SEASON (with four levels, from spring to winter) and MONTH (with twelve levels, considered random and nested in SEASON). Previously, homogeneity of variances and normality was checked using Levene's and Kolmogorov-Smirnov tests, respectively. Heterogeneity was removed using fourth square root and data were normalized subtracting means and dividing by standard deviation. Despite transformations did not remove heterogeneity in all cases, analysis of variance is quite robust to departures from these assumptions, especially when a large number of samples is included (Underwood, 1997).

Exploration of relationships between connectivity results, geographical distances between stations and biological descriptors has been performed using a polynomial regression. As biological

descriptors, abundance, species richness and Bray-Curtis distance between localities of ichthyoplankton, and genetic fluxes (as F_{st} values) of the six studied species were used. To test the influence of very low F_{st} values (very high genetic flux) on the results, we have performed the regressions on three different data sets: including all data, excluding self-flux, and excluding very low genetic differentiation ($F_{st} \leq 0$).

To visualize the spatial structure of genetic fluxes, and compare it with connectivity patterns, it has been applied a non-Metric Multidimensional Scaling analysis (MDS) (Clarke and Warwick, 2001) on the respective triangular matrix of F_{st} and connectivity (considering repetition and $PLD_{30.5}$) of *D. sargus* samples corresponding to the year 2011. This dataset was selected as it contains the higher number of localities inside and outside the Mar Menor.

3. Results

3.1. Computing connectivity

The probability in the Mar Menor of receiving larvae is very low in any station. The mean probability inside the lagoon of receiving larvae from another locality of the lagoon during a month is $3.03E-06/m^2$, and from a locality in the Mediterranean is $1.33E-07/m^2$. In the case of Mediterranean localities, these probabilities are higher and reach $4.72E-07/m^2$ for receiving larvae from the lagoon and $6.82E-06/m^2$ for receiving larvae from other Mediterranean localities.

3.1.1. Effects of PLD and repetition

As expected, connectivity calculations are dependent on considering or not both $PLD_{30.5}$ and repetition. Fig. 2 shows the results of the simulations performed for 1997–98 (13 months) and 2009–2011 (26 months) averaging the 20 offshore stations inside the Mar Menor. When uPLD is considered (Fig. 2a), the probability increases with time with a slow tendency to stabilize, while when considering $PLD_{30.5}$ (Fig. 2b) the probability value is one order of magnitude lower than with uPLD and tend to reach a maximum very quickly (after 3 computation months). The computed probability of receiving particles is always higher when repetition is considered.

3.1.2. Effects of time

Monthly estimates tend to show higher values and higher inter-monthly variability than the cumulated probability (computing all previous months of each period). However, time effect is highly dependent of PLD. Considering $PLD_{30.5}$ makes the cumulated connectivity independent of time (Fig. 2b). It reduces the differences between monthly and cumulate estimates as both are limited by larval duration. It also moderates the importance of repetition (see Table 1)

The ANOVA performed on the probability of receiving particles from other localities considering the factors YEAR (1997–98, 2009–10 and 2010–2011), SEASON (spring, summer, autumn and winter) and MONTH (nested in SEASON) showed that when considering larval $PLD_{30.5}$ there are no differences between periods or seasons (Table 2). There is only significant variability at the scale of months inside each season, but with no defined annual pattern, when independent monthly estimates are performed (YEAR*MONTH(SEASON), $p = 0.00$).

However, when uPLD is considered, a seasonal pattern emerges in all the estimations of connectivity being higher in spring and early summer. This seasonal pattern results in a significant YEAR*SEASON interaction (Co_R, $p = 0.007$; Co_nR, $p = 0.015$) only in the case of cumulative calculations, due to the increasing cumulated probability in the second year of the period

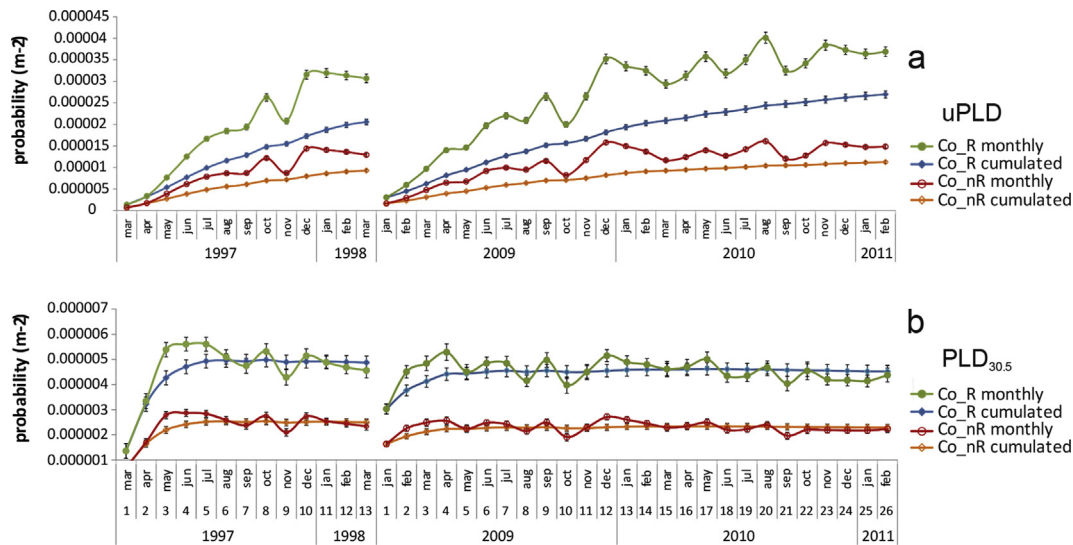


Fig. 2. Results of the simulations performed for the periods 1997-98 (13 months) and 2009-2011 (26 months). Values are mean values (\pm se) for the 20 offshore stations in the inner of the Mar Menor. Graph a) shows the results for particles with unlimited Pelagic Larval Duration (uPLD) and graphic b) considering a Pelagic Larval Duration of 30.5days. Co = connectivity as probability of receiving particles from other stations, R = considering repetition, nR = without repetition. Monthly data show the probability for each month, cumulated shows the cumulated probability for the whole period.

Table 2
Results of the ANOVA performed on the probability estimates of receiving particles from other stations considering the temporal factors YEAR (1997-98; 2009-10 and 2010-11), SEASON (spring, summer, autumn and winter) and MONTH(SEASON) (natural months nested in seasons). R: with repetition; nR: without repetition; MONTH: monthly calculations; uPLD: unlimited pelagic larval duration; PLD_{30.5}: with a pelagic larval duration of 30.5 days.

Source	With PLD _{30.5}			With uPLD		
	df	F-Ratio	p-Value	df	F-Ratio	p-Value
	Co_R_PLD _{30.5}			Co_R		
YEAR	2	4.08	0.108	2	5.038	0.063
SEASON	3	0.767	0.544	2	19.118	0.001
YEAR*SEASON	4	0.51	0.729	5	4.816	0.007
MONTH(SEASON)	8	1.366	0.283	8	1.403	0.268
YEAR*MONTH(SEASON)	16	0.48	0.958	16	5.681	0
Error	27,406			27,406		
	Co_nR_PLD _{30.5}			Co_nR		
YEAR	2	4.22	0.084	2	5.704	0.067
SEASON	3	0.439	0.732	3	14.135	0.001
YEAR*SEASON	5	0.471	0.792	4	4.274	0.015
MONTH(SEASON)	7	1.447	0.254	8	1.215	0.351
YEAR*MONTH(SEASON)	16	0.424	0.977	16	5.594	0
Error	27,406			27,406		
	Co_R_PLD _{30.5} _MONTH			Co_R_MONTH		
YEAR	2	1.333	0.344	2	15.231	0.007
SEASON	3	1.17	0.387	3	6.921	0.013
YEAR*SEASON	5	0.83	0.547	5	1.181	0.364
MONTH(SEASON)	7	1.311	0.307	8	0.986	0.484
YEAR*MONTH(SEASON)	16	7.12	0	15	10.978	0
Error	27,406			27,406		
	Co_nR_PLD _{30.5} _MONTH			Co_nR_MONTH		
YEAR	2	1.333	0.344	2	3.975	0.093
SEASON	3	1.17	0.387	2	6.477	0.021
YEAR*SEASON	5	0.83	0.547	5	1.287	0.318
MONTH(SEASON)	7	1.311	0.307	8	1.363	0.284
YEAR*MONTH(SEASON)	16	7.12	0	16	12.267	0
Error	27,406			27,406		

2009-2011, but not when independent monthly estimates are computed.

In the case of monthly estimates, the only situation for which also emerge differences between years is when considering repetition with uPLD ($p = 0.007$), probably due to same reason. In all the cases exists a significant monthly variability inside each season with a different pattern each year (YEAR*MONTH(SEASON), $p = 0$).

3.1.3. Spatial variability, asymmetry and relationship with distance

Differences in connectivity show a strong spatial pattern and asymmetry. The mean connectivity inside each basin (Mar Menor or Mediterranean) showed no significant differences. This does not imply that all localities receive the same number of particles from the same localities or that all the localities within the lagoon have the same probability of receiving particles from the open sea, as it is shown by the fact that the interaction between factors SEA_I*ST_J

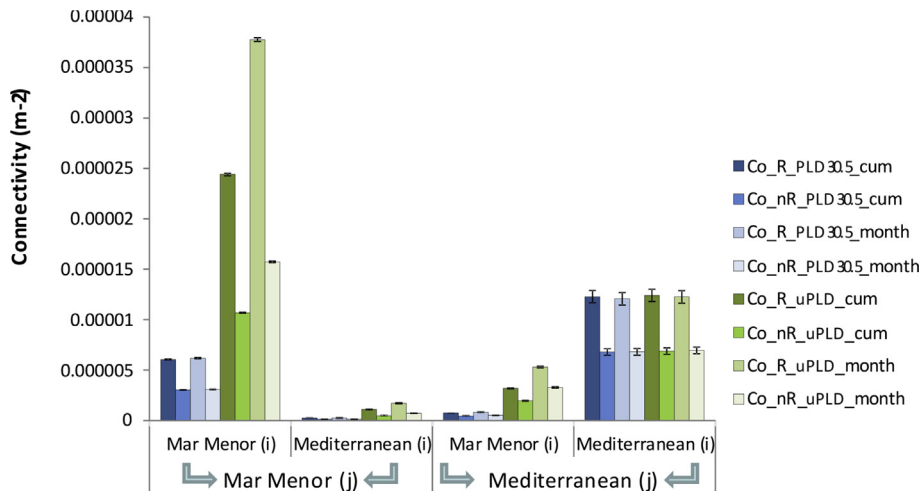


Fig. 3. Mean values of the different connectivity estimations (probability of receiving particles in the case of no repetition) in the Mar Menor and in the Mediterranean stations. (i) are the sending stations and (j) are the receiving stations. Arrows indicate the direction of the flux. co = connectivity, R = considering repetition, nR = without repetition, PLD_{30.5} = with Pelagic Larval Duration of 30.5 days, uPLD = unlimited Pelagic Larval Duration, month = monthly estimates (the contrary is cumulative estimate). error bars correspond to the standard error of the mean.

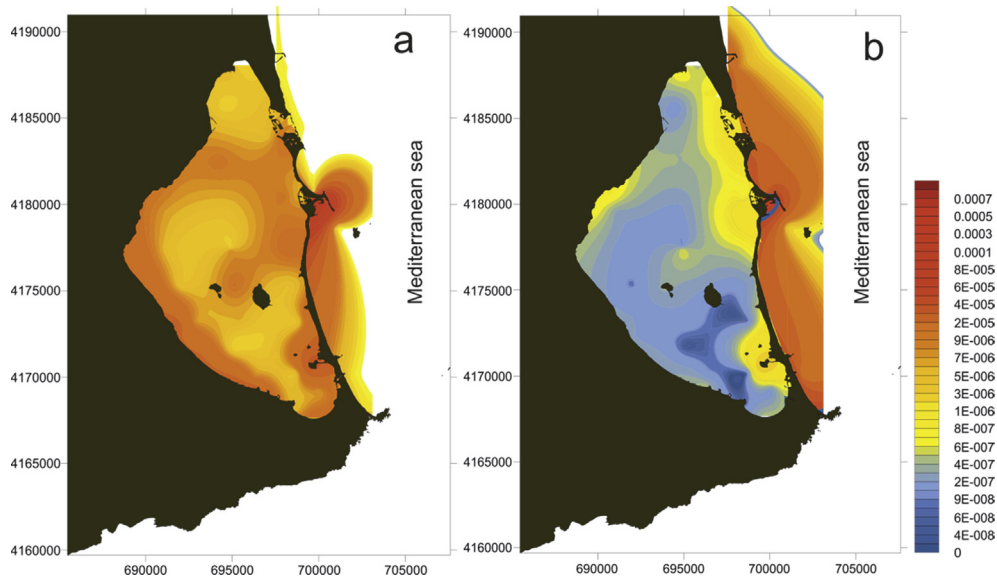


Fig. 4. Spatial distribution of the mean monthly connectivity as the probability of receiving particles from other localities without repetition and with Pelagic Larval Duration of 30.5 days (Co_nR_PLD_{30.5}) between all the stations considered in the study for the year 2010. a) Mean probability (m⁻²) of receiving larvae from the Mar Menor stations b) Mean probability (m⁻²) of receiving larvae from the Mediterranean stations.

Table 4

Relationship between the different estimators of connectivity used and the geographical distance between considered stations for the genetic samples.

Dependent Variable/# cases	Adjusted Multiple R ²	Effect	Coefficient	Std. Error	Std. Coefficient	t	p-Value
CO_R_PLD _{30.5} /2048	0.035	(DISTANCE)	0.000	0.000	1.339	7.739	0.000
		(DISTANCE) ²	0.000	0.000	-2.48	-6.597	0.000
		(DISTANCE) ³	0.000	0.000	1.29	.	.
CO_NR_PLD _{30.5} /2048	0.029	(DISTANCE)	0.000	0.000	1.221	7.035	0.000
		(DISTANCE) ²	0.000	0.000	-2.248	-5.961	0.000
		(DISTANCE) ³	0.000	0.000	1.164	.	.
CO_R_uPLD/2048	0.063	(DISTANCE)	0.000	0.000	1.395	8.187	0.000
		(DISTANCE) ²	0.000	0.000	-2.232	-6.026	0.000
		(DISTANCE) ³	0.000	0.000	1.043	.	.
CO_NR_uPLD/2048	0.049	(DISTANCE)	0.000	0.000	1.207	7.028	0.000
		(DISTANCE) ²	0.000	0.000	-1.901	-5.095	0.000
		(DISTANCE) ³	0.000	0.000	0.876	.	.

Table 5

Results of the polynomial regression (order 3) analyses performed to explore the relationships between Bray-Curtis distances on ichthyoplankton species composition and connectivity variables estimated between the same pairs of stations, both inside and outside the Mar Menor lagoon along the 3 years considered in this study. N = 21632 cases. Variable key: co = connectivity, R = considering repetition, nR = without repetition, PLD_{30.5} = with Pelagic Larval Duration of 30.5 days, uPLD = unlimited Pelagic Larval Duration, month = monthly estimates (the contrary is cumulative estimate).

Independ. Variable	Adj. Mult. R ²	Effect	Coefficient	Std. Error	Std. Coefficient	t	p-Value
co_R_PLD _{30.5}	0.402	co_R_PLD _{30.5}	7,924,894.55	85,399.20	1.27	92.798	0
		co_R_PLD _{30.5} ²	-4.18E+11	8.43E+09	-1.64	-49.628	0
		co_R_PLD _{30.5} ³	5.05E+15	1.33E+14	0.968	38.067	0
co_nR_PLD _{30.5}	0.403	co_nR_PLD _{30.5}	15,271,100.52	160,528.06	1.256	95.13	0
		co_nR_PLD _{30.5} ²	-1.53E+12	3.03E+10	-1.804	-50.609	0
		co_nR_PLD _{30.5} ³	3.38E+16	8.49E+14	1.137	39.812	0
co_R_PLD _{30.5_month}	0.361	co_R_PLD _{30.5_month}	6,938,261.69	76,324.01	1.219	90.905	0
		co_R_PLD _{30.5_month} ²	-3.06E+11	5.97E+09	-1.47	-51.336	0
		co_R_PLD _{30.5_month} ³	3.11E+15	8.22E+13	0.801	37.843	0
co_nR_PLD _{30.5_month}	0.356	co_nR_PLD _{30.5_month}	1.32E+07	142,807.87	1.184	92.238	0
		co_nR_PLD _{30.5_month} ²	-1.09E+12	2.08E+10	-1.505	-52.192	0
		co_nR_PLD _{30.5_month} ³	2.00E+16	5.11E+14	0.862	39.245	0
co_R_uPLD	0.425	co_R_uPLD	3,267,710.97	41,402.38	2.085	78.926	0
		co_R_uPLD ²	-9.26E+10	1.92E+09	-2.823	-48.22	0
		co_R_uPLD ³	7.37E+14	2.06E+13	1.34	35.843	0
co_nR_uPLD	0.423	co_nR_uPLD	7,466,552.52	112,588.75	2.005	66.317	0
		co_nR_uPLD ²	-5.17E+11	1.40E+10	-2.465	-36.864	0
		co_nR_uPLD ³	1.04E+16	4.13E+14	1.053	25.194	0
co_R_uPLD_month	0.417	co_R_uPLD_month	2,087,529.83	27,571.13	2.03	75.714	0
		co_R_uPLD_month ²	-3.89E+10	8.48E+08	-2.726	-45.865	0
		co_R_uPLD_month ³	2.05E+14	5.98E+12	1.299	34.24	0
co_nR_uPLD_month	0.415	co_nR_uPLD_month	4,974,648.62	73,739.00	1.938	67.463	0
		co_nR_uPLD_month ²	-2.33E+11	5.98E+09	-2.361	-39.03	0
		co_nR_uPLD_month ³	3.13E+15	1.13E+14	1.033	27.822	0

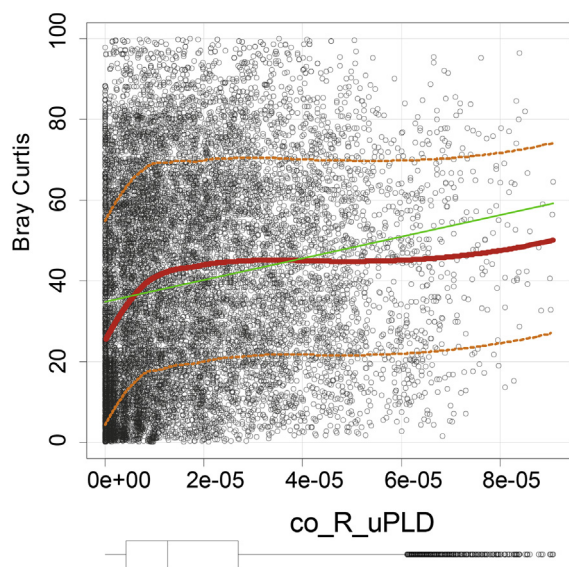


Fig. 5. Relationships between Bray-Curtis distances estimated on ichthyoplankton species composition and cumulative connectivity without considering repetition and with undefined Pelagic Larval Duration (Co_nR_uPLD). Redline: smooth line, dotted lines: spread, green line represents least-square line. Marginal boxplots represent mean values. N = 21632 cases, multiple adjusted R² = 0.425. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

others when considering genetic distances (Fig. 7 a, b). In the same way locality 6 is grouped with 16 and 3 in the first case, but clustered with 38 and 30 in the case of genetic distances. Finally, only in the case of genetic distances the localities from the Mediterranean (27 and 37) are grouped with localities inside the Mar Menor (16 and 3), and these are not the closest to the inlets but on the farthest coast in the inner zone of the lagoon (Fig. 7b).

4. Discussion

Traditionally, genetic markers have been considered an excellent tool to estimate population connectivity (Hellberg et al., 2002; Hedgecock et al., 2007; Leis et al., 2011). By other hand, the use of biophysical and lagrangian hydrodynamic models has been recognized in recent years also as powerful tool for the study of larval dispersal (Werner et al., 2007; Lett et al., 2008; Watson et al., 2010; Leis et al., 2011; Young et al., 2012; Qian et al., 2015; Mitarai et al., 2016; Calò et al., 2018). These models have been applied to study the connectivity between different areas, from the deep sea to networks of marine protected areas (Lett et al., 2010; Andreollo et al., 2013, 2015a, 2015b, 2017; Tanner et al., 2017). However, despite being a crucial process that must be taken into account to manage marine ecosystems (Steneck et al., 2006), most of the research into larval dispersal, retention and connectivity has taken place on fishes in coral reefs (Jones et al., 2009a, 2009b) or came from models based on little or no evidence from direct field data (Gawarkiewicz et al., 2007).

Recently, Ayram et al. (2016) underline that there is a general lack of validation of proposed models and the necessity of increase efforts to obtain occurrence data, genetic data and tracking telemetry to improve the implementation of conservation actions.

At the same time, the importance of connectivity between coastal lagoons and the sea is just starting to be investigated (Lemaire et al., 2000; Webster, 2011; Milana et al., 2012; Quéré et al., 2012; Thomas et al., 2012; Lill et al., 2013; Xueping et al., 2013; Morat et al., 2014; Ramos Guimaraes et al., 2014; Ghezzi et al., 2015), but genetic fluxes have never been tested against hydrodynamic connectivity in these ecosystems.

4.1. Effects of pelagic larval duration, time scales, and repetition on connectivity estimations

Eggs or larval-release location, time, and the distance and the direction of the larval dispersal affect genetic fluxes and are fundamental to define the demography and the genetic structure of

Table 6
Pairwise F_{ST} indices based on DNA markers.

	Localities								
<i>Holothuria poli</i> /16s	2	9	16	30	39				
2. Cabo de Palos									
9. Isla del Ciervo	0.0449								
16. Los Urrutias	0.0446	−0.0108							
30. El Estacio MM	0.043	−0.0098	−0.0035						
39. Torre Horadada	0.0207	0.0659	0.0741	0.0552					
<i>Holothuria poli</i> /CO1	2	9	16	30	39				
2. Cabo de Palos									
9. Isla del Ciervo	0.0024								
16. Los Urrutias	0.0033	−0.0097							
30. El Estacio MM	−0.0079	−0.0017	0.0212						
39. Torre Horadada	−0.0081	−0.0017	−0.0177	0.011					
<i>Cerastoderma glaucum</i>	5	7	16	17	20	24	28	33	
5. La Carrasquilla									
7. Los Nietos	0.21422								
16. Los Urrutias	0.03757	0.17288							
17. Sur del Pedruchico	−0.0231	0.22084	0.0568						
20. Pedruchico	−0.00971	0.20703	0.02821	−0.00355					
24. Los Alcázares	0.0023	0.23519	0.08725	−0.01362	0.00575				
28. Los Narejos	0.03512	0.30278	0.14421	0.0191	0.03012	0.04994			
33. Las Encañizadas MM	0.00811	0.24258	0.08501	0.00237	0.02272	−0.00279	0.14322		
36. Lo Pagán	−0.02069	0.22598	0.05447	−0.01463	−0.01438	−0.00755	0.0124	0.01085	
<i>Pomatoschistus marmoratus</i>	1	16	31	36					
1. Playa Honda									
16. Los Urrutias	−0.0034								
31. Veneziola Med	0.0133	0.00003							
36. Lo Pagán	0.0053	0.0005	0.0108						
Mazarrón Med	0.0149	0.0039	0.0121	0.0013					
<i>Diplodus sargus</i> /2009	27	33							
27. El Estacio Med									
33. Las Encañizadas MM	−0.00114								
37. La Llana	−0.00001	−0.00108							
<i>Diplodus sargus</i> /2011	3	6	16	27	30	33	37		
3. Caravaning_P. Honda									
6. Marchamalo	0.00254								
16. Los Urrutias	−0.00242	0.00042							
27. El Estacio Med	−0.00147	0.00212	0.00011						
30. El Estacio MM	0.00157	0.00132	0.00147	0.00241					
33. Las Encañizadas MM	0.00376	0.00356	0.00311	0.0017	0.00281				
37. La Llana	−0.00173	0.00135	−0.00145	0.00106	0.00086	0.00425			
38. Lo Pagán	0.00163	−0.00155	0.00154	0.00154	−0.00039	0.00069	0.00249		
<i>Diplodus puntazzo</i> /2011	3	6	8	27	30				
3. Caravaning_P. Honda									
6. Marchamalo MM	0.00735								
8. Marchamalo Med	−0.00622	−0.00104							
27. El Estacio Med	0.01929	0.00947	−0.00346						
30. El Estacio MM	0.00256	0.00063	−0.00665	0.01262					
<i>Sparus aurata</i> /2009	3	6	16	27	30	33	37		
3. Caravaning_Playa Honda									
6. Marchamalo MM	0.00254								
16. Los Urrutias	−0.00242	0.00042							
27. El Estacio Med	−0.00147	0.00212	0.00011						
30. El Estacio MM	0.00157	0.00132	0.00147	0.00241					
33. Las Encañizadas_MM	0.00376	0.00356	0.00311	0.0017	0.00281				
37. La Llana	−0.00173	0.00135	−0.00145	0.00106	0.00086	0.00425			
38. Lo Pagán	0.00163	−0.00155	0.00154	0.00154	−0.00039	0.00069	0.00249		
<i>Sparus aurata</i> /2011	3	16	21	30	33	34–27			
3. Caravaning_P.Honda									
16. Los Urrutias	0.00392								
21. El Albuñón	−0.00462	−0.00193							
30. El Estacio MM	0.003	−0.00102	−0.0053						
33. Las Encañizadas	0.00624	−0.00092	−0.00358	0.00344					
34–27. Las Encañizadas Med–El Estacio Med	0.00247	−0.0047	−0.0024	0.00029	0.0035				
38. Lo Pagán	0.00247	0.00624	0.003	0.00392	0	−0.00102			

marine populations. These temporal and spatial factors, reflecting annual and inter-annual circulation patterns, determine the heterogeneity of the process, with a tendency to become more homogeneous for longer advection times (Mitarai et al., 2009), mainly, as our results show, when long life duration in the larval phases exists. Therefore, computation of temporal scales must take into

account that PLD has a strong effect in the estimations of connectivity depending on the duration of the simulations, mainly when repetition is considered. However, both aspects, unrestricted or long PLD and repetition, are worth to be considered in some cases when no exact information is available on PLD of a given species. In these cases, as our results show, including them improves the fit

Table 7

Results of the polynomial regression analyses (order 2) performed to explore the relationships between genetic fluxes (F_{st}) and connectivity variables and geographical distances for different lagoon species. Only when one of the coefficients was significant (bold figures, $p < 0.05$) or marginally significant ($p < 0.075$) the relationship has been included in the table. co = connectivity, R = considering repetition, nR = without repetition, $PLD_{30.5}$ = with Pelagic Larval Duration of 30.5 days, $uPLD$ = unlimited Pelagic Larval Duration, month = monthly estimates (the contrary is cumulative estimate).

Species	Genetic sequence	F_{st} values	Number of Cases	Adj. Multiple R^2	Effect	Coefficient	Standard Error	Std	t	p-Value
<i>Cerastoderma glaucum</i> (Poiret, 1789)	mtDNA CO1	all	82	0.301	(CO_R_PLD _{30.5}) ¹	4231.12	1917.31	4.72	2.21	0.058
					(CO_R_PLD _{30.5}) ²	-1.41E+07	6.46E+06	-4.67	-2.19	0.06
	all	82	0.426	(CO_R_uPLD) ¹	3610.58	1303.56	4.32	2.77	0.024	
<i>Holothuria poli</i> (Delle Chiaje, 1823)	mtDNA CO1	all	82	0.335	(CO_R_uPLD) ²	-1.13E+07	4,137,646	-4.25	-2.73	0.026
					(CO_NR_uPLD) ¹	7865.13	3345.11	3.13	2.35	0.047
	mtDNA 16s	all	27	0.974	(CO_NR_uPLD) ²	-7.50E+07	3.27E+07	-3.05	-2.29	0.051
	mtDNA CO1	≠0	21	0.181	(CO_NR_uPLD) ¹	8.86E+05	101,009	7.17	8.78	0.072
					(CO_NR_uPLD) ²	-1.76E+12	2.03E+11	-7.08	-8.67	0.073
<i>Diplodus sargus</i> (Linnaeus, 1758)	microsatellite	>0	45	0.95	(DISTANCE) ¹	0.00	0.00	1.25	1.80	0.087
					(DISTANCE) ²	0.00	0.00	-1.49	-2.16	0.044
	microsatellite	>0	45	0.956	(CO_R_uPLD) ¹	1854.10	424.95	2.12	4.36	0.049
					(CO_R_uPLD) ²	-1.84E+08	7.23E+07	-1.24	-2.55	0.126
					(CO_NR_uPLD) ¹	3064.05	653.47	2.11	4.69	0.043
<i>Sparus aurata</i> Linnaeus, 1758	microsatellite	>0	70	0.964	(CO_NR_uPLD) ²	-5.04E+08	1.85E+08	-1.22	-2.72	0.113
					(DISTANCE) ¹	0.000	0.00	2.96	18.18	0.003
	microsatellite	>0	70	0.957	(DISTANCE) ²	0.000	0.00	-2.32	-14.24	0.005
					(CO_R_uPLD) ¹	1250.37	133.65	3.53	9.36	0.003
					(CO_R_uPLD) ²	-4.49E+07	5.67E+06	-2.98	-7.92	0.004
					(CO_NR_uPLD) ¹	2058.50	241.87	3.40	8.51	0.003
					(CO_NR_uPLD) ²	-1.26E+08	1.76E+07	-2.86	-7.14	0.006

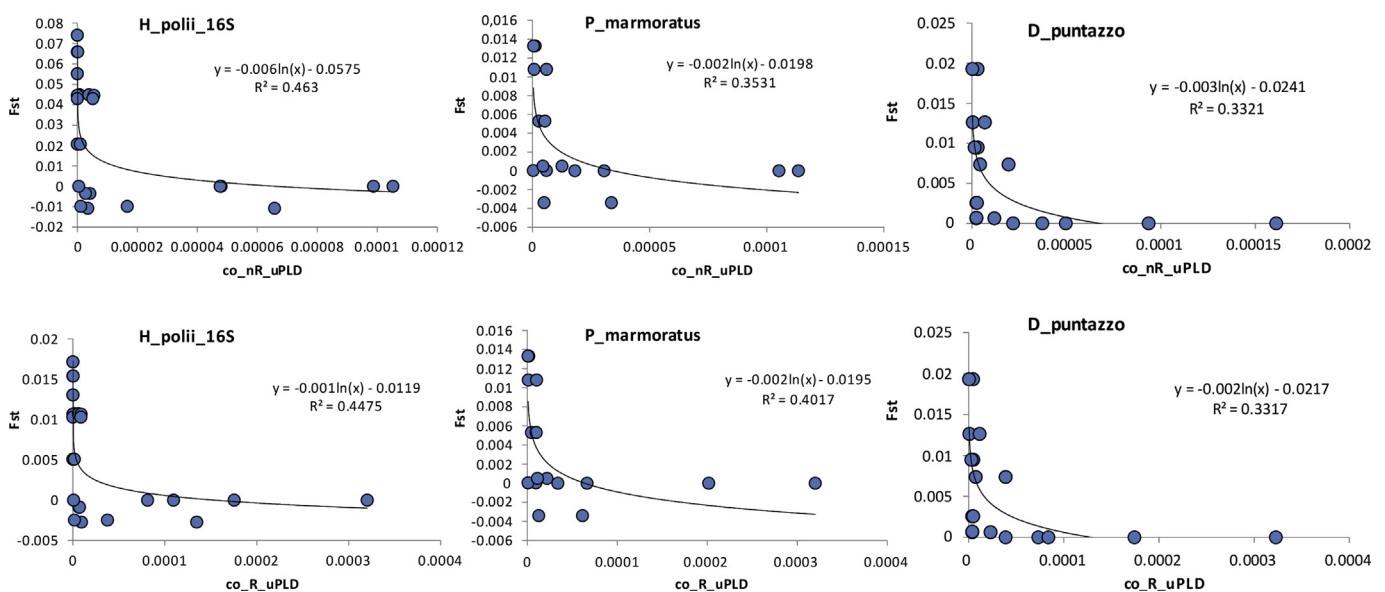


Fig. 6. Best logarithmic regression models for the relationship between genetic distances (F_{st}) and connectivity variables for the Mar Menor studied species.

between hydrodynamic connectivity estimators and biological data. The fact that most of the regression analyses showed higher adjustment when $uPLD$ was considered, suggest that for many species larval life duration probably tends to be higher than the one month used in this work and described in bibliography. Moreover, recent studies based in otolith chemistry in *Sparus aurata* show that larval stage can be highly variable between individuals of the same species (Mercier et al., 2012). A detailed analyses and specific simulations to test the importance of larval duration on connectivity will be necessary to understand the adaptations of organisms to improve its dispersal capabilities.

In the case of ichthyoplankton, the fact that the simulations considering repetition showed lower adjustment when self-Bray-Curtis distances was removed from the analyses, suggest that repetition can be an important process for self-recruitment or for

maintaining the assemblage structure in a given site, but it is less important to increase the connectivity between distant localities. By other hand, for benthic species, repetition not only can improve the chance of self-recruitment but also of coupling larval duration, competency period and finding the adequate location for settlement.

Seasonality is also important when calculating connectivity. When unlimited PLD is considered, a seasonal pattern emerges in all the estimations of connectivity being higher in spring and early summer. It is not an effect of the cumulated probability of receiving particles, as the last season of the simulations corresponds to winter. This pattern is maintained between years. Therefore, it suggests that reproductive time can be important for lagoon species, not only because photoperiod, productivity or water temperatures, but also for increasing connectivity. This seasonality is lost

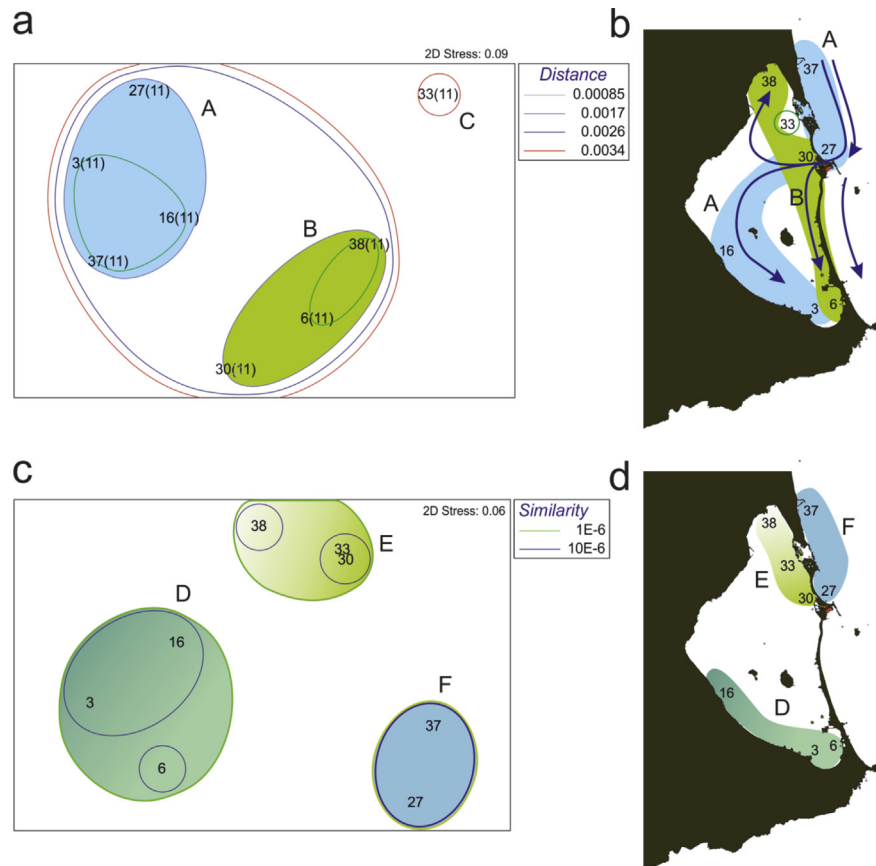


Fig. 7. a) Plot of the results of the non-metric multi-dimensional scaling (MDS) performed on the F_{st} matrix for *Diploodus sargus* (Linnaeus, 1758) localities sampled in 2011. Lines represent the significant groups identified by a cluster analyses using complete linkage method. b) representation of the clusters depicted in the MDS plot in figure a on the Mar Menor map. Arrows indicate the main circulatory currents in the Mediterranean and in the Mar Menor. c) Plot of the results of the non-metric multi-dimensional scaling (MDS) performed on the connectivity matrix (probability of receiving particles from the other station with repetition and with mortality) for *Diploodus sargus* localities sampled in 2011. Lines represent the significant groups identified by a cluster analyses using complete linkage method. d) representation of the clusters depicted in the MDS plot in figure c on the Mar Menor map. Capital letters correspond to the main clusters identified by MDS analyses.

when PLD_{30.5} is included due to the fact that this short larval life cut off the seasonal signal.

4.2. Spatial scales of connectivity

The estimates of average larval dispersal for most of more than 100 species of marine fishes and invertebrates studied on the bases of genetic variation among populations range between 10 and 1000 km (Gaines et al., 2007). However, connectivity, measured as the probability (or the frequency when repetition is computed) of receiving larvae from the sea and from other localities in the Mar Menor, at distances of less than 10 km, is very low (Ghezzi et al., 2015). This makes that, despite the small spatial scales involved, within a lagoon the localities are structured according to a gradient of connectivity between stations and with respect to the sea (Ghezzi et al., 2015), which reproduce a zonation as predicted by the confinement models (Guelorget and Perthuisot, 1983; Guelorget et al., 1983; Pérez-Ruzafa and Marcos, 1992, 1993; Pérez-Ruzafa et al., 2004, 2011a).

Traditionally, models analysing the genetic population structure in coastal marine environments as a function of the distance between samples accept that dispersal between localities was probably related to geographic distance, thus showing positive relationships (Palumbi, 2003). However, in demersal fish species with pelagic larvae, attempts to relate genetic and geographical distances find negative relationships (Fauvelot and Planes, 2002) or

no-relation at all (Pérez-Ruzafa et al., 2006a), suggesting that, at least at medium spatial scales (10¹–10² km) gene flows follows non straight linear paths and are probably determined by the currents (González-Wangüemert et al., 2004). At higher spatial scales, the positive relationships arise again (Pérez-Ruzafa et al., 2006a). By their part, lagrangian hydrodynamic models confirm the complexity and variability of the paths follow by the pelagic eggs and larvae depending on biological or oceanographic factors (Tanner et al., 2017; Calò et al., 2018), but very few studies use them to corroborate the results obtained in base to genetic data in coastal populations.

Other aspect worthy to be considered is that active swimming phases can take advantage of hydrodynamic paths and currents that cannot fit exactly with lagrangian movements.

4.3. The role of connectivity in population genetic structure

For each million larvae produced in one locality, around 3 larvae m⁻² will reach another locality during a month. Logically, mortality due to environmental stress or predation during the pelagic phase or in the recruitment or post-recruitment phases will make these numbers still lower. This low connectivity seems to be a common feature in coastal lagoons, from those considered choked, like the Mar Menor with water residence times close to one year, to the Curonian or Venice with water residence times of 120 and 12 days, respectively (Ghezzi et al., 2015).

However, this small number can be sufficient to maintain high enough genetic fluxes between populations (Vergara-Chen et al., 2010a, b) and our results showed the important role of hydrographical connectivity, dependent on the life strategy of species.

In the case of *Holothuria poli* in the Mar Menor lagoon, a previous genetic study showed high levels of mtDNA diversity and occurrence of exclusive haplotypes coupled with the existence of high gene flow. The 16S gene marker pointed out slight genetic differences between lagoon and no-lagoon populations and the authors considered that the environmental conditions could be acting on haplotype frequencies of both populations, causing the contrasting patterns of genetic structure via selection (Vergara-Chen et al., 2010a).

Pomatoschistus marmoratus genetic study showed similar results, a high mtDNA diversity and low genetic structure as a consequence of high genetic fluxes. In this case, the occurrence of exclusive haplotypes in the lagoon coupled with the existence of high gene flow has been interpreted as an ecological survival strategy in a harsh environment such as the Mar Menor (Vergara-Chen et al., 2010b).

In our study, both species show a significant negative relationship between connectivity and genetic distance (F_{ST}) (therefore, positive with genetic fluxes) while there is no significant relationship with geographical distance. This result reinforces the role of hydrodynamic connectivity in the genetic flux between localities.

The cockle *Cerastoderma glaucum*, with low adult and larval dispersal capability and populations only inside the lagoon, shows high genetic spatial variation. Vergara-Chen et al. (2013) found significant genetic differentiation between 13 localities, with all localities exhibiting high haplotype diversity, low nucleotide diversity, and a high number of exclusive haplotypes.

In agreement with this, *C. glaucum* showed the lowest relationship between genetic distances and connectivity parameters, reinforcing the idea of higher isolation between populations at the spatial scales considered, from 1200 to 18000 m.

Furthermore, only in the case of *C. glaucum* populations, genetic distances and connectivity showed a significant relationship in the simulations with PLD_{30,5} and considering self-distances. The significance and adjusted R^2 were higher in the case of considering repetition. This suggests that this species is probably the only one, among those studied, with a larval duration of less than one month, and also highlights the importance of self-recruitment in the genetic structure of its populations.

In *H. poli*, self-recruitment can also be important, as the adjustment when considering self-distances for the mtDNA 16S was much higher ($R^2 = 0.97$) than when excluding them from the regression analyses, but the significance of the adjustment is only marginal ($p = 0.07$).

D. sargus and *S. aurata* do not show any detectable relationship neither between genetic distance and connectivity, nor with geographical distance when all data are considered (including F_{ST} values ≤ 0). However, a significant relationship emerges when only genetic distances >0 are considered in the analyses. Hedgecock et al. (2007) already pointed out that F_{ST} values close to zero not always express the real connectivity between populations. In our case, it probably means that the highest genetic fluxes are maintained due to active displacements of the individuals, at some extent independently of the hydrodynamic connectivity.

In these species, in fact, genetic distances show a different pattern that lagrangian connectivity for some localities (Fig. 7) suggesting that the colonization of the lagoon by these species do not follow what it is expected for pelagic eggs and larvae. This is in agreement with the fact that no larval phases of these species were found in the ichthyoplankton of the studied area (Pérez-Ruzafa et al., 2004; Quispe, 2014) and the studied individuals correspond

to post-recruits 0+ age class fished with sein-net in the shallow areas of the lagoon and in the Mediterranean (Hernández-García et al., 2015).

As shown in Fig. 7b, considering genetic distances, the localities from the Mediterranean (27 and 37) are grouped with localities 16 and 3, which are located on the farthest coast in the inner zone of the Mar Menor lagoon. At the same time, the cluster conformed by localities located in the inner part of La Manga, the sand bar that separates the lagoon from the sea, excludes locality 33 that appear isolated from all the others (Fig. 7b). These patterns correspond with main circulatory currents in the lagoon (blue arrows in Fig. 7b).

This mismatch indicates in first place that lagrangian hydrodynamic displacements, at least using 2D models, does not necessarily correspond with existing currents, and that some colonization phases of species can use active swimming, but taking advantage of the main currents.

In this way, genetic population structure in a coastal lagoon, results from complex patterns in which hydrodynamic connectivity, probably also combined with active swimming along shore and taking advantage of the main currents in the postrecruit phases, would increase genetic fluxes. Anyway, in migratory species, the possibility that some occasional colonization by passive displacement also exists, as found by Mercier et al. (2012) in Maugio lagoon.

4.4. The role of restricted connectivity in population genetics and assemblage structure

Connectivity between the lagoon and the coastal sea is low, but there is much higher influence of the lagoon on the sea than vice versa. This is something to take into account, since usually it is assumed that lagoon assemblages are dependent on marine colonizers, but it seems that the lagoon can also play an important role in shaping the genetic and species structure of coastal marine populations.

The low probability in the colonization process not only results in a biological zonation according to the confinement models, as mentioned above, but also could lead to subpopulation extinctions (Gaines et al., 2007) and would introduce randomness in the composition of lagoon assemblages depending on the larval abundance for each species in the sea coastal waters. This would explain the low taxonomic similarity between lagoons (including in the same geographical area) (Basset et al., 2006a, 2006b; Pérez-Ruzafa et al., 2007b, 2011a; Barbone and Basset, 2010) and between years in the same lagoon (Sigovini, 2011; Quispe, 2014).

This suggests that the low connectivity between lagoons and sea acts as a resistance to the species and gene fluxes preventing total homogenization and maintaining the heterogeneity and a high complexity in the structure and spatial distribution of the lagoon assemblages. This would explain the high variability between lagoons and between years in the same lagoon, and the spatial heterogeneity in lagoon species composition. At the same time, the randomness of the colonization process, in which a rare allele can be amplified by a bottleneck effect, can explain the high proportion of exclusive or rare haplotypes and alleles in the lagoon populations despite the maintenance of relatively high gene fluxes which open sea populations (Bellec et al., 2010; Vergara-Chen et al., 2010a, b; Mejri et al., 2011; Milana et al., 2012; Vasileiadou et al., 2016). This spatio-temporal variability, both genetic and in species composition (Pérez-Ruzafa et al., 2007a, 2011a), could play an important role in conforming homeostatic mechanisms against eutrophication (Pérez-Ruzafa et al., 2005), human impacts and climate change, and could be a consequence of the restricted connectivity between the lagoon and the sea. Furthermore, the role of coastal lagoons in maintaining, not only the genetic diversity and rare alleles (Pérez-

Ruzafa et al., 2011b) but also species diversity and structure in the coastal marine communities would need more attention and deeper research to develop adequate management strategies.

Due to the asymmetry in connectivity and the larger influence of the lagoon on the sea, the knowledge of the processes determining connectivity between both systems is essential for an adequate coastal zone management and the design of marine policies and maritime strategies also for marine coastal ecosystems.

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