The influence of oceanographic fronts and early-life-history traits on connectivity among littoral fish species

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The spatial distribution of neutral genetic diversity is mainly influenced by barriers to dispersal. The nature of such barriers varies according to the dispersal means and capabilities of the organisms concerned. Although these barriers are often obvious on land, in the ocean they can be more difficult to identify. Determining the relative influence of physical and biotic factors on genetic connectivity remains a major challenge for marine ecologists. Here, we compare gene flow patterns of 7 littoral fish species from 6 families with a range of early-life-history traits sampled at the same geographic locations across common environmental discontinuities in the form of oceanic fronts in the Western Mediterranean. We show that these fronts represent major barriers to gene flow and have a strong influence on the population genetic structure of some fish species. We also found no significant relation between the early-life-history traits most commonly investigated (egg type, pelagic larval duration, and inshore-offshore spawning) and gene flow patterns, suggesting that other life-history factors should deserve attention. The fronts analyzed and the underlying physical mechanisms are not site-specific but common among the oceans, suggesting the generality of our findings.

gene flow | microsatellite | ocean circulation | pelagic stages

The spatial distribution of neutral genetic diversity in aquatic environments, as in terrestrial ones, is mainly generated and maintained by barriers to dispersal. However, although these barriers are often obvious on land, habitat discontinuities in the ocean are much more difficult to distinguish (1). Identifying such barriers is essential in defining the scale of exchange among marine populations, and this information, in turn, is fundamental to our understanding of the dynamic and genetic structure of populations as well as in the management of marine species, including the implementation of marine reserves (2).

Most littoral marine species have restricted adult movement, so their pelagic juvenile stages represent their most important dispersal mechanism (2). In the sea, it is well recognized that movements of pelagic stages are influenced by oceanographic processes, such as upwelling systems, fronts, moving convergences, eddies, and counter currents that can lead to dispersal of hundreds of kilometres (3, 4). Thus, it has been assumed that many marine populations operate as genetically open systems (5–7). However, mounting genetic evidence shows that pelagic stages often fail to fully achieve their dispersal potential (8–11), suggesting that the relationship between dispersal potential and realized gene flow among marine populations is more complex than previously assumed. Assessing the influences that oceanographic factors and early-life-history traits have in determining gene flow remains a major challenge for marine ecologists. Oceanic fronts, sharp discontinuities of physical and biochemical variables, are generated by various physical processes, occur in all oceans, and are likely to represent barriers to faunal exchange (12).

Data on dispersal distances have been collected for relatively few species, representing a limited number of possible dispersal scenarios (13, 14). Thus, high resolution hydrodynamically-based dispersal models have been developed (2, 15). However, recent empirical studies show greater local retention of pelagic stages than predicted by advection models (16–18). Also, it has proved extremely difficult to measure the frequency with which long distance movements occur during such stages (19).

Significant progress has recently been made in our ability to accurately track pelagic stages (20-22), as well as in determining genetic connectivity patterns by combining oceanographic models and molecular genetic data (23-25). However, relatively few empirical studies have investigated how oceanographic conditions influence larval dispersal and ultimately gene flow among marine fishes with varying life-history strategies (7, 26, 27). Also, these few studies have not sampled the same species at the same locations nor have they tested the effects of life-history traits across a well-defined oceanographic barrier and compared the results against barrier-free locations. Thus, the general hypothesis that oceanic fronts may act as a barrier to dispersal for most littoral fish species irrespective of their early-life-history traits remains largely untested. To this end, we compare genetic connectivity patterns of 7 littoral fish species with varied dispersal potentials sampled at the same geographical locations in the Western Mediterranean. Also, we consider how such patterns can be explained by reference to preexisting knowledge of their early-life-history characteristics and of the fronts that may act as oceanographic barriers.

Specifically, we aim to test the following predictions: (*i*) populations separated by oceanic fronts belong to genetically differentiated subunits; (*ii*) populations not divided by fronts are less genetically differentiated; and (*iii*) the degree of connectivity between populations is related to early-life-history traits and dispersal capabilities.

The Species. In this study, we consider 7 cooccurring species from 6 different families, representing a wide spectrum of the main early-life-history characteristics found in littoral fish (Table 1). Early-life-histories vary greatly among marine species. Although

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Table 1. Life-history traits of the different species

Species	Family	Egg type	Larvae distribution	PLD, days
D. vulgaris	Sparidae	Р	0	29–58
M. surmuletus	Mullidae	Р	0	28–35
S. cabrilla	Serranidae	Р	0	21–28
O. melanura	Sparidae	Р	0	14–18
T. delaisi	Tripterygiidae	В	I	16–21
A. imberbis	Apogonidae	MB	I	18–24
S. tinca	Labridae	В	I	9–13

P, pelagic; MB, mouth-brooder; B, benthic; O, offshore (>2 km); I, inshore (<2 km); PLD, pelagic larval duration. Data from refs. 33, 34, and 36.

some species may spawn benthic eggs from which pelagic larvae hatch, other species may display life cycles where both the eggs and the larvae are pelagic, whereas other species may have evolved peculiar forms of parental care such as the use of brood pouches, mouthbrooding, or bearing live young (28, 29). Also, the pelagic larval duration (PLD) as well as the spatial distribution of pelagic stages (i.e., inshore-offshore) also shows great variability among marine species (30–34). Under this scenario, it is expected that species with extended pelagic phases and offshore distributed larvae would be more apt to disperse over greater distances that species with shorter (or no) pelagic phase and inshore distribution (35).

Three of the study species can be considered to have extended PLD with pelagic eggs and offshore larvae, suggesting a high dispersal potential: the Common 2-banded bream (*Diplodus vulgaris*), the Striped red mullet (*Mullus surmuletus*), and the Comber (*Serranus cabrilla*). An intermediate condition is shown by the Saddled bream (*Oblada melanura*), which spawns pelagic eggs and has offshore larvae but with a shorter pelagic duration. The Blackfaced blenny (*Tripterygion delaisi*) and the Cardinal fish (*Apogon imberbis*) are species with low potential for dispersal, producing benthic or mouth-brooded eggs, inshore larvae, and having shorter PLD. Last, the Peacock wrasse (*Symphodus tinca*) has the shortest PLD (also benthic eggs) and should have the least potential for dispersal.

The Fronts. The Western Mediterranean is a well-studied geographical area considered as a "hot-spot" in marine biodiversity with a high level of endemism (36). Conservation strategies may benefit from the inclusion of ocean circulation and population genetic data. The Western Mediterranean is a small-scale ocean system, influenced by the inflow of Atlantic water through the strait of Gibraltar (12). The interaction between lighter Atlantic water and higher density Mediterranean water generates 2 oceanographic fronts, separated by ≈ 600 km, which may affect organismal dispersal (Fig. 14). The Almeria-Oran front (AOF), situated \approx 400 km East of the Strait of Gibraltar, is a sharp semi permanent boundary between surface water masses formed by the convergence of the Atlantic ocean and the Mediterranean sea. It is a thermohaline density front confined to the upper 300 m of the water column, and is characterized by strong density gradients (comparable with the Gulf Stream) and some upwelling areas (1.5 σ T units, from 1,027.5 kg/m³ to 1,026 kg/m³ at the surface) (Fig. 1C) (37). The AOF has been reported to act as a barrier to gene flow in numerous species (38). East of the AOF, the Atlantic water flows north-eastward, reaching the Balearic Islands and forming a second density front in the northern part of the archipelago. This Balearic Front (BF) is a shelf/slope front, present in the upper 200 m, and is characterized by density differences of 0.5 σ T units. This front is similar to shelf/slope fronts on many continental shelves around the world (12, 37, 39). Indeed, the Balearic Sea is a semienclosed basin with many similarities to other semienclosed seas, such as the South China or the Caribbean Seas (Fig. 1B) (39). The characteristics of each front provide a good opportunity to test their effects on gene flow among marine species with varying dispersal capabilities. Also, we compare the results with populations not separated by any front (NF, no front).

Results

Estimates of genetic divergence between populations, measured as F_{ST} , showed significant differences across the AOF for all species except *O. melanura* (Table 2). Comparisons across the BF were also significant for 5 species, the exceptions being *D. vulgaris* and *S. tinca*. Genetic differentiation between populations from Cabo de Gata and Blanes (NF) was only significant for 4 species, and F_{ST} values were generally smaller than those obtained for the populations separated by the BF. By contrast, results from Cabo de Gata-Mallorca (NF) were quite similar to those of Mallorca-Blanes (separated by BF) (Table 2).

Among the study species, *T. delaisi* and *S. cabrilla* showed the most consistent structuring, with significant genetic differences between all populations compared (Table 2). In 2 species, *A. imberbis* and *M. surmuletus*, only Cabo de Gata-Blanes showed no significant difference; these populations were along continuous coastline and were not separated by either oceanic front. The only nonsignificant comparison for *O. melanura* was across

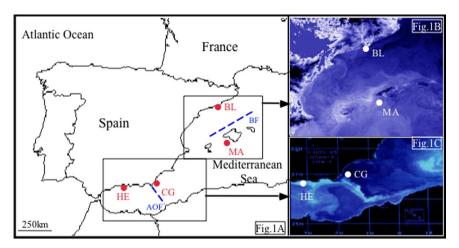


Fig. 1. Sampling locations for the 7 species. (A) HE, Herradura; CG, Cabo de Gata; MA, Mallorca; BL, Blanes; and the locations of the fronts (dotted lines). (B) BF. (C) AOF.

Table 2. Pairwise F_{ST} values for the different species across AOF, BF, and NF

Species	AOF	BF	NF		_
	HE-CG	MA-BL	CG-BL	CG-MA	Mean
D. vul	0.060	0.004	0.008	0.001	0.018
M. sur	0.021	0.134	0.001	0.127	0.071
S. cab	0.014	0.009	0.059	0.036	0.030
O. mel	0.001	0.17	0.052	0.155	0.095
T. del	0.018	0.027	0.038	0.034	0.029
A. imb	0.011	0.060	0.005	0.052	0.032
S. tin	0.033	0.002	0.001	0.001	0.009
Mean	0.023	0.058	0.023	0.058	_
No. Sig	6	5	4	5	—

Significant values (after Bonferroni correction) are shown in bold italics.

the AOF, Herradura-Cabo de Gata. Significant differentiation was shown in 2 of the 4 comparisons of *D. vulgaris*: one pair separated by the AOF, and the other only by distance along continuous coastline (Cabo de Gata-Blanes). Surprisingly, the species expected to show the least gene flow between populations, having benthic eggs, inshore larvae, and the shortest pelagic larval period (Table 1); *S. tinca*, was found to be the species with the least evidence for population structure with only the populations separated by the AOF being significantly differentiated.

Regarding weighted genetic divergence by geographic distance (Fig. 2), for 3 species, the strongest genetic differentiation was found between those populations separated by the AOF, a pattern most clearly shown by *D. vulgaris* and *S. tinca*, and less so by *S. cabrilla*. In the other 4 species, *A. imberbis*, *M. surmuletus*, *O. melanura*, and *T. delaisi*, populations separated by the BF showed the greatest genetic differentiation. These species also showed the greatest overall levels of distance-adjusted differentiation (Fig. 2).

The geographically constrained Bayesian model suggested the existence of 2 genetically differentiated subunits within all species across the sampling area. The spatial location of this discontinuity differed among species. For *D. vulgaris, M. surmuletus,* and *S. tinca,* the genetic discontinuity was found between Herradura and Cabo de Gata, which is congruent with the location of the AOF (Fig. 3 *A, B,* and *G*). For *A. imberbis* and *O. melanura,* a strong genetic discontinuity was observed between Mallorca and Blanes, locations separated by the BF (Fig. 3 *F* and *D*). For *S. cabrilla* and *T. delaisi,* in turn, the clearest genetic discontinuity was detected between Cabo de Gata and Mallorca, locations not separated by either of the fronts (Fig. 3 *C* and *E*).

Discussion

The results of this study allowed us to test 3 predictions, but with very different outcomes. First, we found that, as predicted, both

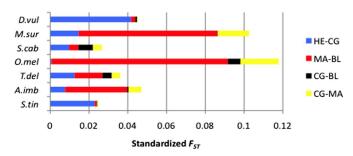


Fig. 2. Standardized F_{ST} (genetic divergence per geographic unit) among pairwise adjacent sampling locations of *D. vulgaris*, *M. surmuletus*, *S. cabrilla*, *T. delaisi*, *O. melanura*, *A. imberbis*, and *S. tinca* species.

the AOF and BF appeared to have a strong influence on population genetic structure of the study species. The second prediction, that populations not separated by fronts would be less genetically differentiated, was supported by the distanceadjusted F_{ST} figures and the Bayesian spatial plots, although a clear picture did not emerge from the raw F_{ST} data. Last, we found no clear relationship between the early-life-history traits investigated (egg type, PLD, and inshore-offshore spawning) and gene flow patterns. This finding suggests that genetic connectivity patterns cannot be readily predicted from the dispersal potential estimated from these early-life-history traits. Perhaps, other biophysical processes such as larval behavior, ontogeny, and mesoscale variability at short spatiotemporal scales may (also) influence genetic connectivity among marine fish populations.

The Effects of the AOF on the Genetic Structure of Littoral Fishes. We

estimated a significant effect of the AOF on genetic differentiation among 6 out of the 7 study species; although, the extent of the differentiation was different among species. Thus, it can be suggested that the AOF can restrict gene flow among populations of species with pelagic stages of various durations, whether they are largely spent inshore or offshore. In addition to the front itself, other environmental and biological factors may also contribute to the genetic structuring observed in this area. For example, flow patterns in the Alboran Sea (40, 41) coupled with frontal density formation may result in favourable conditions for egg and larval development, leading to behavioural and physiological responses to reduce transport and increase settlement, promoting retention.

D. vulgaris has pelagic eggs, offshore larvae, and a PLD of 29–58 days. By contrast, *S. tinca* has benthic eggs and inshore larvae with a PLD of a mere 9–13 days. However, these species showed similar levels of genetic differentiation across the AOF. Similarly, populations of *T. delaisi* and *S. cabrilla* on one hand, and those of *A. imberbis* and *M. surmuletus* on the other, showed very similar patterns of genetic differentiation despite the differences in their life-history traits (Table 1). The only species not showing significant genetic differentiation across the AOF was *O. melanura*, a species showing intermediate values for traits that might be expected to be associated with genetic structuring.

Our results agree with the majority of studies (38), which have shown evidence that significant population differences can be found across the AOF, even for species that have very long pelagic larval stages (\approx 4 months) (42). Some previous studies have also reported a lack of significant genetic differentiation for species with relatively weaker presumed dispersal capabilities, such as those with shorter PLDs (\approx 30 days) or benthic eggs (43). Similarly, in our study, *O. melanura* showed no significant genetic differentiation across the AOF, despite its presumably limited larval dispersal capabilities. However, in this species, it might be suggested that gene flow across the AOF could be facilitated by movements of the shoaling benthopelagic adults.

Our study indicated contrasting levels of divergence among the 2 sparid species, *D. vulgaris* and *O. melanura*. Different results have also been noted in previous studies of closely-related species within the area. Significant differences among populations of the anglerfish species *Lophius budegassa* have been found, but not among those of *Lophius piscatorius*, which has a qualitatively similar life history (42). Likewise, a gene flow break for 3 out of 5 sparid species investigated was found (43), and later it was shown that patterns were consistent within species irrespective of whether mitochondrial and nuclear (allozyme) markers were used (44). Thus, although the AOF can be an effective barrier to gene flow for most marine species, there are exceptions, which cannot be easily predicted from their early-lifehistory traits nor the genetic markers used. Explaining why closely-related species with similar life-history traits show strik-

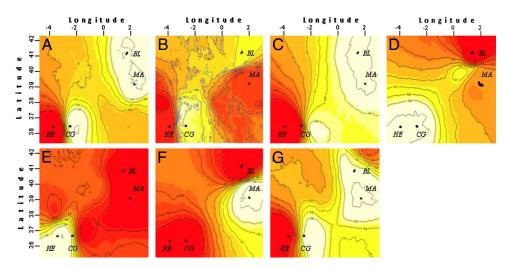


Fig. 3. Map of posterior probabilities of population membership and spatial location of genetic discontinuities for populations of *D. vulgaris* (*A*), *M. surmuletus* (*B*), *S. cabrilla* (*C*), *O. melanura* (*D*), *T. delais* (*E*), *A. imberbis* (*F*), and *S. tinca* (*G*) species. Contour lines indicate the spatial position of genetic discontinuities between populations. Lighter colours indicate higher probabilities of population membership.

ingly different patterns of gene flow remains a challenge worthy of further research. The use of coupled biophysical models holds great promise in this regard (45, 46).

The Effects of BF on the Genetic Structure of Littoral Fishes. Like the AOF, the BF also reduces gene flow in most species, except for D. vulgaris and S. tinca, species lying at opposite poles of the distribution of predicted dispersal capabilities. It was particularly surprising to find evidence for high levels of gene flow in the inshore-living S. tinca, which has benthic eggs and short larval duration. Not only are the Mallorca and Blanes populations separated by the front, but a littoral species might be expected to show little gene exchange between continental and insular populations. The mating and settlement behavior of the species might explain this apparently anomalous result. Like other species of the genus Symphodus, spawning takes place in nests built with branching algae that are often destroyed and transported by waves (47). Because such algal clumps are also suitable habitat for settlers (48), passive transportation through drifting algae could help homogenize gene pools across the BF. This hypothesis, which merits further research, highlights the possible importance that life-history traits other than PLD, may have on the connectivity of marine populations.

Likewise, environmental and biological factors in addition to the BF may have also contributed to the genetic structure observed in the other species. The effect of the BF may be intensified by the existence of habitat discontinuities between insular and continental populations. The oceanographic features of offshore habitats can differ substantially from those of coastal waters (36), and the survival of inshore-spawned larvae may be poor, compared with that of offshore-spawned larvae. Therefore, although it would appear that offshore larvae are also constrained by the front, the Balearic Islands display partial hydrodynamic interactions with the continent (49). This intermittent connection may allow for passive transport of early-life stages of some species with pelagic eggs and offshore larvae, such as D. vulgaris. Not only has this species the largest PLD in this study, but it reproduces in autumn, when the density gradients of the BF are reduced (39). This early-life-history trait suggests that the PLD and the seasonality of the fronts might be key elements allowing larvae, at least of this species, to reach the archipelago. Another habitat discontinuity that could pose a natural barrier is the deep-water trench of >1,000 m that separates the Balearic Islands from the continent (50). Restriction of gene flow by deep water has been shown for other marine species (51–53).

The Genetic Structure in the Absence of Fronts. From inspection of the raw F_{ST} figures, it would appear that populations not separated by fronts are no less genetically differentiated (Table 2). However, the standardized F_{ST} values indicate that the fronts are associated with a substantial restriction in gene flow (Fig. 2), a pattern also evident from the maps of posterior probabilities (Fig. 3).

In the comparison between the continental populations of Cabo de Gata and Blanes, 4 species (D. vulgaris, S. cabrilla, O. *melanura*, and *T. delaisi*) were significantly different. This differentiation may have been a result of the considerable distance between the localities, suggesting isolation by distance. The species M. surmuletus, A. imberbis, and S. tinca showed no significant genetic differentiation. No common life-history characteristics readily explain the absence of genetic differentiation between these 2 localities. The adults of these species are relatively sedentary, suggesting that larval dispersal could be more relevant in connecting populations. We did not have information about all species differences in larval behavior or preferred position in the water column as such traits could influence the response of larvae to currents (54). For example, *M. surmuletus* larvae are neustonic (found in surface waters), whereas S. cabrilla larvae are typically found in deeper layers. This difference could affect their transport as much as their inshore-offshore gradient. Future studies may need to consider how these traits affect genetic connectivity.

The continental populations at Cabo de Gata and the insular populations at Mallorca were significantly differentiated in 5 out of the 7 species. In fact, the levels of differentiation for this comparison were more similar than those obtained between populations separated by the BF, Mallorca, and Blanes (mean $F_{ST} = 0.058$). Of course, Blanes is also much closer to Mallorca than Cabo de Gata is, so the standardised F_{ST} figures were much higher for the populations separated by the BF, for all species except *S. cabrilla* (Table 2, Fig. 2), consistent with the third prediction.

Genetic Differentiation and Early-Life-History Characteristics. No evidence was found that a single life-history trait is strongly related to population genetic differentiation, whether in the presence or absence of oceanographic barriers. Some studies

have found that early-life-history traits are poor predictors of population genetic structure (7, 55), whereas others have found a clear relationship between early-life-history and gene flow (29, 56). This discrepancy indicates that population structure cannot always be explained by simple predictors. Other biological characteristics may have additional and significant influence on the connectivity between populations, including larval and adult behavior, and reproductive and recruitment strategies (57). Also, small-scale hydrographic variability and local processes may have ecologically meaningful effects on population connectivity (45).

In summary, by using a multispecies approach, our results demonstrate that the spatial location of genetic discontinuities between populations differed among species. Biotic factors, such as egg type, PLD, and inshore-offshore spawning, proved to be poor predictors of population structure, showing not necessarily that they are unimportant, but rather that they may be insufficient in the absence of further knowledge. Also, our results highlight the relationship between gene flow patterns and barriers to dispersal such as ocean fronts. The fronts analyzed and the underlying physical mechanisms are not site-specific but common among the oceans, suggesting the generality of our findings. Oceanic fronts could isolate populations of many species, increasing their tendency to self-recruitment and increasing their vulnerability. This isolation could have important implications in conservation-management policies for marine resources (58), particularly in semienclosed areas, such as the Mediterranean, South China, or Caribbean Seas, considered as hot-spots for marine biodiversity (36). Therefore, the design of a network of marine reserves or any other conservationmanagement strategy should be influenced by the scale of genetic connectivity produced by the combination of oceanographic features and life histories of species.

Materials and Methods

Sample Collection and Genetic Analysis. During 2004–2007, a total of 1,197 adults from 7 different marine fish species were sampled at the same 4 locations along the Spanish Mediterranean coast and the Balearic Islands (Fig. 1.4). All samples were obtained by scuba diving. A mean of 47.5 individuals per site and species were analyzed [see supporting information (SI) Table S1]. A total of 63 species-specific microsatellite loci (mean 9 loci per species) were successfully amplified by PCR and analyzed to determine the genetic diversity and population structure of each species (see *SI Text* and Tables S2–S8). Popula-

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tion structure was investigated by using raw and distance-adjusted *F_{ST}* values, whereas Bayesian methods were used to seek spatial genetic discontinuities.

Spatial Genetic Structure. The effect of the oceanographic fronts on gene flow levels within and among species was assessed through 2 different approaches, at both the population and individual levels. First, at the population level, pairwise values of F_{ST} and their estimated probabilities were calculated within species by 10,000 random permutations by using GENETIX v. 4.02 (59). Permuted F_{ST} values were compared with observed values to estimate the probability of randomly achieving a value greater than or equal to the observed. The alternative hypothesis of significant genetic differentiation was accepted if this probability was equal to or <0.05. Also, we standardized population F_{ST} values by dividing each pairwise value by its corresponding pairwise geographic distance. In this way, a genetic distance per geographic distance unit was obtained and used to evaluate the relative effect of each front on each species.

At the species level, spatial locations of genetic discontinuities (i.e., genetic boundaries) along the sampling area were determined by using the R package GENELAND (60). The program makes use of a geographically constrained Bayesian model that explicitly takes into account the spatial position of sampled multilocus genotypes without any prior information on the number of populations and degree of differentiation between them. Geographical coordinates were assigned to each individual by randomly choosing *n* spatial locations encompassed within a 10-km radius from each of the 4 sampling locations, by using the Mapping toolbox in MATLAB v.7. (Mathworks), where n equals the number of individuals per species sampled at a given location. Thus, the same geographic coordinates were used for individuals of all species sampled at the same site. The inference algorithm was launched by using the Dirichlet distribution as prior for allele frequencies with 20,000 MCMC iterations using spatial information. Then, the algorithm was rerun with an additional 20,000 MCMC iterations, fixing the value of K (i.e., number of populations) to that determined by the mode of the posterior distribution of the MCMC chain, and setting the Poisson processes equal to the number of sampled individuals per species.

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