

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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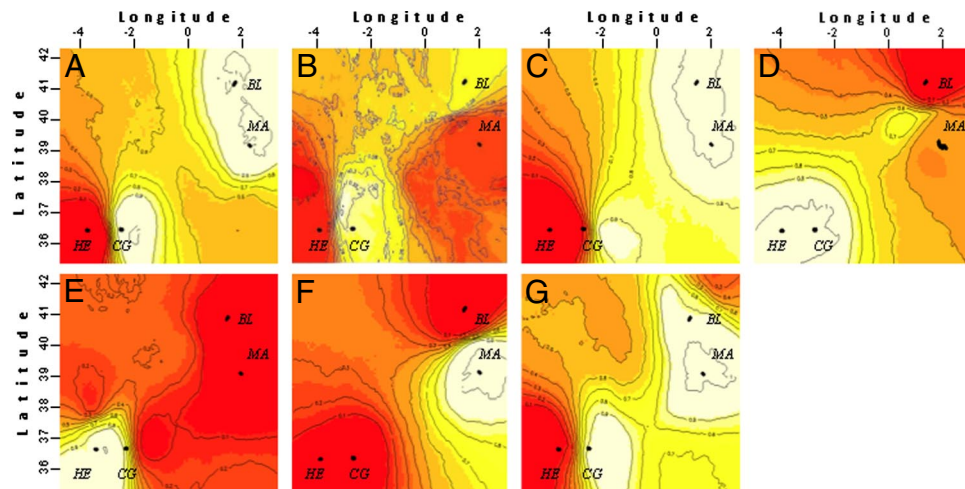


Fig. 3. Map of posterior probabilities of population membership and spatial location of genetic discontinuities for populations of *D. vulgaris* (A), *M. surmuletus* (B), *S. cabrilla* (C), *O. melanura* (D), *T. delaisi* (E), *A. imberbis* (F), and *S. tinca* (G) species. Contour lines indicate the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

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