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ECOGRAPHY

Brevia

Revisiting long-distance dispersal in a coastal marine fish

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Dispersal is any movement of individuals from a source location (e.g. birth or breeding site) to another where establishment and reproduction may occur (Clobert et al. 2012). Dispersal shapes species distribution and plays a key role in species persistence under global change. It also has evolutionary (e.g. gene flow, adaptation) and biogeographic (e.g. range shift, transmission of disease) consequences (Álvarez-Noriega et al. 2020). Specifically, long-distance dispersal that occurs beyond a threshold distance not reached by most individuals has the potential to reshape genetic variation and species geographic range (Luo and Li 2023). While it has often been reported for plants (Jordano 2017), long-distance dispersal is still difficult to observe over large spatial scales (Van der Stocken et al. 2019). A recent meta-analysis indicates that the spatial extent of dispersal observed in marine organisms with a larval dispersal phase depends on the spatial scale of the sampling (mean of 40 km) and not on the potential dispersal inferred from biophysical models (Manel et al. 2019). Therefore, long-distance dispersal for non-migratory marine species is rarely documented and likely underestimated (Manel et al. 2019), while it determines their capacity to migrate towards more favorable environmental conditions (Nanninga and Manica 2018) or to generate spillover far from marine protected areas (MPAs, Russ and Alcalá 2011). In this study, we identified five pairs of closely related individuals of an exploited Mediterranean fish species, the white seabream *Diplodus sargus*, using a rigorous statistical framework of six relatedness estimates coupled to a parentage assignment program. These five pairs were all distant from more than 1300 km, suggesting exceptional long-distance individual dispersal events of more than 650 km.

To capture such exceptional long-distance dispersal events, we performed an exhaustive sampling design – along a 4000 km coastline – that encompasses the full geographic range of the white seabream *D. sargus* across the Mediterranean Sea. We genotyped a total of 297 individuals at 8206 single nucleotide polymorphisms (SNPs) (Boulanger et al. 2022) to shed light on long-distance dispersal movements over one generation. We estimated six relatedness coefficients among pairwise individuals, and



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we used a maximum likelihood method to assign sibship (Method, Supporting information). From these analyses, we detected a total of five pairs of closely related individuals ($5/43\,954 = 0.01\%$ of all pairwise comparisons), comprising three full siblings and two half-siblings. These five pairs showed the highest estimates regardless of the method used (Supporting information). For these five pairs, 80% of the relatedness coefficients were > 0.25 , where 0.25 is indicative of individuals that have at least one ancestor in common and share one quarter of their genotype (Supporting information). Only the selected related pairs have relatedness coefficients > 0.25 . Heterozygosity values were estimated per individual and per SNPs to ensure the quality of the genomic dataset and overcome contamination bias (Supporting information); none of the related individuals were finally removed. This high proportion of pairs of related individuals could be expected, due to the high variance in reproduction success reported for this exploited and protandrous hermaphrodite species, with only a small proportion of adults contributing to the reproduction in yearly cohorts (Planes and Lenfant 2002). The median marine geographic distance (Methods, Supporting information) separating the closely related individuals was 2063 km (SD = 873 km, Interquartile range = 1506–2196

km; Range = 1350–2222 km), revealing exceptional long-distance dispersal events for the white seabream that have never before been reported (Fig. 1A). One pair was sampled at the same site, located in the Gulf of Lion in France. The four other related pairs were sampled more than 1350 km apart (Fig. 1A).

Most of the long-distance dispersal events connected eastern and western Mediterranean populations (Fig. 1B) across a marked gradient of sea surface temperature (SST, average temperature = 24.83°C , range = $22.70\text{--}27.28^{\circ}\text{C}$, Supporting information). We found that a maximal distance of 2221 km separated one full sibling pair (Fig. 1B). This distance is six times longer than the maximal dispersal distance estimated by a biophysical model of larval dispersal, i.e. 355 km (Legrand et al. 2019), and 22 times longer than the adult dispersal distance found in the literature for this species (> 100 km) (Giacalone et al. 2022). Even if individuals from the same pair dispersed in opposite directions from the spawning site, the dispersal distances reported here are still one order of magnitude longer than previously estimated. Our results demonstrate that white seabream individuals can spread much further than expected by biophysical models of larval dispersal. Exceptional adult migrations probably

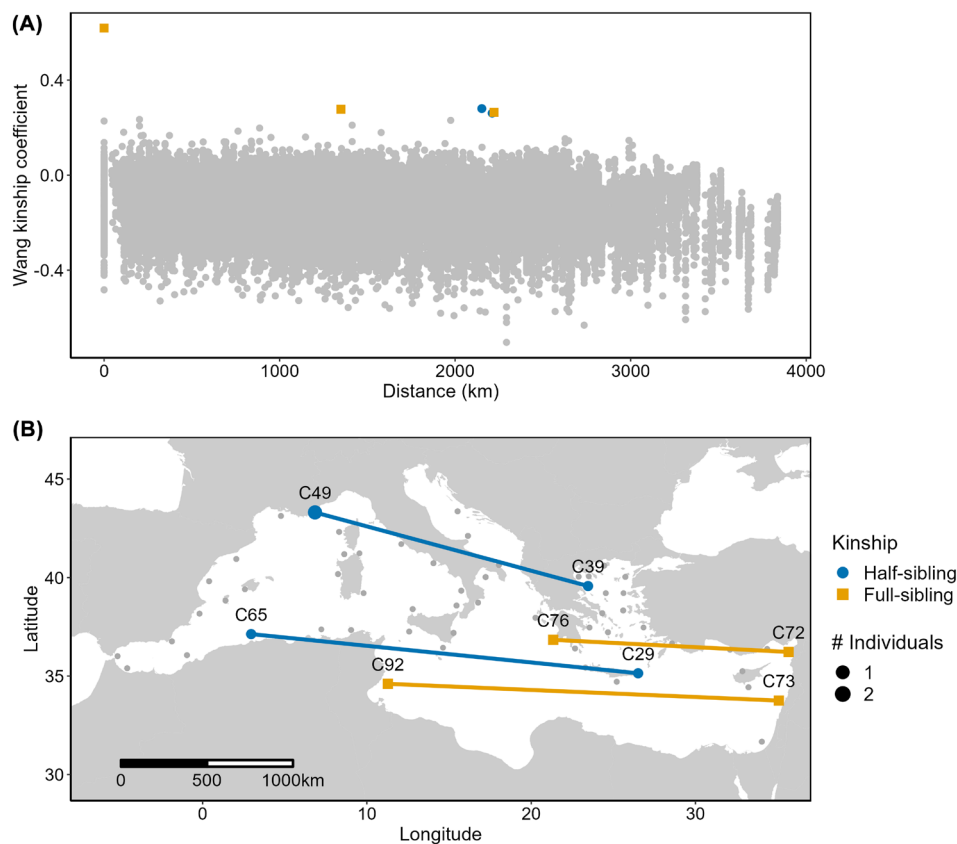


Figure 1. Long-distance dispersal of related *Diplodus sargus* individuals (A) distribution of the 95 percentiles (i.e. > 0.0160) for the Wang relatedness coefficient inferred from 8206 neutral single nucleotide polymorphisms (SNPs) along a gradient of geographic distance across the Mediterranean Sea. Colors represent the five pairs of closely related individuals which are either full siblings (brown) or half-siblings (blue) and showed the highest Wang coefficients (> 0.25). (B) Location of the 297 individuals sampled across the Mediterranean Sea. Pairs of related individuals are colored as in (A) and lines indicate these pairs. The pair sampled at the same site is not represented.

contribute to these extreme events, as previously documented (Abecasis et al. 2009), as well as larval rafting and active larval dispersal (Baptista et al. 2019).

The Mediterranean Sea is considered as a ‘hotspot’ of both climate change and marine biodiversity, harboring 4–18% of all known marine species (Coll et al. 2010). SSTs are predicted to increase by 2.7°C before the end of the century, threatening many marine species that cannot easily escape from this semi-enclosed area (Lasram et al. 2010). In our study area, the mean annual SST is expected to increase from 19.9 to 21.4°C in 2050 with the most pessimistic emission scenario (IPCC Relative Concentration Pathway 8.5, Moss et al. 2010), and from 26.0 to 28.0°C for the hottest month. Long-distance dispersal of favorable mutations adapted to warming could then be particularly critical to ensure the species’ survival. Following this scenario, long-distance migrants from the eastern Mediterranean basin could rapidly bring hot-adapted alleles into the cooler – and becoming potentially vulnerable – western populations. This niche shift of western populations can be critical to escape regional extirpation under climate change. However, this hypothesis requires further investigations, since the method employed in this study cannot reveal the direction of individual dispersal and whether these niche shifts are primarily evolutionary or not.

Evidence of such long-distance dispersal also has implications for the design of MPAs in the overcrowded but poorly protected Mediterranean Sea, since species dispersal extent should determine their size and spacing. Long-distance dispersal can potentially connect distant and isolated MPAs. In the Mediterranean Sea, 70% of no-take MPAs are geographically isolated (> 42 km), and the closest no-take MPAs are on average 77 km away (ranging from 0 to 225.3 km) (Supporting information). The dispersal values obtained here (> 650 km) suggest that even the most isolated MPAs could be connected by a few individuals, ensuring gene flow and migration towards favorable environments.

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Author contributions

Stéphanie Manel: Conceptualization (leading); Formal analysis (equal); Funding acquisition (lead); Writing – review and editing (lead). **Emilie Boulanger:** Conceptualization (supporting); Formal analysis (equal); Writing – review and editing (equal). **Laura Benestan:** Conceptualization (supporting); Formal analysis (equal); Writing – review and editing (supporting). **David Mouillot:** Conceptualization (equal); Writing – review and editing (equal). **Alicia Dalongeville:** Conceptualization (supporting); Formal analysis (equal); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

All the codes and data required to reproduce the statistical analyses are available at: <https://gitlab.mbb.univ-montp2.fr/bev/long-dispersal-distance>.

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fbg79cvs> (Boulanger et al. 2021).

Supporting information

The Supporting information associated with this article is available with the online version.

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