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Unraveling the physics of connectivity and dispersal in Mediterranean coastal marine populations: the case of the Alboran and Adriatic seas

Irene Nadal Arizo

Directores: Jesús García Lafuente y Simone Sammartino

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Unraveling the physics of connectivity and dispersal in Mediterranean coastal marine populations: the case of the Alboran and Adriatic seas

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UNIVERSIDAD DE MÁLAGA
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DECLARACIÓN DE AUTORÍA Y ORIGINALIDAD DE LA TESIS PRESENTADA PARA OBTENER EL TÍTULO DE DOCTOR

D./Dña. IRENE NADAL ARIZO

Estudiante del programa de doctorado DINÁMICA DE LOS FLUJOS BIOGEOQUÍMICOS Y SUS APLICACIONES de la Universidad de Málaga, autor/a de la tesis, presentada para la obtención del título de doctor por la Universidad de Málaga, titulada: UNRAVELING THE PHYSICS OF CONNECTIVITY AND DISPERSAL IN MEDITERRANEAN COASTAL MARINE POPULATIONS: THE CASE OF THE ALBORAN AND ADRIATIC SEAS

Realizada bajo la tutorización de JESÚS GARCÍA LAFUENTE y dirección de JESÚS GARCÍA LAFUENTE y SIMONE SAMMARTINO

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HACEN CONSTAR:

Que el trabajo recogido en la presente memoria, titulada “Unraveling the physics of connectivity and dispersal in Mediterranean coastal marine populations: the case of the Alboran and Adriatic seas”, presentada por Irene Nadal Arizo, ha sido realizada bajo nuestra dirección y tiene, a nuestro juicio, contenido científico suficiente, de lo que informamos favorablemente en orden a su presentación y defensa para optar grado de Doctora Internacional por la Universidad de Málaga.

Para ello, firmamos la presente en Málaga a 12 de junio de 2024:

Jesús García Lafuente Simone Sammartino

“El mar

me alimenta,

el mar

me sustenta.

A mí,

a mi familia…

El mar me contenta,

el mar

me atormenta…

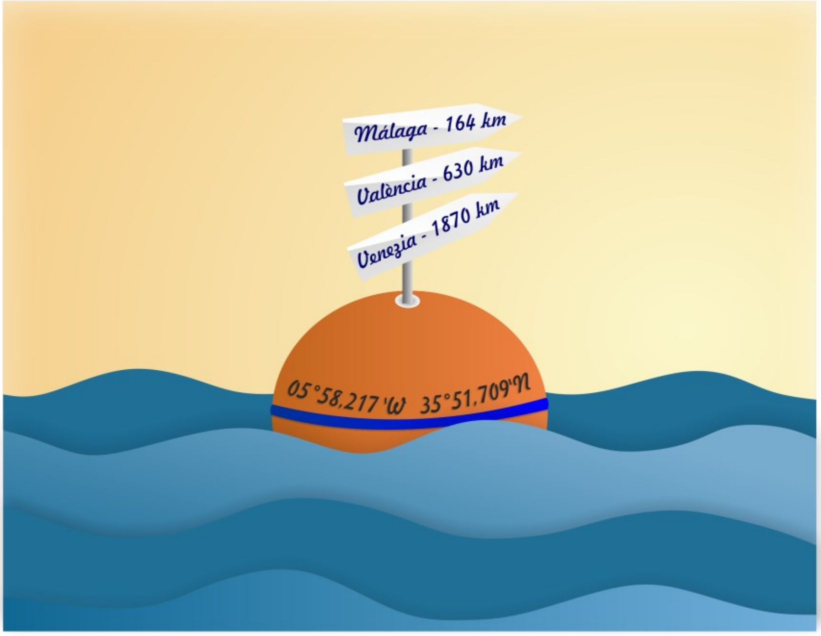
El mar

es mi vida,

el mar

es mi hogar…”

Ricardo Villar Martínez, *El poeta de los mares*



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Cuando acaba un doctorado, en cierto modo, se cierra un ciclo para dejar paso a otra etapa de la vida. Ahora, mirando atrás, reconozco lo importante que ha sido este periodo y todas aquellas personas que han formado parte de él. Sin ellas, no sería quien soy hoy, así que quiero dar las gracias a todos los que, de una forma u otra, me han guiado, acompañado y apoyado, ya sea en el ámbito profesional o personal, en este viaje tan especial.

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List of publications

Publications arising from this thesis

The present thesis is presented in the form of a "thesis by compendium of publications". To this aim, a total of four scientific papers are collected, which have been published (1-, 2-, 3-) or are being prepared for submission for publication (4-) in scientific journals, all of which belong to the first quartile in the Journal Citation Report (JCR). The listed works deal with the hydrodynamics that regulate the connectivity and dispersal patterns of different populations of interest in the regions of the Strait of Gibraltar and the Alboran Sea (1-, 3-, 4-) on the one hand, and the Adriatic Sea (2-) on the other.

1- **Nadal, I.**, Sammartino, S., García-Lafuente, J., Sánchez Garrido, J. C., Gil-Herrera, J., Hidalgo, M., & Hernández, P. (2022). Hydrodynamic connectivity and dispersal patterns of a transboundary species (*Pagellus bogaraveo*) in the Strait of Gibraltar and adjacent basins. *Fisheries Oceanography*, *31*(4), 384-401. https://doi.org/10.1111/fog.12583.

2- **Nadal, I.**, Picciulin, M., Falcieri, F. M., García-Lafuente, J., Sammartino, S., & Ghezzo, M. (2024) Spatio-temporal connectivity and dispersal seasonal patterns in the Adriatic Sea using a retention clock approach. Frontiers in Marine Science, 11:1360077. https://doi.org/10.3389/fmars.2024.1360077.

3- García-Lafuente, J., **Nadal, I.**, Sammartino, S., Korbee, N., Figueroa, F.L. (2023) Could secondary flows have made possible the cross-strait transport and explosive invasion of *Rugulopteryx okamurae* algae in the Strait of Gibraltar?. *PLOS ONE*, *18*(5): e0285470. https://doi.org/10.1371/journal.pone.0285470.

4- **Nadal, I.**, Sammartino, S., Sánchez Garrido, J. C., García-Lafuente, J., Korbee, N., Figueroa, F.L. Modeling spread of an alien alga under different temporal scenarios in the Strait of Gibraltar and adjacent basins. In preparation for submission to the journal Marine Pollution Bulletin in the following months of the year 2024.

Other scientific publications during the doctoral period

During the period of my doctoral thesis, I contributed to two additional scientific works that are not included in this dissertation. These contributions are hereby listed as scientific merits:

5- García-Lafuente, J., Sammartino, S., Huertas, I. E., Flecha, S., Sánchez-Leal, R. F., Naranjo, C., **Nadal, I.**, & Bellanco, M. J. (2021). Hotter and Weaker Mediterranean Outflow as a Response to Basin-Wide Alterations. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.613444 .

6- Sánchez-Garrido, J. C., & **Nadal, I.** (2022). The Alboran Sea circulation and its biological response: A review. *Frontiers in Marine Science*, 9. https://doi.org/10.3389/fmars.2022.933390.

Eleven contributions to national congresses are listed below as additional merits:

7- **Nadal, I.,** Sánchez Garrido, J. C., Sammartino, S., García-Lafuente, J., Korbee, N. & López-Figueroa, F. (2024, July 10-12). Dispersal modeling of the invasive algae *Rugulopteryx okamurae* in the Strait of Gibraltar and adjacent basins [Oral presentation]. Physical Oceanography Encounter 2024 (EOF) - IX International Symposium on Marine Science (ISMS2024). Catholic University of Valencia. Valencia, Spain.

8- **Nadal, I.**, Picciulin, M., Falcieri, F. M., García-Lafuente, J., Sammartino, S., & Ghezzo, M. (2024, July 10-12). Spatio-temporal patterns of connectivity and dispersal in the Adriatic Sea [Poster]. Physical Oceanography Encounter 2024 (EOF) - IX International Symposium on Marine Science (ISMS2024). Catholic University of Valencia. Valencia, Spain.

9- **Nadal, I.,** Ghezzo, M., Falcieri, F.M., Sammartino, S., & García-Lafuente, J. (6-9 septiembre 2023). Patrones de dispersión y conectividad en el Mar Adriático [Poster]. I Congreso Iberoamericano Jóvenes Investigadores del Mar. University of Almería. Almería, Spain.

10- **Nadal, I.**, García-Lafuente, J., Sammartino, S., Sánchez-Garrido J. C., Korbee, N. & López-Figueroa, F. (6-8 julio 2022). On the interaction between the macroalgae *Rugulopteryx okamurae* and the hydrology of the Alboran Sea [Poster]. VII Expanding Ocean Frontiers conference (EOF) – VIII International Symposium on Marine Science (ISMS2022). University of Las Palmas de Gran Canaria. Las Palmas de Gran Canaria, Spain.

11- **Nadal, I.**, Sammartino, S., García-Lafuente, J., Sánchez Garrido, J. C., Gil-Herrera, J., Hidalgo, M., & Hernández, P. (6-8 julio 2022). Hydrodynamic connectivity and dispersal patterns in the Strait of Gibraltar: Implications for a transboundary species [Oral presentation]. VII Expanding Ocean Frontiers conference (EOF) – VIII International Symposium on Marine Science (ISMS2022). University of Las Palmas de Gran Canaria. Las Palmas de Gran Canaria, Spain.

12- **Nadal, I.**, Muñoz López, P., Sammartino, S., García-Lafuente, J., & Cabello, J. (6-9 septiembre 2021). Estructura y variabilidad de las propiedades termohalinas y corriente en el Estuario del Guadalquivir [Oral presentation]. III Congress of Young Researchers (JISDELMAR). University of Granada. Motril, Spain.

13- **Nadal, I.,** García-Lafuente, J., Sammartino, S., Muñoz López, P., & Cabello, J. (6-9 septiembre 2021). Interacciones entre la propagación de la onda de marea y el efecto de la fricción en el Estuario del Guadalquivir [Poster]. III Congress of Young Researchers (JISDELMAR). University of Granada. Motril, Spain.

14- **Nadal, I.,** García-Lafuente, J., Sammartino, S., Muñoz López, P., & Cabello, J. (5-7 julio 2021). Interacciones entre la propagación de la onda de marea y el efecto de la fricción en el Estuario del Guadalquivir [*Online* oral presentation]. VI Expanding Ocean Frontiers conference (EOF). Polytechnic University of Catalonia. Barcelona (Virtual conference), Spain.

15- **Nadal, I.,** García-Lafuente, J., Sammartino, S., Cabello, J. & Muñoz López, P., (16-18 junio 2021). Tidal propagation and frequency responses in the Guadalquivir Estuary [*Online* oral presentation]. 9th International Workshop On Marine Technology (MARTECH). University of Vigo (Virtual conference). Vigo, Spain.

16- **Nadal, I.** Sammartino, S., Sánchez Garrido, J. C., & García-Lafuente, J. (1-4 octubre 2019). Connectivity patterns of the blackspot seabream (*Pagellus bogaraveo*) in the Alboran Sea [Poster]. II Congress of Young Researchers (JISDELMAR). University of Málaga. Málaga, Spain.

17- **Nadal, I.,** Sammartino, S., Sánchez Garrido, J. C., & García-Lafuente, J. (1-4 octubre 2019). Tidal dynamics effect on the connectivity patterns of the blackspot seabream (*Pagellus bogaraveo*) in the Alboran Sea [Oral presentation]. II Congress of Young Researchers (JISDELMAR). University of Málaga. Málaga, Spain.

List of abbreviations

Abbreviation		Chapter(s)
AdDW	Adriatic Deep Water	1, 4
ADCP	Acoustic Doppler Current Profiler	5, 6
AJ	Atlantic Jet	1, 3, 6
AOF/AO	Almería-Oran front	1, 3
AS	Alboran Sea	3
AS	Adriatic Sea	4
CCG	Central Cyclonic Gyre	1, 3, 6
CS	Camarinal Sill	5, 6
EAC	Eastern Adriatic Current	1, 4, 7
EAG	Eastern Alboran Gyre	1, 3, 6, 7
ELS	Early-Life-Stages	3
GSA	Geographical Sub-Area	3, 4
ISW	Ionian Surface Water	1
LIW	Levantine Intermediate Water	1, 2, 3
MITgcm	Massachusetts Institute of Technology General Circulation Model	2, 3, 6
MPoP	Maximum Percentage of Particles	3
NACW	North Atlantic Central Water	1, 6
NAdDW	North Adriatic Dense Water	1, 4
PLD	Pelagic Larval Duration	1, 2, 3, 4
RCM	Retention Clock Matrix	4
SAW	Surface Atlantic Water	1
SHYFEM	Shallow water HYdrodynamic Finite Element Model	2, 4
SoG	Strait of Gibraltar	1, 3, 5, 6, 7
Sv	Sverdrup (1 Sv = 10^6 m·s^{-1})	1, 3, 6

ToMC	Time of Maximum Connectivity	3
WAC	Western Adriatic Current	1, 4, 7
WAG	Western Alboran Gyre	1, 3, 6, 7
WMDW	Western Mediterranean Deep Water	1, 6

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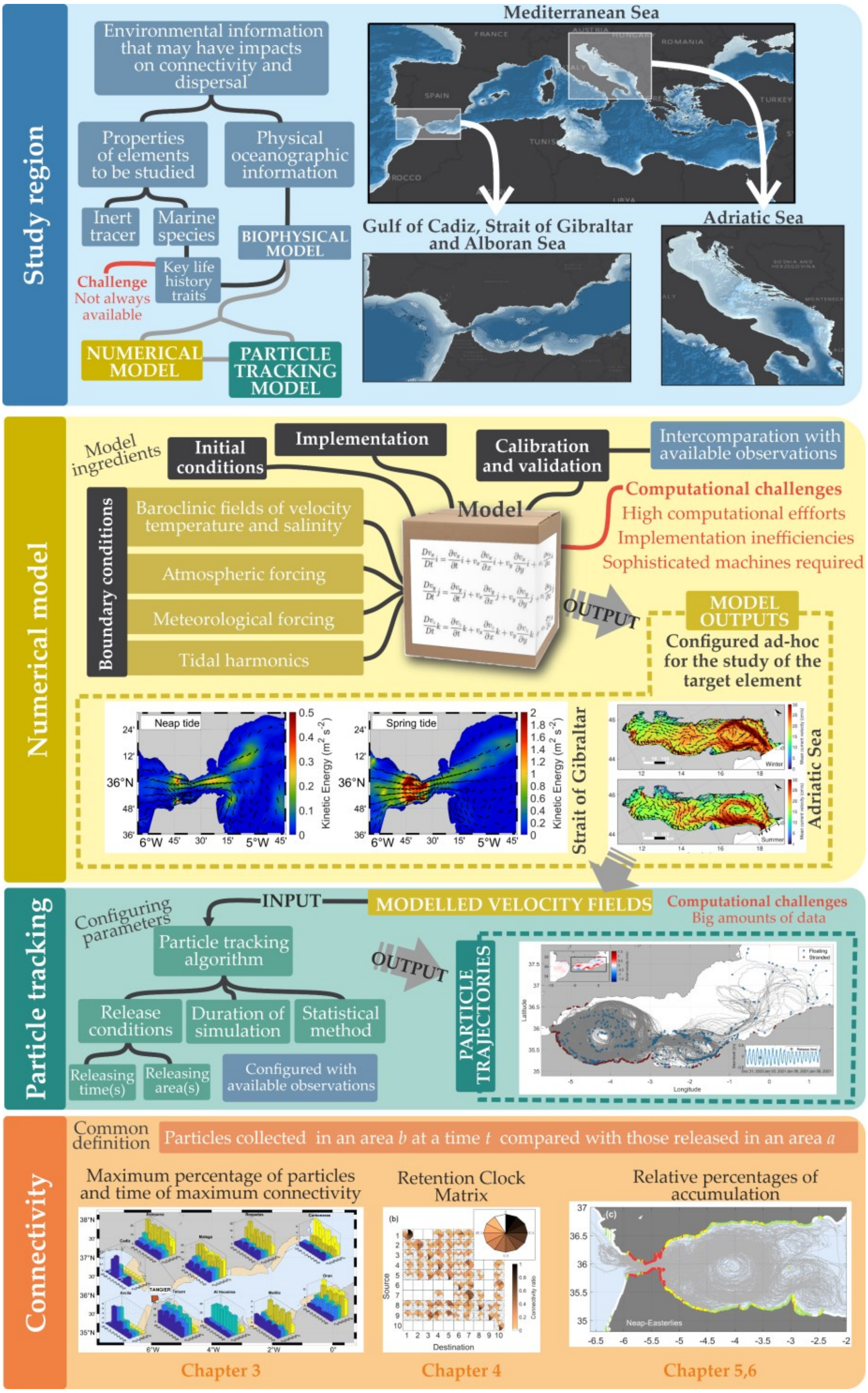
Scheme of the research: one-page thesis



Study region

Environmental information that may have impacts on connectivity and dispersal

Properties of elements to be studied

Physical oceanographic information

Inert tracer

Marine species

Key life history traits

Challenge
Not always available

BIOPHYSICAL MODEL

NUMERICAL MODEL

PARTICLE TRACKING MODEL

Mediterranean Sea

Gulf of Cadiz, Strait of Gibraltar and Alboran Sea

Adriatic Sea

Numerical model

Model ingredients

Initial conditions

Implementation

Calibration and validation

Intercomparation with available observations

Boundary conditions

Baroclinic fields of velocity temperature and salinity

Atmospheric forcing

Meteorological forcing

Tidal harmonics

Model

Computational challenges
High computational efforts
Implementation inefficiencies
Sophisticated machines required

OUTPUT

MODEL OUTPUTS
Configured ad-hoc for the study of the target element

Strait of Gibraltar

Adriatic Sea

Particle tracking

Configuring parameters

INPUT

MODELLED VELOCITY FIELDS

Computational challenges
Big amounts of data

Particle tracking algorithm

Release conditions

Duration of simulation

Statistical method

Releasing time(s)

Releasing area(s)

Configured with available observations

OUTPUT

PARTICLE TRAJECTORIES

Connectivity

Common definition

Particles collected in an area *b* at a time *t* compared with those released in an area *a*

Maximum percentage of particles and time of maximum connectivity

Retention Clock Matrix

Relative percentages of accumulation

Chapter 3

Chapter 4

Chapter 5,6

1 General Introduction

1.1 State of the art

1.1.1 Motions in the marine environment: an overview

The marine environment is a vast, complex and dynamic system encompassing a broad range of fluid motions interacting at several spatio-temporal scales (Pineda et al., 2007). At the seaside, the occurrence of wind-driven surface waves with periods ranging from seconds to minutes and wave heights from centimeters to several meters is a common observation (Ocampo-Torres, 2001). Tides are an ever-present phenomena throughout the ocean, although generally more pronounced in proximity to large bathymetric features such as the entrance to a gulf, bay, channel, or estuary (Sirviente et al., 2023). Longshore currents are another visible phenomenon within the surf zone (Boon, 2004). Even propagating internal waves, often generated through the interaction of the tidal flows with the bottom topography, may be detected by the naked eye in specific spots (Sánchez-Garrido & Vlasenko, 2009).

The set of oceanic fluid motions readily observable to the human eye represents a subset of the full spectrum of ocean motions known (Figure 1.1), ranging from molecular processes to decadal oscillations and climate variability on scales from seconds to centuries and from centimeters to thousands of kilometers. These motions are responsible for transporting seawater properties along with plankton, larvae, and debris, over long distances (van Sebille et al., 2020). It is a start to have an idea of how diverse processes and variables occurring in the ocean might influence the distribution of such matter at different spatio-temporal scales.

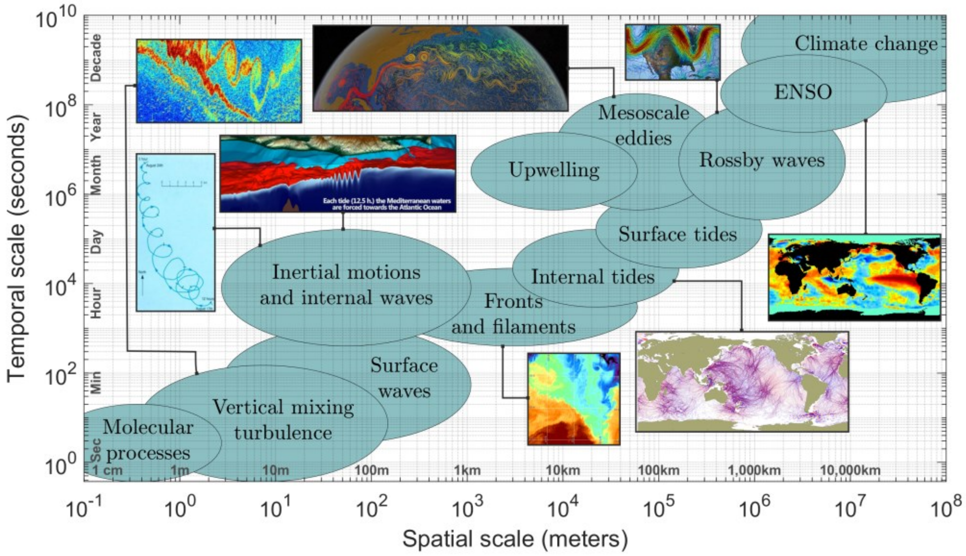


Figure 1.1. Spatio-temporal scale at which different oceanographic phenomena occur. Adapted from Dickey, 2001.

Small-scale turbulence is an ubiquitous eddy motion state of geophysical fluids responsible for mixing that influences sediment resuspension, mediates nutrient uptake, and affects the community structure of planktonic organisms in a multitude of ways (Margalef López, 1997), including alterations in grazing activity, motility, and growth (Megrey, 2001; Zhao et al., 2020). At similar spatio-temporal scales, surface waves generated in the upper layer of the ocean, have an effect on both mean currents through the action of the flux of momentum (Xue et al., 2023), and on the net transport of organisms and solutes in the nearshore environment, thereby influencing the dynamics of certain marine populations (Monismith & Fong, 2004).

In most coastal areas worldwide, oscillatory flow driven by tidal currents represents a dominant form of motion advecting shallow-water organisms. A relevant mechanism for this transfer is the interaction between topography and stratified tidal flow, which generates freely propagating internal waves that regulate the magnitude of vertical transport of certain organisms within the water column (Sentchev & Korotenko, 2003). Inertial oscillations, often resulting from extreme wind events such as storms, operate similarly to tidal processes and have been reported to pump nutrients from below the mixed layer into the euphotic zone, where they can be utilized by phytoplankton, thus altering the grazing activity (Esposito et al., 2023). Persistent winds also influence upwelling and downwelling, which affect nutrient availability, particularly during certain seasons, and are crucial to the coast-wide and regional ecology (Trautman & Walter, 2021).

At the opposite extreme of the spectrum, planetary processes such as those linked to interannual (North Atlantic Oscillation, NAO; El Niño Southern Circulation, ENSO), and decadal (Pacific Decadal Oscillation, PDO) climatic modes also have environmental impacts through alterations in ocean-atmosphere interactions and nutrient and light availability (Daud et al., 2019; Graham et al., 2023; Pineda & López, 2002). For instance, anomalously high temperatures and diminished wind-driven upwelling in the Northeastern Pacific during El Niño events, occurring every two to seven years, have been shown to reduce larval abundance and settlement, potentially resulting in wide-scale ecological disruption (Pineda et al., 2018; Pineda & López, 2002).

The complex environment in which marine organisms reside offers a multitude of pathways and scales that ultimately determine the extent of connection or separation of individuals within and among local populations (Cowen & Sponaugle, 2009). An understanding of the spatial and temporal variability in the exchanges of such individuals is of paramount importance in numerous theoretical and practical applications (Brown et al., 2016). When applied to marine organisms, biological traits and the life history of the species concerned, particularly during the earliest stages of life, are of equal importance (Demmer et al., 2022). These biophysical interactions ultimately determine and regulate population dynamics. The focus of the subsequent Section is on these issues.

1.1.2 The idea and relevance of connectivity and dispersal

Most marine species are distributed in geographically discrete locations across their spatial range (Antell et al., 2020), resulting from the interactions between the biological and ecological characteristics of the species and the spatially diverse marine habitats (Costello & Chaudhary, 2017). The relationships between these habitat units are maintained through the transport of individuals at various life stages, from eggs and larvae to juveniles and adults (Lipcius et al., 2019). Over the years, researchers have employed a variety of key terms to describe these dynamics of populations in the marine environment (Pineda et al., 2007), the most widely used being "dispersal" and "connectivity" (Cowen & Sponaugle, 2009).

In a general sense, dispersal can be defined as the outcome of all processes responsible for the transport (advection) and spread (diffusion) of a cloud of passive particles representing small fluid parcels, small amounts of tracers, or passively drifting individuals (Mayorga-Adame et al., 2022). When applied specifically to the context of marine organisms, dispersal represents the tendency of individuals to move, settle, and ultimately reproduce away from their native habitats and parents, a behavior that influences numerous evolutionary and ecological processes (Monroy et al., 2017). This usage is common in the terrestrial literature, where dispersal is typically described as a probability density function of dispersing individuals versus distance from a source (Pineda et al., 2007). The patterns of linkage or isolation of dispersants are summarized under the concept of connectivity. Connectivity refers to the extent to which passive particle exchange occurs between distinct locations (P. D. Taylor et al., 1993). It may therefore be applied not only to analyze interactions between individuals within a population (Ormerod et al., 2011), but also to estimate heat (Tamsitt et al., 2018) and momentum fluxes (Edson et al., 2013), and exchanges of other suspended particulate matter, including sediments (Najafi et al., 2021) and pollutants (Fifani et al., 2021).

Because of its broad definition and growing relevance, the term "connectivity" has been introduced and applied in a multitude of fields. As such, several interpretations exist, with the main differences between them being the scale of applicability of the study (Kadoya, 2009). In ecological terms, population connectivity is of common usage (Cowen et al., 2007; Cowen & Sponaugle, 2009; Fogarty & Botsford, 2007; Pineda et al., 2007). It refers to the degree to which spatially separated populations are linked by dispersal of individuals that are part of a metapopulation, defined as an ensemble of populations of the same species distributed across habitable areas (Cowen et al., 2007). Demographic connectivity is used to describe the number of dispersers that are exchanged between populations (Kendrick et al., 2017). Genetic connectivity concerns the efficient transfer of gene flow between distant populations (Legrand et al., 2022). Sediment connectivity refers to the degree to which a system controls the transfer of sediment between different landforms or landscape units (Bracken et al., 2015). Such definitions represent only a sample of the multitude of potential usages, with arguably the most relevant being those that link the influence of connectivity processes on ecological function and ecosystem services, a definition that is often referred to as functional connectivity (Hidalgo et al., 2017).

Depending on the magnitude of the environmental phenomena involved and other biological parameters, such as the size of the dispersing agents, diverse spatial differences can be identified in the exchange of individuals. These differences range from very low levels of connectivity between populations, where population structure and size are maintained only through self-recruitment (i.e., closed populations), to high levels of connectivity that occur through large dispersal of larvae between meta-populations (i.e., open populations) (Cowen et al., 2000). It is therefore essential to have detailed knowledge of not only the magnitude, but also the spatio-temporal scales over which connectivity operates, in order to understand the structure of marine populations and their interrelationships (Siegel et al., 2008).

Spatio-temporal scales of connectivity are mediated by the successful exchange of individuals (Gaines et al., 2007). This is particularly relevant for early life stages, when spores, eggs, and developing larvae can be treated, at least to some extent, as passive plankton (Simpson et al., 2013). Examples include most pelagic species, some of which spend their entire lives as plankton (holoplankton) or only their larval stages as plankton (meroplankton and ichthyoplankton) (Ibáñez-Tejero et al., 2019), but also many benthic species, which typically are characterized by a relatively stationary phase (sessile or sedentary juveniles and adults) preceded by a planktonic stage (propagules and larvae) during which dispersal occurs (Legrand et al., 2019). As such, dispersal distances, hence connectivity, is determined by the time that individuals spend in planktonic life stages (D'Aloia et al., 2015), commonly defined as spore or propagule duration, or pelagic larval duration (PLD, hereafter). The duration of this stage varies greatly from species to species, ranging from hours (e.g. giant kelp, with a spore duration of ~30 hours, Reed et al., 2006), to days (e.g. black-faced blenny fish; with a PLD of ~16 days, Schunter et al., 2019), and up to months (e.g. black rockfish, with a PLD of ~6 months, Miller & Shanks, 2004; or rock lobster, with a PLD up to ~18 months, Bradford et al., 2015).

The temporal and spatial scales over which connectivity varies during the pelagic stage rely on the spawning phase (Le Corre et al., 2012), the timing and location of which is in turn determined by multiple external factors, including system hydrodynamics and larval behavior (Shanks, 2009). Certain hydrodynamic conditions may increase larval dispersal distances (e.g., wind-driven surface currents and tides), while others may act to decrease them (e.g., eddies, turbulence). Therefore, it is reasonable to expect variability in connectivity patterns not only among species, but also among regions and time periods of a given study (Le Corre et al., 2012). In this regard, marine populations residing in environmentally sheltered regions may be less susceptible to strong directional advection, implying relatively limited dispersal, which in turn could lead to higher local retention and juvenile survival, and increased population connectivity within the region (Figure 1.2a). In contrast, in exposed environments, where the confluence of tides, wind-driven currents, and small-scale turbulence is present, dispersal may lead to lower individual retention, resulting in lower juvenile survival and reduced population connectivity (Figure 1.2b). By the time individuals reach maturity, they are too large to be influenced by the beneficial or detrimental effects of these environmental parameters and are expected to migrate to their adult habitat by ontogenetic migration.

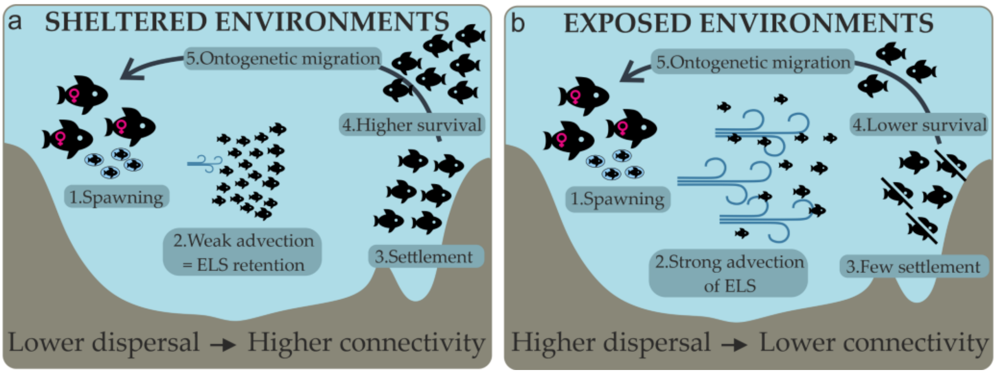


Figure 1.2. Hypothetical linkage between spawning of eggs and adult ontogenetic migrations in sheltered (a) and exposed (b) regions. Sketch adapted from Brown et al. (2016).

Dispersal and connectivity between different sites or populations is of particular relevance in the context of the design of marine protected areas (MPAs), with several studies having already demonstrated the effectiveness of such areas for the long-term conservation of the ecosystem and surrounding fisheries (Batista et al., 2011; Dominique, 2011; Gaines et al., 2010; Marcos et al., 2021). Particularly, defining the MPA optimal size and structure has been shown to directly influence their effectiveness (Muntoni, 2015). This is directly related to the objectives of the definition of an MPA. When designed for ecosystem conservation, MPAs should be large enough to retain a substantial portion of early life stages production (Marcos et al., 2021). If the objective is to optimize fisheries, the dimension of the MPA should be sufficient to increase the density and size of fish populations, and allow a proportion of individuals to spillover beyond their boundaries into surrounding fished areas (Guidetti & Claudet, 2010). If the MPA is designed as a network, individual MPAs should be self-sustaining or adequately connected to other MPAs via larval dispersal (Planes et al., 2009).

Connectivity knowledge can be employed not only to oversee specific marine areas of conservation concern, but also to identify, monitor and regulate marine invasive alien species, i.e., organisms introduced outside their natural range (Assis et al., 2015; Hansen et al., 2024; Schilling et al., 2023). Additionally, understanding the dynamics of species with pelagic planktonic larval phases capable of long-range dispersal via ocean currents may enable the identification of sites suitable for early warning systems (Crivellaro et al., 2022). In many respects, knowledge of dispersal patterns and resulting connectivity estimates is of paramount importance to the management of a given marine ecosystem.

1.1.3 Some notions on the methods to estimate connectivity

As awareness of connectivity as a key component for understanding and managing certain marine populations has emerged, considerable effort has been invested in developing and applying a variety of methods to obtain information on population dynamics (Gaines et al., 2007; Hidalgo et al., 2017). Even so, knowledge of connectivity of specific marine species and specific geographic regions remains scarce (Podda & Porporato, 2023). This is certainly true in the case of the Mediterranean Sea, despite being an ideal location for such studies due to its well-studied oceanographic patterns (Bethoux et al., 1999; Calò et al., 2013; Daskalaki et al., 2022). Yet, the importance of the Mediterranean environment as a biodiversity hotspot (Beca-Carretero et al., 2024) and the cumulative human threats that marine populations continuously face (Micheli et al., 2013), make the connectivity research an urgent endeavor.

In their comprehensive literature review on methods for estimating population connectivity, particularly in the Mediterranean context, Calò et al. (2013) identified genetic techniques, otolith analysis, and modeling tools as the most advanced and commonly used approaches for estimating marine connectivity in the nearshore environment. Estimating population connectivity through genetics requires measuring gene flow (Pascual & Macpherson, 2016), which is often inferred indirectly by analyzing the movement of alleles or genes between populations (Palumbi, 2003), but can also be assessed directly through parentage analyses (Planes et al., 2009), which calculate the probability that a given individual originated from a particular source population or set of parents (Hedgecock et al., 2007). Both approaches rely on molecular markers, such as microsatellites, allozymes, and mitochondrial DNA (Hauser & Ward, 1998; Féral, 2002; Meer et al., 2015), which are powerful tools for identifying genetic differentiation between populations (Ferrari et al., 2023), detecting barriers to gene flow for specific species (Schunter et al., 2011), and estimating the origins and number of migrants of a given population, among others (Deudero et al., 2017). Otolith analysis through morphometrics and microchemistry techniques also provides valuable information on aging, growth, and, by back-calculation, the date of spawning, hatching, and settlement of propagules for certain fish populations (Campana, 1999; Morat et al., 2014).

Yet, knowledge of population connectivity usually requires an understanding of the origins and trajectories of dispersing individuals within local or sub-populations (Cowen et al., 2007; Pineda et al., 2007). Visual tracking is the only direct method available to accomplish this but, mainly for practical reasons, has been less applied to dispersing larvae (Nolasco et al., 2018). Alternatively, advances in computational abilities have led to non-direct estimation progress based on circulation models coupled with Lagrangian particle-based algorithms (van Sebille et al., 2018). Lagrangian connectivity studies involve the analysis of sets of virtual particles representing fluid parcels, tracers, or passively drifting individuals, to identify their pathways, associated timescales and transports between distinct oceanic regions (Rühs, 2018). Classic applications involve forward simulations, where particles virtually released from potential source regions are tracked through simulated currents to their final settlement sites (Torrado et al., 2021). Other techniques include backtracking the particles from the settlement areas by running the particle tracking simulations in reverse (Y. Wang et al., 2019), which yields insights into the origin of specific species and enables the delineation and monitoring of the path's history of established populations (Kwon et al., 2019). The primary objective of both techniques is to estimate dispersal kernels, i.e. the probability distributions of spatial spread (Nathan & Muller-Landau, 2000), which can inform decisions regarding the management of certain populations and geographic regions (D'Aloia et al., 2015).

By now, the study of connectivity with Lagrangian algorithms has been of great benefit for interdisciplinary applications. For instance, it has revealed the impacts of marine currents on certain populations, providing valuable information for ecosystem management (Hariri et al., 2024). It has been utilized to understand the migratory pathways of several marine populations, such as plankton blooms (Ser-Giacomi et al., 2023), bluefin tuna eggs and larvae (P. Mariani et al., 2010), rays and skates (Marandel et al., 2018), marine birds (Schneider, 1991), juvenile turtles (Lalire & Gaspar, 2019), and juvenile sharks (Bonnin et al., 2021), among other specimens (Rodríguez-Díaz & Gómez-Gesteira, 2017). It has been used to assess the accumulation of plastic debris in the Mediterranean (Soto-Navarro et al., 2020) and on the world's shorelines (Lebreton et al., 2019). It has been implemented even to provide rapid and accurate forecasts to minimize damage during maritime emergencies, including the search and rescue of a person lost at sea (Ličer et al., 2020), and the evaluation and management of oil spills, such as the Prestige accident in NW Spain in 2002 (Sotillo et al., 2008), and the Deepwater Horizon oil spill in the Gulf of Mexico in 2010 (Mariano et al., 2011).

The cited examples represent only a selection from a growing array of novel tools, methods, and multidisciplinary approaches that are being applied to provide efficient solutions for marine ecosystem assessment and management (van Sebille et al., 2018). At the same time, several of the cited studies also raise concerns about the methodological challenges facing marine connectivity research. The following Section focuses on these issues.

1.1.4 Methodological challenges

Despite the considerable progress that has been achieved in the development of techniques for studying connectivity in the marine environment, the efforts are still limited by numerous processes related to physical oceanography, ecology (Cowen & Sponaugle, 2009), ocean modeling, marine spatial planning, and even administration and jurisdiction

(Popova et al., 2019). The multitude of available tools is itself a challenge, as it can be laborious to navigate and find the optimal technique for estimating connectivity (Novi et al., 2021). The selection of a methodology introduces further complexities into the development of complex and often expensive research tasks, which usually require sophisticated instrumentation and technology (Hidalgo et al., 2017).

Challenges in understanding population connectivity arise from the difficulty of obtaining direct observations of target individuals and tracking their movements, especially during early developmental stages (Sale & Kritzer, 2003), given their small size and still poorly understood interactions with the physical realm (Darnaude et al., 2022). Its knowledge is further constrained by the frequent inaccessibility to the marine environment (Hidalgo et al., 2017), although the literature suggests that even when accessed, certain population aspects, such as the phenotype-environment mismatch or the specific-species reproductive strategy, are not directly measurable (Pineda et al., 2007). Once accessible, large sample sizes are demanded to achieve high accuracy in inferring population structure using experimental approaches, both genetic and otolith based, which are often constrained by the limited number of individuals available and the associated costs (Deudero et al., 2017; Fumagalli, 2013; Schemmel et al., 2022). However, several genetic studies indicate that even with the most sensitive molecular markers and the largest sample sizes, there may still be small discrepancies in the level of gene flow between populations (Hauser & Ward, 1998; Fumagalli, 2013), and molecular markers, that are highly sensitive to such changes, may not be sufficient to identify populations with minimal degrees of isolation (Hauser & Ward, 1998; Kasapidis & Magoulas, 2008)

Ultimately, this leads to uncertainties in the knowledge of small-scale, biologically dominated processes and information, such as larval taxonomy, community diversity, biomass, and abundance, which are essential for predicting effective dispersal patterns (Ferraro & Failler, 2022). The consequences of these limitations are twofold, as ecological information, especially on the spatio-temporal distribution of spawners (e.g. where, when and how many), is crucial for initializing biophysical coupled models of passive larval modeling and for interpreting their results (Hidalgo et al., 2017). Therefore, most biophysical models are hypothesis-driven and assume poorly known biological parameters, leading to uncertainty in population connectivity estimates (Calò et al., 2018).

The difficulty of quantifying connectivity is particularly acute in the nearshore environment, which is challenging to measure by both experimental and numerical approaches (Siegel et al., 2003). The transition from small spatio-temporal scales within the coastal environment to larger scales offshore requires a balance between fine-scale sampling strategies nearshore and more extensive offshore (Greenberg et al., 2007). Variation across scales of specific processes is also a challenge for modeling efforts, as simultaneous resolution of mesoscale (and even smaller) scales is currently problematic (Werner et al., 2007), despite recent advances in model nesting techniques (e.g., Mogé et al., 2019). Notwithstanding these constraints and the inevitable simplification of the biotic component, numerical models are still optimal tools that provide reliable results to delineate the main patterns of connectivity, with some studies having already demonstrated their high explanatory capacity in reproducing the observed inter-annual recruitment variability (Hidalgo, Rossi, et al., 2019). In particular, the low cost associated with exploring different environmental scenarios provides a valuable tool for assessing population connectivity and its variability across different spatiotemporal scales (B. Jones, 2014).

1.2 Motivation, objectives, and structure of the PhD thesis

From the preceding analysis, it becomes evident that a comprehensive understanding of the dynamics of marine ecosystems, the management of fishery resources to optimize fisheries, the regulation of marine invasive species, as well as the design of marine protected areas, necessitate an in-depth knowledge of dispersal and connectivity. These processes are significantly influenced by oceanographic features, the magnitude of which is usually enhanced in nearshore environments, which normally are highly complex dynamic regions dominated by small-scale turbulence processes, advection and diffusion acting at different spatio-temporal scales.

Certain regions of the Mediterranean, widely recognized as one of the world's most important environmental biodiversity hotspots, provide specific examples of such complexity. Among these, the Alboran Sea and the Adriatic Sea are of particular note. Advances in connectivity and dispersal in these regions, along with guidance on how to integrate this information into management actions, require urgent attention. However, the difficulties encountered in quantifying nearshore connectivity, whether by observational or numerical methods, have led to a lack of understanding of the linkages between the hydrodynamics of those Mediterranean regions and the biological characteristics of the species present there.

Aiming to contribute to a better understanding of these dynamics-of-populations, the objective of this PhD is to provide a picture of the potential patterns of connectivity and dispersal of important population groups at different regional scales in the Mediterranean Sea. It focuses on the two aforementioned relevant regions: (1) the Strait of Gibraltar and the adjacent Alboran Sea, a transition basin between the Mediterranean Sea and the Atlantic Ocean strongly influenced by the Atlantic water flow, and (2): the Adriatic Sea, a semi-enclosed water body characterized by a peculiar topography and a large number of freshwater sources. Lagrangian transport algorithms coupled with results from high-resolution hydrodynamic models implemented in these regions, are the numerical tools applied to the study of application cases of species of interest.

The dissertation is organized as follows:

(I) The present chapter (**Chapter 1**) is divided into two main sections. The first (1.1. State of the art) has thus far presented an overview of the fluid motions responsible for the transport of tracers in the marine environment (1.1), a discussion of the main concepts of population dynamics (1.1.2), and a description of the commonly used methodologies and encountered challenges in the applications of such studies (1.1.3 and 1.1.4). Subsequent section

(1.3. General hydrodynamics of the study regions) describes the hydrodynamic processes occurring within the study areas, whose knowledge is essential for conducting population-dynamics studies.

(II) **Chapter 1** outlines the methodology employed for the study of connectivity in subsequent chapters. It is divided into three main sections. The first part (2.1. Numerical model) provides an overview of the necessary background material about the numerical models used in this thesis. The second part (2.2. Lagrangian particle tracking) examines the basis of Lagrangian particle trajectory calculations. The third part (2.3. Connectivity computation) briefly describes the methodologies employed for the quantification of connectivity.

(III) In **Chapter 3,** a high-resolution circulation model implemented in the regions of the Strait of Gibraltar, Gulf of Cadiz and Alboran Sea, is coupled to a Lagrangian tracking algorithm to gain insight into the sustainability of an appreciated and overexploited resource of the Spanish and Moroccan fisheries, the blackspot seabream (*Pagellus bogaraveo*). Several scenarios consisting of different spatial (depths and sites) and temporal (tidal phase and strength) initial conditions simulating spawning are analyzed to identify the most likely pathways of dispersal.

(IV) In **Chapter 4**, a high-resolution model is coupled to a Lagrangian tracking software to examine the hydrodynamics that regulate connectivity of particles in the Adriatic Sea. Lagrangian particles, representing eggs and larvae with typical biological characteristics of generic marine organisms inhabiting the region, are released throughout the basin at different times during a test year to identify the most likely pathways of individual dispersal.

(V) In **Chapter 5**, the plausible causes of the spreading of the marine invasive alien algae *Rugulopteryx okamurae* in the Strait of Gibraltar is evaluated by revisiting historical current-meter profiles collected in the Strait of Gibraltar. Cross-strait connections are analyzed, and favorable opportunity windows and unfavorable scenarios are provided.

(VI) In **Chapter 6**, the trajectories of the invasive algae *Rugulopteryx okamurae* as vectors of biological pollution are examined, by means of a high-resolution model coupled to a Lagrangian algorithm in the Strait of Gibraltar and adjacent basins. Various scenarios consisting of different temporal initial conditions (tidal phase and strength, and winds) are analyzed to identify the most unfavorable scenarios of particle accumulation in the shorelines.

(VII) **Chapter 7** offers an integrated discussion of the findings presented in previous chapters, presents the directions for future works, and provides a comprehensive overview of the thesis.

1.3 General hydrodynamics of the study regions

Hydrodynamic models applied to studies of connectivity should reach sufficient resolution in coastal areas and resolve at least the mesoscale satisfactorily (Fox-Kemper & Menemenlis, 2008). These processes are essential for connectivity and, therefore, knowledge of the hydrodynamics, circulation patterns, and variability of the interest regions is fundamental to construct numerical models and interpret their outcomes in the interest regions (García-Lafuente, Sanchez-Garrido, et al., 2021).

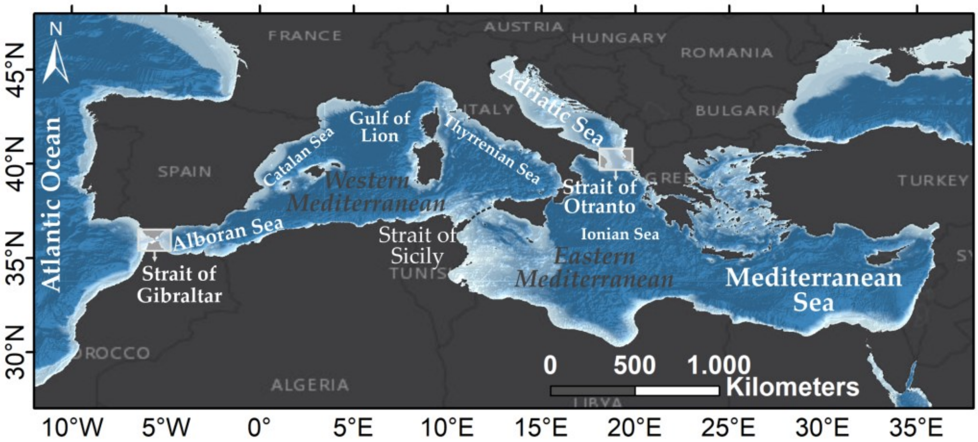


Figure 1.3. Map showing the Mediterranean Sea, the Strait of Sicily dividing the Mediterranean into western and eastern basins, and the two regions of interest, the Alboran and Adriatic Seas, connected to the Mediterranean by the Straits of Gibraltar and Otranto, respectively. Some relevant sites mentioned in the text are also indicated.

This dissertation deals with the dynamics of dispersal and connectivity occurring within two relevant sub-basins of the Mediterranean Sea (Figure 1.3), namely, the Alboran Sea and the Adriatic Sea. A summary of the oceanographic characteristics of both regions follows.

1.3.1 The Alboran Sea

The Alboran Sea is the westernmost basin of the Mediterranean Sea, bounded on the west by the Strait of Gibraltar (SoG, hereafter), and on the east by the north-south line connecting the locations of Almeria and Oran (Sánchez-Garrido & Nadal, 2022). It is the first to receive Atlantic waters flowing through the SoG, of clear interest to the Alboran Sea, for which a preliminary description of its dynamics follows. The SoG is the narrow (~14 km at its narrowest section) and shallow (~300 m at its shallowest section in Camarinal Sill) gateway that separates the Mediterranean Sea from the Atlantic Ocean (Farmer et al., 1988; García Lafuente, Alvarez Fanjul, et al., 2002). The horizontal density gradients drive a two-way exchange with a surface inflow of Atlantic waters and a counterflow of Mediterranean waters beneath (García-Lafuente et al., 2017), which is ultimately forced by the freshwater deficit of the Mediterranean Sea (Bethoux et al., 1999). On average, the volume transport through the Strait is slightly less than 1 Sv in both directions (1 Sv = 10^6 m^3/s, Sammartino et al., 2015).

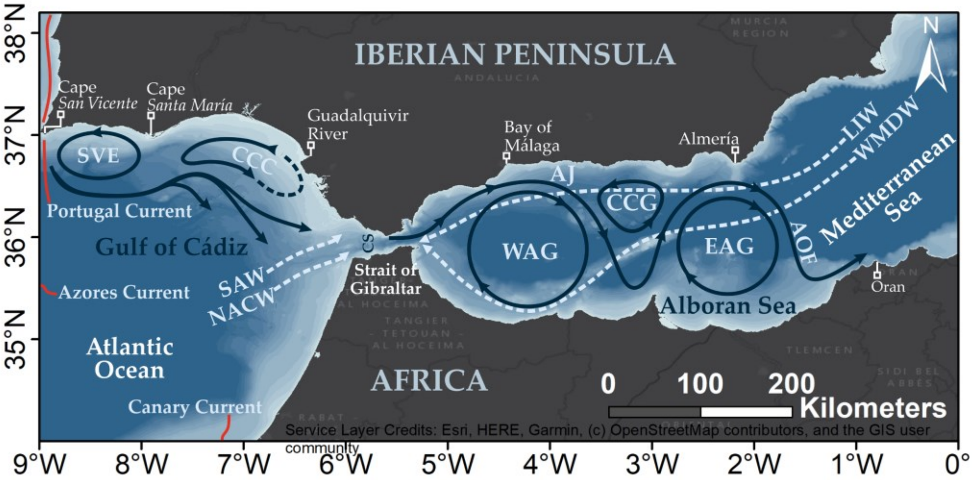
Two water masses contribute to the inflow: the North Atlantic Central Water (NACW), which are mode waters originated at mid-high latitudes of the North Atlantic by isopycnic convection (Soto Navarro, 2012), and the Surface Atlantic Water (SAW), which results from shallow NACW that is modified by atmosphere-ocean interactions (Criado-Aldeanueva et al., 2012). The main water masses of the outflow are the Levantine Intermediate Water (LIW) and the Western Mediterranean Deep Water (WMDW). The LIW is formed in the Eastern Mediterranean (see Figure 1.3) by evaporation and is characterized by a salinity maximum of 38.5 when it reaches the Strait of Gibraltar (Millot, 2013). The WMDW is formed by diapycnal convection in the Gulf of Lion, in the northwestern part of the Western Mediterranean basin (see Figure 1.3) associated to strong winter heat loss and is among the coldest Mediterranean Waters (θ=12.9 °C) (García-Lafuente et al., 2021). Other less common water masses present in the Mediterranean outflow are the Winter Intermediate Water (WIW), formed in the continental shelf of the Catalan Sea (Juza et al., 2013), and the Tyrrhenian Dense Water (TDW), formed mostly by the mixing between WMDW and LIW in the Tyrrhenian Sea (Iacono et al., 2021).

The exchange flow through the SoG is strongly influenced by tides (García-Lafuente et al., 2000), especially in the vicinity of the Camarinal Sill, where the flow direction in either layer, Atlantic and Mediterranean, is periodically reversed. During the ebb tide (high-to-low water), water flows to the east in both layers, while during the flood (low-to-high water), it flows to the west. The eastern exit of the strait, although still subject to tidal modulation, does not undergo a change in direction, maintaining an eastward current (the outflow undergoes a change in direction with the tide). The contrary happens in the western exit, where it is the outflow that tends to keep direction whereas the inflow changes periodically with the tide. The sub-inertial modulation, related to the meteorological forcing (Candela et al., 1989; García Lafuente, Alvarez Fanjul, et al., 2002), also modifies the baroclinic exchange by significant fractions of their average values at few-days' timescale, although it is much less than tidal fluctuations of flows.

The circulation in the uppermost 100-150 m of the Alboran Sea is therefore mainly driven by the Atlantic water, which enters the Alboran Sea from the Strait in the form of a frontal baroclinic jet, the so-called Atlantic Jet (AJ) (Viúdez, 1997), with flow velocities of up to 1 $m \cdot s^{-1}$. In its way eastward, the AJ surrounds two mesoscale anticyclonic and oligotrophic gyres usually present in the basin, the Western and the Eastern Alboran Gyres (WAG and EAG, respectively, see Figure 1.4) (Sánchez-Garrido et al., 2013), the EAG being less common, especially in winter (Renault et al., 2012). Between the WAG and the EAG lies a third mesoscale cyclonic gyre of smaller size (CCG).

Regarding the deeper circulation, the LIW flows towards the Strait close to the Spanish shelf, whereas the WMDW does it along the African coast in the south, possibly conveyed by the bottom topography (García-Lafuente et al., 2017). The accumulation of LIW flow along the north shelf shallows the pycnocline towards the north Alboran Sea and therefore favors nutrient pumping to the photic layer by eventual wind-driven upwelling events. Primary productivity on the north coast is thus enhanced with regards to the African coast. Another source of surface fertilization is the AJ itself, which is locally enriched in its entrance due to strong tidal mixing (Sánchez-Garrido et al., 2015). Local fertilization along the AJ has been also reportedly associated to its ageostrophic frontal dynamics (Oguz et al., 2014). Sub-mesoscale cyclonic eddies released from the Strait and advected by the AJ along its periphery represent another potential source of nutrient supply into the Alboran Sea (Sánchez-Garrido et al., 2015).

The Gulf of Cadiz, situated on the Atlantic side of the Strait of Gibraltar, is the source of the waters of the AJ. Consequently, it is also of evident interest to the Alboran Sea, for which a brief description is provided below.



Service Layer Credits: Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Figure 1.4. Map of the Gulf of Cádiz and Alboran Sea, showing the Strait of Gibraltar, and patching its general circulation: on the Atlantic Side, the Coastal Counter Current (CCC) and the Cape San Vicente gyre (SVE), and on the Mediterranean Side, the Atlantic Jet (AJ), the Western and Eastern Alboran Gyres (WAG and EAG, respectively), the Central Cyclonic Gyre (CCG) and the Almería-Oran front (AOF). The Canary, Azores, and Portuguese currents alluded to in the text flow southward, eastward, and northerly, respectively, in the North part of the Atlantic not shown. For illustration purposes, an imaginary branch representing the course of these currents is shown in red. The most relevant water masses are also displayed, following sketches from Kinder & Bryden (1990).

The Gulf of Cadiz is a sub-basin of the North Atlantic Ocean located west of the Strait of Gibraltar. Its most prominent geographic features in the north are the Capes San Vicente and Santa María (Figure 1.4). The surface circulation patterns on the shelf are wind-driven and characterized by two cyclonic eddies (García-Lafuente et al., 2007). One gyre flanks the western side and extends from Cape San Vicente to Cape Santa María. The other, formed by the Coastal Counter Current (CCC), occupies the eastern shelf from Cape Santa María to the Guadalquivir River (Teles-Machado et al., 2007). These eddies promote the upwelling of nutrient-rich deep waters, creating highly productive zones that are exploited by mesopelagic species (Sánchez-Garrido et al., 2015). The offshore boundary of these eddies is defined by an eastward-flowing branch of the Portuguese-Canary Current. Within the Gulf, part of this current flows towards the Strait of Gibraltar, while another recirculates anticyclonically. The central Gulf is also influenced by the eastern branch of the Azores Current, which feeds into the Portugal Current (Barton, 2001), and by the Canary Current, flowing along the northwestern coast of Africa.

1.3.2 The Adriatic Sea

The Adriatic Sea is a semi-enclosed basin in the northernmost Mediterranean Sea (Figure 1.3, Figure 1.5). The bathymetry is characterized by a strong asymmetry, shallow in the upperpart, gradually deepening towards the middle, and rising sharply to ~1270 meters at the lower part in the Otranto Sill (Cushman-Roisin et al., 2001). It is connected to the Ionian Sea via the Strait of Otranto, a ~75-km-wide and ~800-m-deep channel where different water masses are exchanged (Orlić et al., 1992). The surface flow circulation is generally cyclonic (Russo & Artegiani, 1996). It consists of a northwestward current along the eastern coast, the Eastern Adriatic Current (EAC), composed of Levantine Intermediate Water (LIW) and Ionian Surface Water (ISW), and a fast, coastally confined southeastward current, the Western Adriatic Current (WAC) along the western coast (Figure 1.5).

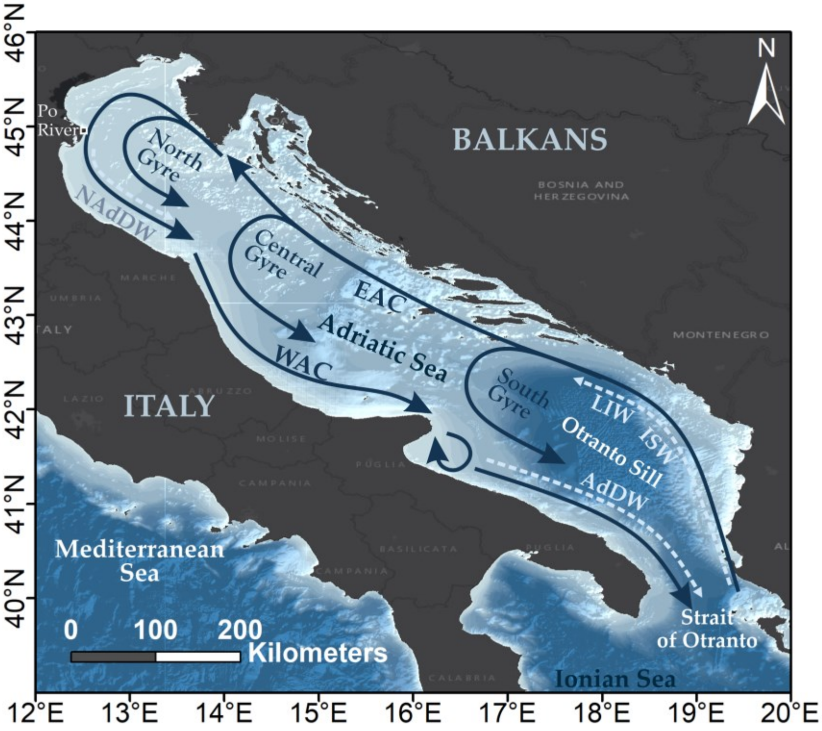


Figure 1.5. Map of the Adriatic Sea sketching its general circulation: the Western and Eastern Adriatic Currents (WAC and EAC, respectively) and the North, Central and South Cyclonic Gyres. The most relevant water masses are displayed, following sketches from Russo & Artegiani (1996). Some of the relevant locations are also displayed.

The WAC exports fresher waters in the surface layer and denser water below it to the Ionian Sea (Figure 1.5). The surface water of the WAC is formed in the northern Adriatic and is principally due to the Po River, whose mouth is located in the northwestern part of the basin and whose mean annual discharge is 1500 m^3/s (Russo & Artegiani, 1996). The bottom portion of the WAC is a density-driven current, consisting of North Adriatic Dense Water (NAdDW) which is formed during winter in the central part of the basin (Malanotte-Rizzoli et al., 1996). Another characteristic dense water, namely Adriatic Deep Water (AdDW), formed by the NAdDW contribution and by the diapycnal convection in the deep Otranto Sill (Vilibić et al., 2012), exits the Adriatic Sea at the bottom, pressed against the continental margin of the western flank of the Strait of Otranto (Russo & Artegiani, 1996).

2 Methodology

2.1 Numerical model

A cardinal element of this thesis is the outcome of general circulation models, intended to represent the time evolution of the velocity field and thermohaline properties (i.e. temperature and salinity) of the water column in a large domain encompassing the regions under study. The purpose of this section is to revise the architecture of the models employed, that will be coupled to the Lagrangian modules for the study of population dynamics in the cited nearshore environments. Specifically, two numerical models used in the following chapters are scrutinized: MITgcm (c.f. Subsection 2.1.3) and SHYFEM (c.f. Subsection 2.1.4). Some notions on the knowledge of general circulation models follow.

2.1.1 Governing equations

In the field of environmental science, a numerical model is frequently described as a tool that employs numerical integration techniques to solve the fundamental governing equations of fluid dynamics (Kowalik & Murty, 1993). The governing equations for a fluid in a rotating system is a set of equations based on the Newton's second law applied to a non-inertial reference system, along with another equation for mass conservation, which for water, a fluid basically incompressible, can be transformed in another for volume conservation. The deduction of these equations, which is a classic topic of geophysical fluid dynamics, is long and somewhat complicated and is out of the scope of this dissertation. They can be found in many textbooks (Cushman-Roisin & Beckers, 2006; Gill, 1982; Kundu et al., 2012; McWilliams, 2006; Stewart, 2009). The equations, using a standard nomenclature, are written here for the sake of a better understanding of the numerical models, which is the objective of this Chapter:

$$\frac{\partial u}{\partial t} - 2\Omega \sin\varphi\, v + u\frac{\partial u}{\partial x} + v\frac{\partial u}{\partial y} + w\frac{\partial u}{\partial z} = -\frac{1}{\rho}\frac{\partial p}{\partial x} + F_x \qquad [2.1]$$

$$\frac{\partial v}{\partial t} + 2\Omega \sin\varphi\, u + u\frac{\partial v}{\partial x} + v\frac{\partial v}{\partial y} + w\frac{\partial v}{\partial z} = -\frac{1}{\rho}\frac{\partial p}{\partial y} + F_y \qquad [2.2]$$

$$\frac{\partial w}{\partial t} + u\frac{\partial w}{\partial x} + v\frac{\partial w}{\partial y} + w\frac{\partial w}{\partial z} = -\frac{1}{\rho}\frac{\partial p}{\partial z} - g + F_z \qquad [2.3]$$

(ρ the density, Ω the rotation rate of earth, φ the latitude, g the acceleration of gravity, u, v and w the velocity components in the x, y and z dimensions, and F_i the components of frictional and any other body force as, for instance, tidal forces derived from the tidal generation potential). Additionally, these equations are complemented by the classical advection-diffusion equation that applies to variables such as temperature [2.4], salinity [2.5], or other biochemical substances (tracers), which are based on conservation laws.

$$\frac{\partial T}{\partial t} + u\frac{\partial T}{\partial x} + v\frac{\partial T}{\partial y} + w\frac{\partial T}{\partial z} = K_H\left(\frac{\partial^2 T}{\partial x^2} + \frac{\partial^2 T}{\partial y^2}\right) + K_Z\frac{\partial^2 T}{\partial z^2} \qquad [2.4]$$

$$\frac{\partial S}{\partial t} + u\frac{\partial S}{\partial x} + v\frac{\partial S}{\partial y} + w\frac{\partial S}{\partial z} = K_H\left(\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2}\right) + K_Z\frac{\partial^2 S}{\partial z^2} \qquad [2.5]$$

(T temperature, S salinity, and K_H and K_z the horizontal and vertical eddy diffusivities, respectively). Again, their deduction is somewhat cumbersome and is not provided here. It can be found in the above-referred textbooks.

2.1.2 General considerations on the setup of ocean models

The configuration of a numerical model for the reproduction of the hydrodynamics of specific regions involves various key steps, which are generally analogous for all models (Oke et al., 2016). These include the generation of a model grid, the preparation and interpolation of bathymetry, initial and boundary conditions, calibration, validation, and verification procedures prior to its application, which in turn are contingent on the region to be simulated. Guidance on model building procedures is widely documented in the environmental modeling community (Griffies & Adcroft, 2008; Kowalik & Murty, 1993; Rahman, 2019; J. J. Williams & Esteves, 2017) and, therefore, a detailed description of the step-by-step instructions is unnecessary. However, general considerations are relevant to the description of the numerical tools used in this thesis, for which an overview description of general setups of ocean models is given below. A scheme of the steps involved is shown in Figure 2.1.

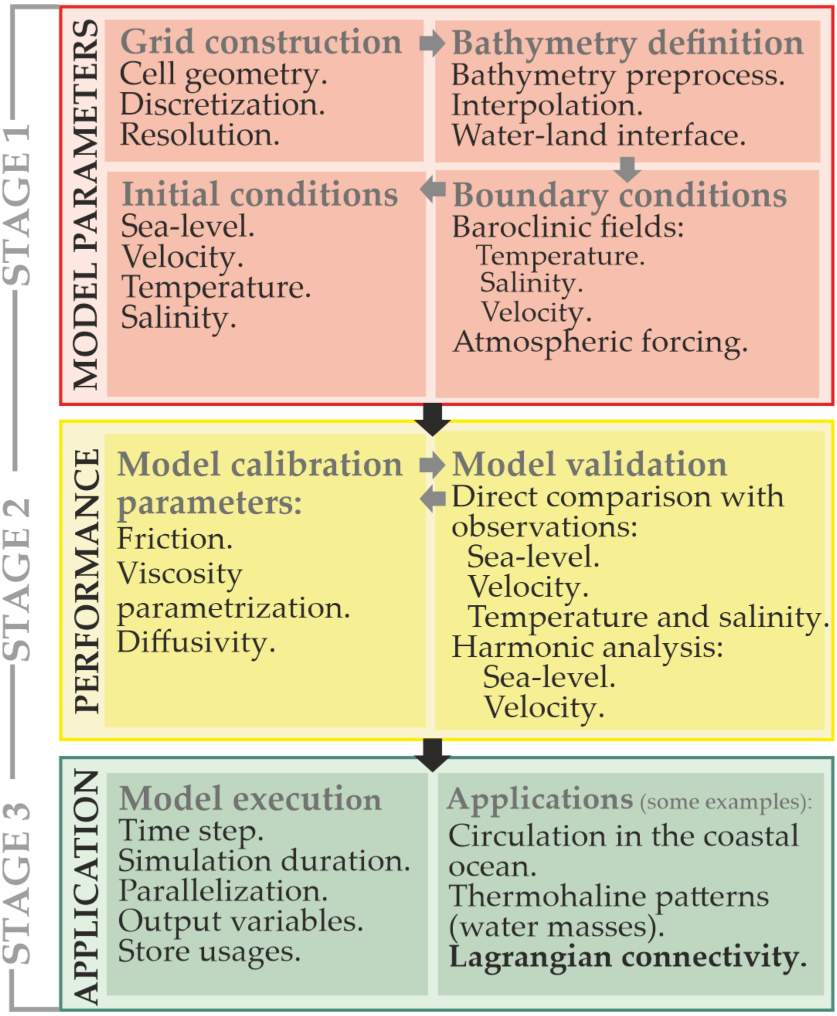


Figure 2.1. Schematic diagram of some of the typical stages required for a hydrodynamic model setup.

With a pre-determined spatial extent, the initial phase of the model construction process involves selecting and configuring the model grid and bathymetry (Stage 1, Figure 2.1). This involves deciding on the cell geometry (i.e. shape and size), the horizontal and vertical resolution, and the discretization of cells (Bomers et al., 2019). Traditionally, structured curvilinear grids have been employed as an effective way of discretizing the model domain to provide a high density of grid points in a particular region (e.g. MITgcm model; Marshall, Hill, et al., 1997). A further prevalent approach is to configure the modeling domain as a flat plane defined by structured Cartesian coordinates, but this often results in a loss of realism, unavoidable due to distortions caused by conformal map projections (Riha, 2017). The restrictions of structured domains are particularly acute when representing nearshore environments with complex geometric features such as main channels, branches, and floodplains. In such cases, the most commonly employed approach is the use of unstructured meshes (e.g. SHYFEM model; Umgiesser et al., 2004), by dividing the model domain into triangles, a process that is relatively straightforward and allows for considerable flexibility in terms of shape (Loseille, 2017). However, they are also associated with lower numerical accuracy (Ventosa-Molina et al., 2017). The advantages and disadvantages of the fully structured and fully unstructured grids have led to a recent combination of the two grid types (e.g. Delft3D Flexible Mesh model; Mogé et al., 2019), although much effort for optimization and improvement still must be done (Bomers et al., 2019).

The use of accurate bathymetry is another critical factor in modeling studies, especially in coastal and shelf sea applications, and efforts must be made to ensure that the best and most recent bathymetric information is used. The selection of the interpolation method (e.g. linear, nearest neighbor, inverse distance weighted, or spline), is of great importance and depends on the data density and the requirements of the model (Amoroso et al., 2023). Initial and boundary conditions are also configured at this stage, including oceanic states at the model boundaries and sea-atmosphere interactions. The approach to forcing the model typically consists of a one-way nesting scheme in which the model variables (e.g. velocity, temperature, salinity) are relaxed at the open boundaries within a buffer region. In general, ocean circulation models do not incorporate tides. There are specific global ocean models developed for the purpose of forecasting the tidal sea surface elevation signal within the ocean, which typically employ sea-surface height (SSH) data derived from satellite altimeters and coastal tide gauges. The output from these global tidal models, which consists of tidal constants (i.e., amplitude and phase for many tidal constituents) throughout the domain, is used to provide tidal forcing to regional ocean circulation models, such as those applied in this memory.

Once the geometry and spatial extent of the model have been configured, calibration and validation are the two major steps in the subsequent stage of model implementation (Stage 2, Figure 2.1). Calibration requires the adjustment of certain model parameters to achieve optimal model performance for specific locations and applications, which typically include bed roughness and friction factors, and horizontal eddy viscosity and diffusivity, among others (Zapata et al., 2019). In this step, sensitivity analyses are commonly performed to test the robustness of the model and to identify errors by finding unexpected relationships between inputs and outputs. Validation, on the other hand, involves running a model with the parameters determined during the calibration process and comparing the predictions with observations, not necessarily used in the calibration process. This is usually done by direct comparison of the observed and simulated variable time series or, for certain nearshore environments, by comparison of the tidal constants derived from observations and model output using standard harmonic analysis (Pawlowicz et al., 2002). A close agreement between model predictions and measurements indicates that the model is both calibrated and valid.

The final crucial stage is the execution and application of the model to study a particular process of interest. At this stage (Stage 3, Figure 2.1), decisions are made regarding the model's computational parameters, such as the time step (i.e., the increment of time simulated in each iteration) and the total simulation duration. Also, the configuration of the output variables to be stored is determined, typically planned ad-hoc for subsequent coupling to Lagrangian algorithms. Given the significant computational resources typically required, these simulations are often run on supercomputers with hundreds of processors located in specialized research centers (Kowalik &

Murty, 1993). In this context, parallelization, which involves dividing a task into smaller sub-tasks that are simultaneously processed across multiple processors, significantly reduces execution time by effectively distributing the workload (Lee et al., 2014). The outcome of simulations is finally represented by the model outputs, which encapsulate the variables representing the hydrodynamic temporal evolution of the studied region.

Numerous applications have been developed for representing such oceanic fluids, many of which utilize three-dimensional numerical models applied to oceans, marginal seas, coastal areas, estuaries, and rivers. Examples of these models include TELEMAC (Galland et al., 1991), DELFT3D (Roelvink & Banning, 1995), MITgcm (Marshall, Hill, et al., 1997), SHYFEM (Umgiesser et al., 2004), OpenFOAM (Nilsson & Page, 2005), ROMS (Shchepetkin & McWilliams, 2005), HYCOM (Chassignet et al., 2009), FVCOM (Wu et al., 2011), ELCOM (Leon et al., 2012), MPIOM (Jungclaus et al., 2013), NEMO (B. Jones, 2014), and SCHISM (Zhang et al., 2016), among many others. It thus seems reasonable to utilize an existing model instead of developing a new modeling system for studying a particular application. In this research, the potential of two hydrodynamic models, MITgcm (Subsection 2.1.3) and SHYFEM (Subsection 2.1.4) to accurately represent the main circulation patterns in the areas under study is explored. A detailed description of each model is provided below.

2.1.3 MITgcm

The first numerical model employed in this thesis is the Massachusetts Institute of Technology General Circulation Model (MITgcm), a flexible tool designed for the study of the atmosphere, ocean and climate (Marshall, Adcroft, et al., 1997; Marshall, Hill, et al., 1997). The model solves the fully non-linear, non-hydrostatic Boussinesq form of the Navier-Stokes equations with a spatial finite-volume discretization on a curvilinear grid (Marshall, Adcroft, et al., 1997; Marshall, Hill, et al., 1997). The model is written in FORTRAN, a language widely used in computational fluid dynamics and is compiled and run on UNIX/LINUX-based systems. Source code can be found on the MITgcm group web site (http://mitgcm.org/).

MITgcm is used by a large global research community with broad applications. For instance, it has been applied to provide an accurate prediction of sea ice in the Arctic (Yuan et al., 2024) and the Nordic Seas (Jensen et al., 2018). It has been employed to gain understanding of certain lake-dynamics (Dorostkar et al., 2022; Safin et al., 2021; Walsh, 2020). It has been applied to analyze extreme heat events occurring on the Red Sea (Sun et al., 2019), to assess mesoscale variability in the Caribbean Sea (Boog et al., 2019), and to study the dynamics of the ocean current-induced in the Green Island (Hsu et al., 2020). Yet, the primary uses for this model involve the examination of regional-to-large scale ocean dynamics. Among these, one of the most relevant and near applications to the region of interest in this thesis is the study of the fluid dynamics of the Mediterranean Sea (Sannino et al., 2009, 2022), and particularly, the Strait of Gibraltar and adjacent basins (Sánchez-Garrido et al., 2011, 2013). The latter application is the one in use in this thesis and the following description is a brief overview.

2.1.3.1 Setup for the Strait of Gibraltar and adjacent basins

The model is implemented on a curvilinear grid that spans the Gulf of Cadiz, starting from 9.4°W, and extends to the eastern limit of the Alboran Sea, at 1.6°E (Figure 2.2). The model's horizontal resolution and vertical discretization are unequal, being highest horizontally in the Strait of Gibraltar and near the surface in the vertical dimension. The bottom topography is derived from four bathymetric sources: (1) the multilayer bathymetric product from the EMODnet Digital Terrain Model (EMODnet Bathymetry Consortium, 2018), (2) the ecocartography campaign developed by the Spanish Ministry of Agriculture, Fisheries and Food between 2000 and 2012 for the Gulf of Cadiz (Gaide et al., 2018), (3) the high-resolution topobathymetric map of the southeastern Spanish continental shelf produced by the Spanish Oceanographic Institute and the General Secretariat of Maritime Fisheries (Acosta Yepes et al., 2006), and (4) the high-resolution coastline of the OpenStreetMap project (OpenStreetMap contributors, 2015).

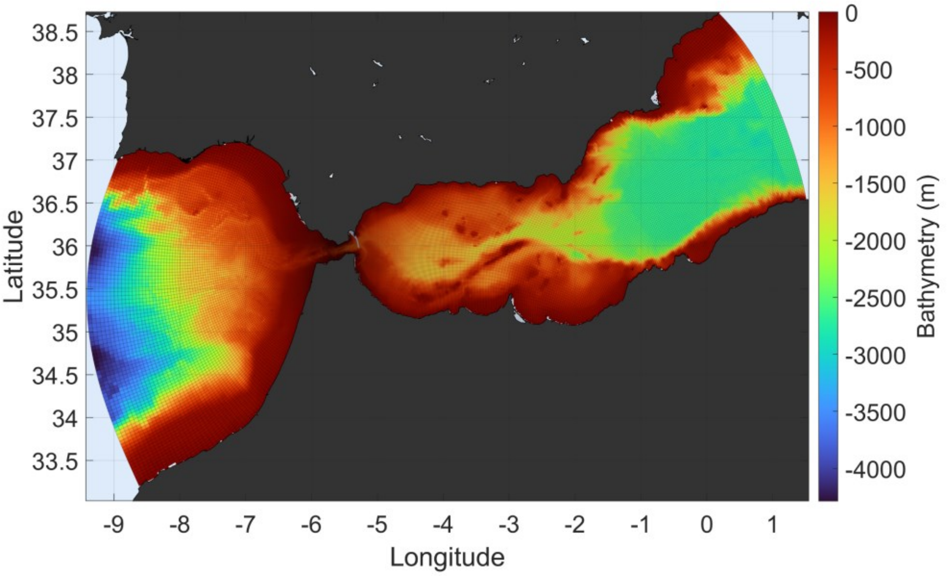


Figure 2.2. Numerical grid and bathymetry of MITgcm application in the Strait of Gibraltar and adjacent basins.

At the two lateral open boundaries (the west - Atlantic Ocean, the east - Western Mediterranean Sea), the hourly baroclinic (density varying) fields of temperature, salinity, and zonal (u) and meridional (v) components of velocity orthogonal to the boundary are imported from the CMEMS-IBI model for simulations up to 2021 (Sotillo et al., 2015), and from the Mediterranean Sea Physics Analysis and Forecast System (CMEMS MED-Currents, EAS6 system; Clementi et al., 2021), for simulations from 2021 onwards. The operational storm surge NIVMAR model (Álvarez-Fanjul et al., 2001) provides meteorologically-driven barotropic (vertically integrated) flows to account for the remote effect of the atmospheric forcing over the Mediterranean basin. These flows are imposed at the two open boundaries by prescribing a vertically homogeneous velocity at the grid cells of the boundary which, integrated over the whole contour, reproduces the barotropic flow from NIVMAR model. In a relatively small region strongly influenced by tidal currents such as the Strait of Gibraltar, tides must be imposed as boundary conditions in the domain contours. A barotropic tidal velocity is prescribed at the same nodes and following the same procedure as before. The barotropic tidal velocity is computed via tidal prediction using the outputs of the MOG2D-G High Resolution barotropic model (Carrère & Lyard, 2003), developed by Legos/CNRS. Tidal constituents employed in the prediction are M_2 (lunar semidiurnal) S_2 (solar semidiurnal), N_2 (lunar elliptical semidiurnal), K_2 (luni-solar declinational semi-diurnal), K_1 (luni-solar diurnal), O_1 (lunar diurnal), P_1 (solar diurnal), and Q_1 (lunar elliptical diurnal). The atmospheric forcing at the sea surface, including wind stress, humidity, air temperature, and shortwave and longwave radiation, is computed using data from atmospheric reanalysis (Hersbach et al., 2023).

Previous applications of the implementation of MITgcm in this area have demonstrated the model's efficacy and reliability, and the results have been published in several high-scored international journals. Examples of such studies are the investigations of the dynamics of the Bay of Algeciras at tidal and subinertial scales (Sammartino, García Lafuente, et al., 2014; Sammartino et al., 2017; Sánchez-Garrido et al., 2014), including a validation of the surface fields using the Lagrangian trajectories of a set of surface drifters released in the Strait area (Sotillo et al., 2016). The MITgcm model is therefore deemed suitable for the study of Lagrangian connectivity. In particular, it will be employed in the following chapters:

(1) In Chapter 3, the prior version of MITgcm is used to simulate the hydrodynamics of the region of interest (Strait of Gibraltar and adjacent basins) from November 2004 to April 2005 to cover the most active spawning months of the modeled species, the blackspot seabream (*Pagellus bogaraveo*).
(2) In Chapter 6, the most recent version of MITgcm is used in a two-level nesting representation to improve its already high performance in simulating the complex hydrodynamics of this area in the year 2021, which could shed light on the causes of the expansion of the seaweed *Rugulopteryx okamurae* across the Strait of Gibraltar and the Alboran Sea.

2.1.4 SHYFEM

The second numerical model employed in this thesis is the Shallow water HYdrodynamic Finite Element Model (SHYFEM), developed by the Institute of Marine Science, CNR, Venice, Italy (Umgiesser et al., 2004). SHYFEM is based on the solution of the primitive equations considering an incompressible fluid and applies hydrostatic and Boussinesq approximations. It runs on an unstructured grid with a staggered horizontal discretization of the Arakawa B-grid type (Bellafiore & Umgiesser, 2010). SHYFEM is particularly well suited for solving the hydrodynamics of domains characterized by complex geometries and bathymetries, such as lagoons, coastal seas, estuaries, and lakes. In such domains, the finite element method allows local refinements of the resolution to achieve finer accuracy in regions where the physical phenomena are more complex, while saving computational resources. The source code can be accessed via the SHYFEM GitHub repository (https://github.com/SHYFEM-model/shyfem), which also contains illustrative examples of model configurations and detailed descriptions of the model development process.

To date, SHYFEM has been successfully applied to simulate hydrodynamics in several areas, including the Mediterranean Sea (S. Mariani et al., 2015), several coastal lagoons (De Pascalis et al., 2012; Ghezzo et al., 2015), the Po River-Delta-Sea system (Maicu et al., 2018), and the Adriatic Sea, where most applications have been developed (Bellafiore & Umgiesser, 2010; Federico et al., 2017; Ferrarin et al., 2016, 2017). The latter region is the subject of Chapter 4 of this thesis, for which a brief description is given below.

2.1.4.1 Setup for the Adriatic Sea

The model is implemented on an unstructured numerical grid that encompasses the Strait of Otranto and the entire Adriatic Sea (Figure 2.3). The horizontal and vertical resolutions are uneven, with the highest resolution occurring near the surface and the shoreline. The numerical grid consists in approximately 110,000 triangular elements with a resolution that varies from a few dozen kilometers in the open sea to a few hundred meters along the coast and tens of meters in the inner lagoon channels. The bathymetry of the Adriatic Sea and its lagoons combines multiple datasets with varying spatial resolutions and measurement methods, all of which utilized the IGM42 reference datum (Ferrarin et al., 2019).

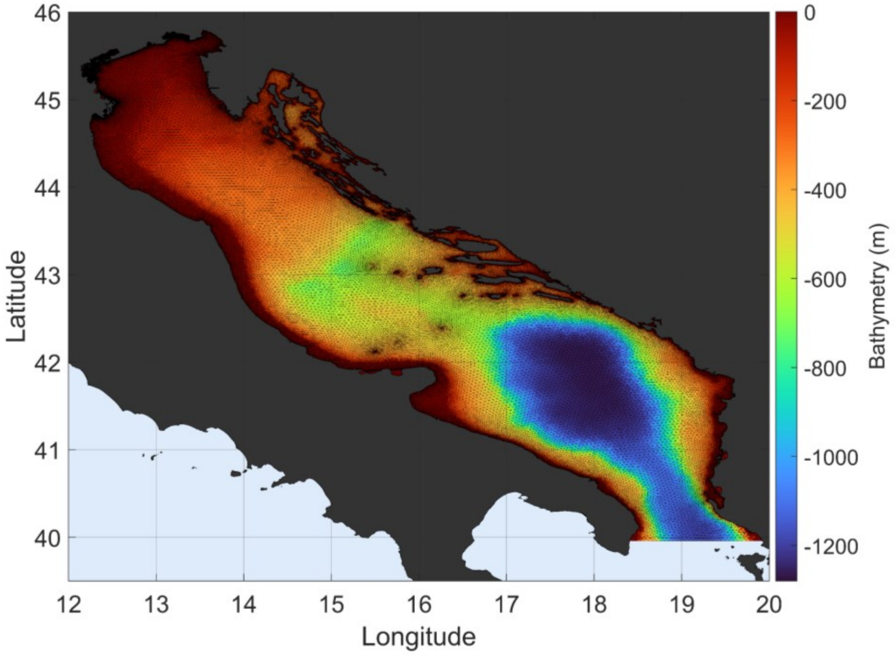


Figure 2.3. Numerical grid and bathymetry of SHYFEM application in the Adriatic Sea.

It considers five boundary conditions, including the sea level, velocity, temperature and salinity at the Strait of Otranto, and freshwater discharges from 17 tributaries (see details in Ferrarin et al., 2019). The sea level and the current velocity conditions are imposed through the hourly tidal signal provided by the FES2012 global tidal model (Carrere et al., 2013). The daily water level, baroclinic velocity, water salinity and temperature are provided by the Mediterranean Forecast System (Tonani et al., 2008), available via the Copernicus Marine Environmental Monitoring Service (http://marine.copernicus.eu/). Daily freshwater discharges at river boundaries are obtained, where available, from automatic hydrometric stations closest to river mouths, through calibrated stages, or from monthly and annual climatological values (Ferrarin et al., 2019 and references therein).

The atmospheric forcing, including pressure and wind, is provided by the ECMWF ERA5 atmospheric reanalysis (Hersbach et al., 2023).

The application of the SHYFEM model to the Adriatic Sea has been validated in previous works, demonstrating the ability to accurately reproduce tidal propagation, storm surge, water flows at the lagoons' inlets, and water temperature and salinity variability (Ferrarin et al., 2008, 2010; Ghezzo et al., 2011; Umgiesser et al., 2004). For this reason, it is further considered to be an appropriate tool for simulating the Lagrangian transport of virtual particles in this region. In particular, the model will be employed in Chapter 4, where the SHYFEM output from 2018 will be utilized to assess the influence of hydrodynamics on connectivity, dispersal, and retention patterns in the Adriatic Sea.

2.2 Lagrangian particle tracking

In terms of particle tracking, there exist basically two approaches for the numerical simulation of dispersing agents, categorized as Eulerian and Lagrangian. In computational fluid dynamics, the Lagrangian particle tracking is commonly defined as a numerical technique for tracing Lagrangian particle paths within a Eulerian frame (Schröder & Schanz, 2023). In essence, the objective of Lagrangian analysis is to describe the fluid motions by tracking the movement of individual fluid parcels based on the particle motion equations (Rühs, 2018). As the particle displaces, it follows a curve in space called the Lagrangian particle trajectory. The velocity of the Lagrangian particle is thus the time derivative of the trajectory position, and must be equal to the local Eulerian velocity at each point crossed in space and time:

$$\frac{\partial \vec{x}}{\partial t} = \vec{v}(\vec{x}, t) \tag{2.6}$$

Where $\vec{v}$ is the vector velocity with components u, v and w in the x, y and z directions, and $\vec{x}$ is the particle coordinate in the three directions. When the nth particle is located at the point $\vec{x}(t) = x$, its position in $t + \Delta t$ can be updated as:

$$\vec{x}(t + \Delta t) = \vec{x}(t) + \vec{v}(\vec{x}(t), t)\Delta t \qquad [2.7]$$

The time integration of the trajectory equation [2.7] can be obtained via explicit or implicit time-stepping, as well as in the form of analytical solutions. The simplest explicit time-stepping method is the so-called Euler method, for which the velocity at a given point of the trajectory in space and time is multiplied by a time step Δt. Better accuracy of the trajectories can be obtained by using higher-order methods for the integration of equation [2.7], such as the 4th order Runge-Kutta scheme, which involves determining the position of a passive tracer by starting from a known initial condition and applying a weighted average of four successive increments between time steps t_n and $t_{n+1} = t_n + \Delta t$. The solution from $\vec{x}_n$to $\vec{x}_{n+1} = \vec{x} + \Delta t$ can therefore be written as:

$$\vec{x}_{n+1} = \vec{x}_n + \frac{1}{6}\,\Delta t(k_1 + 2k_2 + 2k_3 + k_4) \qquad [2.8]$$

where,

$$k_1 = \vec{v}(\vec{x}_n, t_n) \qquad [2.9]$$

$$k_2 = \vec{v}\left(\vec{x}_n + \frac{1}{2}k_1\Delta t, t_n + \frac{1}{2}\Delta t\right) \qquad [2.10]$$

$$k_3 = \vec{v}\left(\vec{x}_n + \frac{1}{2}k_2\Delta t,\ t_n + \frac{1}{2}\Delta t\right) \qquad [2.11]$$

$$k_4 = \vec{v}(\vec{x}_n + k_3\Delta t,\ t_n + \Delta t) \qquad [2.12]$$

and v_j is the velocity delivered at each iteration t_j.

Thus, a simulated Lagrangian trajectory inherently carries information about the displacement, but also about the Lagrangian velocities of a given virtual fluid particle. In addition, it is possible to store salinity and temperature (if simulated) values along the trajectory by interpolating spatially and temporally the respective gridded simulated Eulerian fields onto the particle positions.

2.2.1 Applications

Aiming at describing the flushing patterns in the Bay of Algeciras, Sammartino et al. (2017) employed virtual Lagrangian drifters and a tracking algorithm specifically adapted to the curvilinear grid of the numerical model MITgcm implemented in the region. The three-dimensional velocity field provided by the numerical hydrodynamic model was used to determine the trajectory that a virtual particle at a given horizontal position, depth and time, would follow when subjected to these currents.

In addition, many third-part particle tracking software packages have been developed, each offering unique capabilities tailored to specific scientific needs, ranging from broad ocean circulation studies to focused biological and environmental applications. The packages OceanParcels (Lange & Van Sebille, 2017), and OpenDrift (Dagestad et al., 2018) are amongst the most common applications, which are versatile modules to simulate the transport of diverse type of elements, such as plastics, pollutants, and water parcels. Other models, such as Ichthyop (Lett et al., 2008) or PaTATO (Fredj et al., 2016), are specifically designed for marine propagule dispersal and simulate the transport and behavior of larvae, incorporating biological processes such as vertical migration and mortality. Other tools, such as TrackMPD (Jalón-Rojas et al., 2019), and TRACMASS (Döös et al., 2013), are designed to analyze the transport and transformation of water masses, focusing on pathways and transformations that involve changes in heat and salinity. Finally, models such as Ariane (Muller et al., 2009) and Deft3D-PART (Mogé et al., 2019) are used for general particle tracking in three-dimensional oceanographic contexts, helping to study complex flow patterns and particle dynamics in the marine environment. In this research, the potential of two Lagrangian algorithms to accurately represent the dispersal patterns of certain target individuals under study is explored:

(1) In Chapter 3, the two-dimensional algorithm developed by Sammartino et al. (2017) is utilized as the numerical tool to investigate the hydrodynamics that influence the connectivity of the blackspot

seabream (*Pagellus bogaraveo*), which is an exploited fishery species in both Spanish and Moroccan waters.

(2) In Chapter 4, the software OpenDrift is employed as the numerical tool to examine the hydrodynamics that regulate connectivity in the Adriatic Sea. Lagrangian particles, representing eggs and larvae with typical biological characteristics of generic marine organisms inhabiting the region, are released throughout the basin at different times during a test year to identify the most likely pathways of individual dispersal.

(3) In Chapter 6, OpenDrift is again used to assess the environmental impact of the alien macroalga *Rugulopteryx okamurae* over the Strait of Gibraltar, the Gulf of Cadiz and the Alboran Sea. Particles are released in different scenarios consisting of a combination of environmental conditions.

2.2.1.1 OpenDrift

OpenDrift is an open-source python-based software application developed by the Norwegian Meteorological Institute (Dagestad et al., 2018). It consists of several particle-based sub-models used to predict the transport and destination of different types of objects or substances drifting in the ocean (Dagestad et al., 2018). The sub-models incorporate environmental variables to compute the advection of the seeded particles, including eastward and northward velocities, waves and winds, among other variables, which are loaded as objects called "readers". The basic sub-module, OceanDrift, considers the particles as passive, i.e. the transport is determined by the time the particles spend drifting in the ocean. Bioecological properties such as motility, migration, and birth and death rates are not considered.

Multiple parameters can be configured when running a simulation, including the number and distribution of seeded particles (or drifters), the size and shape of the seeding area, the simulation time step, and the integration method (e.g., Euler or Runge-Kutta), among others. Once all parameters are set and the simulation is run, OpenDrift generates output files in NetCDF format containing information on particle trajectories, including geographic coordinates (latitude and longitude) over time, and environmental properties such as velocities and thermohaline (if simulated) values along the trajectory.

2.3 Connectivity computation

A key quantitative measure of population connectivity is the source distribution matrix, where each cell is the number of particles (p) released from a certain source i (along the vertical axis) and collected in a certain destination j (along the horizontal axis), so $C_{i,j}$ is the probability that an individual or group of individuals of population i will move to population j after a certain tracking time:

$$C(i,j) = \frac{p_j}{p_i} \qquad [2.13]$$

The diagonal cells of this matrix (where $i = j$) represent the local retention, which is the number of individuals that remain in the region where they were originally released, including those individuals that leave and eventually return to their source area (Cowen et al., 2007). Therefore, connectivity ratios (C), ranging from 0 to 1, quantify the strength of connectivity between different sites, with higher (lower) values indicating stronger (weaker) or more (less) favorable connections between subsites. This approach provides only a partial representation of connectivity, neglecting crucial temporal information, such as the identification of areas with different individual retention characteristics over time (e.g. boxes that rapidly disperse, both disperse and recruit, or recruit only). To overcome this limitation, three different approaches are defined:

In Chapter 3, an alternative definition of connectivity is adopted by calculating the maximum percentage of particles collected in each landing area, together with the time at which it occurs, throughout the entire duration of the simulation, which is 60 days, corresponding to the maximum PLD estimated for blackspot seabream (Peleteiro-Alonso et al., 1997):

$$C(i,j) = \max\left(\frac{p_j(t)}{p_i}\right) \quad [2.14]$$

In Chapter 4, a more-recent approach consisting of a "retention clock matrix" is used to track the temporal changes in source-sink connections, where the release event is described as a circular clock that tracks the number of particles (p) over the entire time scale of interest (Defne et al., 2016):

$$C(i,j,t_n) = \frac{p_j(t_n)}{p_i(t_0)} \quad [2.15]$$

In Chapter 6, connectivity is assessed as the probability of algal accumulation for the affected coastlines. To estimate these accumulation rates along the coastal zone, the coastline is divided into 630 segments (n), each ~1000 m long and ~100 m wide. For each simulated period, the accumulation per segment (A_n) and the total accumulation for all segments ($A_T = \sum_1^n A_n$) are obtained. The relative percentage of accumulation for each region is then calculated by dividing the amount of settled particles in each segment by the total accumulation as:

$$\%\mathrm{RA} = \frac{A_n}{A_T} \cdot 100 \quad [2.16]$$

Further details on the development of these methodologies and sensitivity analysis of each quantification measure will be provided in subsequent chapters.

3 Hydrodynamic connectivity and dispersal patterns of a transboundary species (*Pagellus bogaraveo*) in the Strait of Gibraltar and adjacent basins

Nadal, I., Sammartino, S., García-Lafuente, J., Sánchez Garrido, J. C., Gil-Herrera, J., Hidalgo, M., & Hernández, P. (2022). Hydrodynamic connectivity and dispersal patterns of a transboundary species (*Pagellus bogaraveo*) in the Strait of Gibraltar and adjacent basins. *Fisheries Oceanography*, 31(4), 384-401. https://doi.org/10.1111/fog.12583.

Base de datos 2023: JCR/ Factor de Impacto: 1.9/ Cuartil: Q1

Abstract

The blackspot seabream (*Pagellus bogaraveo*) is a benthopelagic fish species highly appreciated by consumers and an important target of the Spanish and Moroccan fisheries in the transcontinental waters of the Strait of Gibraltar area. It is also one of the most exploited resources of the region, which has led to a situation of overexploitation and a notable drop of catches. To gain insight into the sustainability of this resource and certain patterns of the spatial adaptation of the species, a high-resolution circulation model coupled to a Lagrangian tracking module has been employed to investigate the dispersal pathways of blackspot seabream, using eggs and larvae (early-life-stages, ELS) as purely passive particles advected by currents. Several spawning scenarios consisting of different spatial (depths and sites) and temporal (tidal phase and strength) initial conditions have been analyzed to identify the most likely pathways of ELS dispersion. Eastward transport by the Atlantic Jet exiting the Strait of Gibraltar is the most influencing process in that dispersion. Regarding temporal fluctuations, fortnightly tidal modulation is the prevailing factor to determine the horizontal paths of the ELS, spring tides being the cause of the greatest scattering of propagules. Spawning depth in the Strait of Gibraltar is a critical condition, as revealed by the model sensitivity tests. Potential implications of the results of the study

Keywords

Alboran Sea, blackspot seabream, early-life-stages (ELS), hydrodynamic connectivity, pelagic larval duration (PLD), Strait of Gibraltar, transboundary stock

4 Spatio-temporal connectivity and dispersal seasonal patterns in the Adriatic Sea using a retention clock approach

Nadal, I., Picciulin, M., Falcieri, F. M., García-Lafuente, J., Sammartino, S., & Ghezzo, M. (2024) Spatio-temporal connectivity and dispersal seasonal patterns in the Adriatic Sea using a retention clock approach. *Frontiers in Marine Science*, 11:1360077. https://doi.org/10.3389/fmars.2024.1360077.

Base de datos 2023: JCR/ Factor de Impacto: 2.8/ Cuartil: Q1

Abstract

Hydrodynamic features play a key role in determining the dispersal and connectivity of fish populations, especially in highly energetic areas determined by currents, river flow, and meteorologically induced fluctuations. Understanding how species interact with these physical processes is essential for managing vulnerable populations and identifying areas that require effective conservation efforts. This study examines the hydrodynamics that regulate connectivity in the Adriatic Sea, a shallow and semi-enclosed basin that is widely recognized as one of the most important areas in the Mediterranean Sea for protection. A high-resolution hydrodynamic model coupled with a Lagrangian tracking module serves as the numerical tool. Lagrangian particles, representing eggs and larvae with typical biological characteristics of generic marine organisms inhabiting the region, are released throughout the basin at different times during a test year to identify the most likely pathways of individual dispersal. The temporal component of connectivity is highlighted using a previously developed retention clock matrix over different larval durations. Seasonality is a critical factor in dispersal, with greater variability and reduced efficiency in winter compared to summer. The potential implications of the results for improved assessment and management of high value marine species in the basin are discussed.

Keywords

Adriatic Sea, numerical modeling, hydrodynamic connectivity, dispersal patterns, Retention Clock Matrix

5 Could secondary flows have made possible the cross-strait transport and explosive invasion of *Rugulopteryx okamurae* algae in the Strait of Gibraltar?

García-Lafuente, J., **Nadal, I.,** Sammartino, S., Korbee, N., & Figueroa, F. L. (2023). Could secondary flows have made possible the cross-strait transport and explosive invasion of *Rugulopteryx okamurae* algae in the Strait of Gibraltar? *PLOS ONE*, *18*(5), e0285470. https://doi.org/10.1371/journal.pone.0285470.
Base de datos 2023: JCR/ Factor de Impacto: 2.9/ Cuartil: Q1

Abstract

Presently, the Strait of Gibraltar is undergoing an unprecedented invasion of the alien alga *Rugulopteryx okamurae* of North Pacific origin. According to the scarce literature, the algae first settled in the south shore, probably following commercial exchanges with French ports where it was accidentally introduced together with Japanese oysters imported for mariculture. There is no certainty, however, that the algae first colonized the south shore of the Strait and, from there, spread to the north. It could well have been the opposite. Whatever the case, it spread all over the Strait and surrounding areas with amazing rapidity. Human-mediated vectors (algae attached to ship hulls or fishing nets, for example) can be behind the spread from the shore initially settled to the algae-free shore on the opposite side. But it could also have happened by means of hydrodynamic processes without direct human intervention. This possibility is assessed in this paper by revisiting historical current meter profiles collected in the Strait of Gibraltar searching for secondary cross-strait flows. All the stations present an intermediate layer of northward cross-strait velocity near the interface of the mean baroclinic exchange along with a surface layer above of southward velocity, whose lower part also overlaps the interface zone. The first one would back the south-to-north transport of algal fragments, the second one, the north-to south. In both cases, algae must reach the depth of the interface. The vertical velocity field in the area, which far exceeds the small sedimentation velocity of the algae, allows their vertical displacements throughout the water column. Its endurance to survive under the weak or no light conditions that will prevail during the cross-strait transport and its capability of reactivating the metabolism after this unfavorable period, offers chances for colonizing the opposite shore. Therefore, the propagation of the algae by hydrodynamic processes, without human intervention, cannot be ruled out.

Keywords

Strait of Gibraltar, invasive alga, secondary flows, cross-strait velocity

6 Modeling spread of an alien alga under different temporal scenarios in the Strait of Gibraltar and adjacent basins

6.1 Abstract

The expansion of the invasive macroalga *Rugulopteryx okamurae* across the Alboran Sea and northeastern Atlantic since its introduction through the Strait of Gibraltar has been rapid, but the mechanisms by which this successful colonization has occurred have not been fully understood. By using two nested high-resolution hydrodynamic models coupled to a Lagrangian particle tracking algorithm, we tested whether the trajectories of the invasive alga as vectors of biological pollution can be explained by numerical passive dispersal. Virtual tracers, representing free spores, thalli fragments, or detached mats of *Rugulopteryx okamurae* were periodically released in the Strait of Gibraltar during the year 2021. Dispersal simulations indicate that the algal spores first spread eastward before spreading westward, with transport by the Atlantic Jet leaving the Strait of Gibraltar being the most influential process. Tidal strength, followed by winds, is a dominant agent, with spring tides and easterly winds generally promoting higher particle accumulation inside the Alboran basin. The terminal settling velocity of particles is a critical condition, as revealed by a model sensitivity test. The potential utility of numerical tools in elucidating the dispersal dynamics of introduced and expanding species, identifying high-risk areas, and formulating management strategies for these species is discussed.

6.2 Introduction

Marine invasive alien species cause biological pollution and pose a significant threat to the marine environment, potentially leading, in some cases, to a reduction in biodiversity and ecological functionality (Solís-Díaz et al., 2022). Recent concerns regarding bioinvasions (i.e. the successful establishment and spread of alien species) have focused on exotic macroalgae (Mannino et al., 2021; Tsirintanis et al., 2022; van der Loos et al., 2023), whose proliferation affects native community structures and diversity through competitive resource interactions, including light and nutrients (Strong & Dring, 2011). The Mediterranean Sea has become a hotspot for such algal invasions, with several species introduced via diverse pathways, including ballast water discharge, mariculture, and fishing activities (Z. Wang et al., 2022; Fortič et al., 2023). However, the management and control of the introduced species are impeded by the limited understanding of their origins and dispersal mechanisms in the invaded regions.

Among these, *Rugulopteryx okamurae* (Dictyotales, Phaeophyta), an alien macroalga, has been identified as a particularly concerning and hard-to-manage invader in the Mediterranean (EU, 2022). Native to the northwestern Pacific Ocean, the brown alga was first detected in the Mediterranean in 2002 in the coastal lagoon of Thau (southwestern France) (Verlaque et al., 2009). In 2016, a subsequent arrival occurred in the Strait of Gibraltar (SoG) off the coast of Ceuta (Altamirano-Jeschke et al., 2016). Shortly after, thousands of tons of decomposing *R. okamurae* biomass were found along the coasts on both sides of the SoG (Altamirano-Jeschke et al., 2016; Ocaña Vicente et al., 2016) and fishing fleets reported an alarming decline in catches due to the extreme clogging of the alga in their nets (refer to Figure 1 from Báez et al., 2023). In the SoG and surrounding areas, the seaweed has rapidly colonized diverse marine habitats, ranging from shallow to deeper waters (0-40 m depth; García-Gómez et al., 2021), displacing organisms inhabiting soft and rocky seafloors in illuminated and shaded areas (García-Gómez et al., 2018; Estévez et al., 2022), and causing significant alterations to the local biota (Sempere-Valverde et al., 2021; Ferreira-Anta et al., 2023).

Its extraordinarily high connectivity potential, i.e. the effective linkage between the releasing sources and the receiving regions, is facilitated by its dispersal through floating drifting thalli at practically any depth in the water column (Mateo-Ramírez et al., 2023), prolific vegetative production

(Altamirano-Jeschke et al., 2016), survival under adverse environmental conditions, such as low or no light (García-Lafuente et al., 2023; Mateo-Ramírez et al., 2023), and wide thermal variations (Rosas-Guerrero et al., 2021). To date, this has resulted in the continued expansion of *R. okamurae* to a large part of the Atlantic and Mediterranean coastal areas (Figure 6.1b,c,d), including the southern and eastern Iberian Peninsula (García-Gómez et al., 2020; Mateo-Ramírez et al., 2023; Rueda et al., 2023; Terradas-Fernández et al., 2023), northern Africa (Aamri et al., 2018), southeastern France (Ruitton et al., 2021), southern Italy (Bellissimo et al., 2023), southwestern Portugal (Liulea et al., 2023), and the Macaronesia Islands (Faria et al., 2022), where it is causing severe environmental, health, and economic impacts (De la Lama-Calvente et al., 2024).

The impacts and adaptability of *R. okamurae* in the Mediterranean environment have been the subject of extensive research recently (García-Gómez et al., 2018, 2020, 2021; Sempere-Valverde et al., 2021; Mercado et al., 2022; Florido et al., 2023). However, critical aspects such as the processes driving their distribution and the origins of their invasive success still remain to be understood. Muñoz et al. (2019) employed an environmental favorability model to predict the alga's expansion within the Mediterranean, highlighting the Alboran Sea coastlines as particularly conducive environments. Subsequent observations in the northern Alboran partially validated this prediction (Mateo-Ramírez et al., 2023; Rueda et al., 2023), although a detailed distribution and density of the settled populations in the basin remain largely undefined. In a more recent observational study, García-Lafuente et al. (2021) explored the origin of the algal invasion and raised the hypothesis that hydrodynamic processes, in addition to human-mediated vectors (e.g. ballast water and hull fouling from shipping), were partially responsible for its nearly simultaneous appearance on both sides of the SoG. While the well-known two-way exchange in the Strait makes a direct link unlikely, the authors suggest that cross-strait currents at certain depths could be responsible for either the northward or southward algal spread.

Both arguments are candidate processes to be addressed by Lagrangian particle tracking simulations. When coupled with high-resolution numerical models capable of accurately representing circulation features, Lagrangian algorithms are valuable tools for examining the physical processes that affect the dispersal of virtual particles in the marine environment. Dispersing agents in these approaches commonly represent passive target organisms or elements, such as plankton, algae, or debris, whose active mobility is null or negligible when compared to the effect of drift by ocean currents. In particular, numerical results provide significant advantages in invasive species management by identifying potential source locations and paths of marine non-indigenous species, assessing the risk of invasions, and designing early warning systems (Crivellaro et al., 2022). The aim of our study is therefore to employ a Lagrangian tool with virtual tracers representing free spores, thalli fragments, or detached mats of *Rugulopteryx okamurae*, to test whether the trajectories of the invasive alga as vectors of biological pollution can be explained by numerical passive dispersal. The work focuses on the SoG, the location where the macroalga concentrated before its aggressive colonization, and its adjoining basins, the Alboran Sea and the Gulf of Cadiz, which have been significantly affected by the algal invasion so far. An existing numerical model of this region has been refined, particularly in the Strait, to enhance its already high performance in simulating the complex hydrodynamics of this area that could contribute to explain and manage the algal spreading.

The structure of the work is as follows: Section 6.3 provides an overview of relevant circulation features of the regions of study, including a brief literature review of the occurrences of *Rugulopteryx okamurae* in the Mediterranean Sea and northeastern Atlantic since its first detection in the SoG. Section 6.4 describes the hydrodynamic model used to represent the main circulation features, including two subsections on the model domain, initialization, and validation. After assessing its performance, the model results are used to force a Lagrangian particle tracking algorithm, whose simulation details are described in Section 6.5. Section 6.6 presents the results of this work in terms of particle accumulation in shorelines, with subsections examining the accumulation ratios in particular months, the dependence of the terminal settling velocity on the numerical results, and the implications of the model results for species management. Finally, Section 6.7 contains the concluding remarks.

6.3 Relevant hydrodynamic features of the study area

The SoG is the only passage connecting the Atlantic Ocean to the Mediterranean Sea, a semi-enclosed basin where evaporation exceeds precipitation and river runoff (Bethoux, 1979). To compensate for the resulting net buoyancy loss, a two-way exchange occurs therein: lighter Atlantic waters ($S<36.5$), mainly North Atlantic Central Water (NACW), enter the Mediterranean invading the Alboran Sea at the surface (Echevarría et al., 2002), while saltier Mediterranean waters ($S>38.2$), mainly Levantine Intermediate Water (LIW) and Western Mediterranean Deep Water (WMDW), flow towards the Atlantic Ocean underneath (Naranjo et al., 2015). On average, the volume transport is slightly less than 1 Sv in both directions (1 Sv = 10^6 m^3/s).

The mean exchanged flux is subject to variability on different time scales, ranging from tidal to subinertial, seasonal and interannual, modifying its velocity and direction (García Lafuente, Alvarez Fanjul, et al., 2002; García-Lafuente et al., 2000, 2007, 2009). The interaction between tides and topography produces one of the world's most unique internal tides, capable of vertically displacing the interface depth by over 100 meters and inducing substantial temperature and salinity fluctuations at tidal frequencies (Sánchez-Garrido et al., 2011). Also, barotropic flow variability, driven by atmospheric pressure differences between the Atlantic Ocean and Mediterranean Sea, can significantly alter the baroclinic exchange on timescales ranging from a few days to a few weeks (García Lafuente, Alvarez Fanjul, et al., 2002).

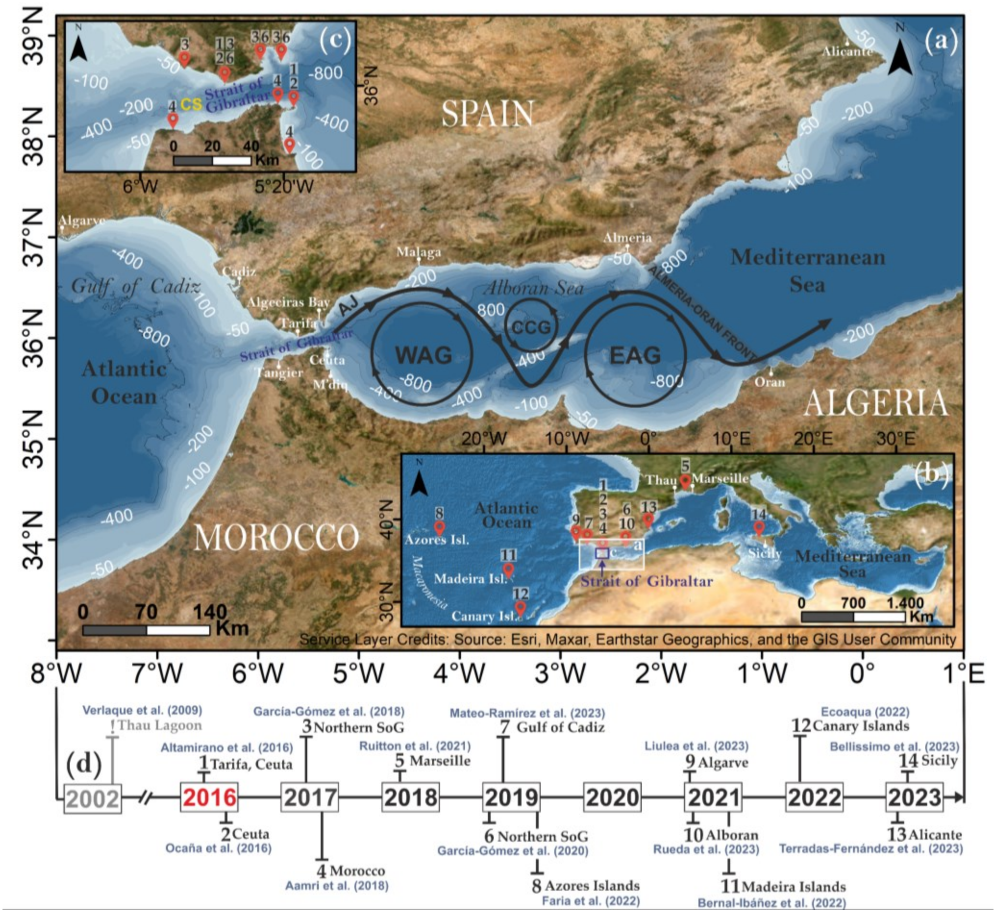


Figure 6.1. (a) Map of the study area showing bathymetric features and outlining its prevailing surface circulation: the Atlantic Jet (AJ), the Western and Eastern Alboran Gyres (WAG, EAG, respectively), and the Central Cyclonic Gyre (CCG). (b) Map of the northeastern Atlantic Ocean and the Mediterranean Sea, highlighting the location of the Alboran Sea (white square) and the SoG (purple square), and spotting records of *Rugulopteryx okamurae* through a sequential number code, where 1 is the first reported detection in the SoG in 2016 and 14 is, to our knowledge, the last reported record to date. (c) Zoomed-in-view of map (b) in the SoG, with a label that indicates the position of the main sill of the Camarinal (CS). (d) Timeline plot of the 14 records of *Rugulopteryx okamurae* spotted in maps (b,c) from the existing scientific literature.

The upper-layer of Atlantic water enters the Alboran Sea through the formation of a swift Atlantic Jet (AJ), which extends over the surface from 0 to 200 m (Figure 6.1a), and features velocities of ~1 m/s (Sánchez-Garrido & Nadal, 2022). In its way eastward, it follows a wavy path around the Western and the Eastern Alboran Gyres (WAG and EAG, respectively; see Figure 6.1a), two mesoscale anticyclonic and oligotrophic gyres typically present in the basin, the EAG being less common, especially in winter (Renault et al., 2012). Between the WAG and the EAG lies a third mesoscale cyclonic gyre of smaller size, referred as the Central Cyclonic Gyre (CCG), which promotes upwelling conditions that enhance primary production in the area (Sánchez-Garrido & Nadal, 2022). The eastern boundary of the Alboran circulation system is marked by the Almería-Oran front, which flanks the eastern side of the EAG (Tintoré et al., 1988; Sanchez-Vidal et al., 2004).

Winds in the Alboran Sea are mainly zonal. Easterly and westerly winds blow with nearly equal magnitude and are equally likely to occur, with slight seasonal variations. The strongest winds in both directions typically occur in winter, while the mildest winds occur in summer, when easterlies are slightly more frequent than westerlies. The overall zonal orientation of the Alboran Sea coastline makes it suitable for wind-driven coastal upwelling to occur on either the northern or southern coast of the basin (Sánchez-Garrido & Nadal, 2022).

6.4 Hydrodynamic model

6.4.1 Model description and initialization

The result of two-nested numerical models, whose code is based on the MIT General Circulation Model (MITgcm hereafter, Marshall, Adcroft, et al., 1997; Marshall, Hill, et al., 1997) have been applied in this study. MITgcm has been previously used to accurately represent the circulation features of this particular region (Sánchez-Garrido et al., 2011, 2013), among other works), and was further employed by Sammartino et al. (2017) in a successful three-level nesting implementation in the Bay of Algeciras (eastern margin of the SoG, see Figure 6.1a). A detailed description of the equations and technical details of the model can be found in the cited works.

The two nested models are formulated on an orthogonal curvilinear Arakawa C-grid with vertical discretization on Z-levels (Figure 6.2). The first nesting layer, referred to as the regional model hereinafter, matches the domain with the previous version of the same model (e.g. Sammartino et al., 2017), albeit at a higher horizontal (~200 instead of ~600 m within the Strait) and vertical (72 instead of 46 Z-levels) resolution. The second layer, referred to as local model, is focused on the SoG and is nested at a 1:5 downscaling ratio relative to the first domain (see insets of Figure 6.2), resulting in a minimum grid spacing of ~45 m, the highest resolution available for modeling the SoG to date. The bottom topography in both domains is derived from four bathymetric sources, namely, the multilayer bathymetric product from the EMODnet Digital Terrain Model (EMODnet Bathymetry Consortium, 2018), the ecocartography campaign developed by the Spanish Ministry of Agriculture, Fisheries and Food between 2000 and 2012 for the Gulf of Cadiz (Gaide et al., 2018), the high-resolution topobathymetric map of the southeastern Spanish continental shelf produced by the Spanish Oceanographic Institute and the General Secretariat of Maritime Fisheries (Acosta Yepes et al., 2006), and the high-resolution coastline of the OpenStreetMap project (OpenStreetMap contributors, 2015).

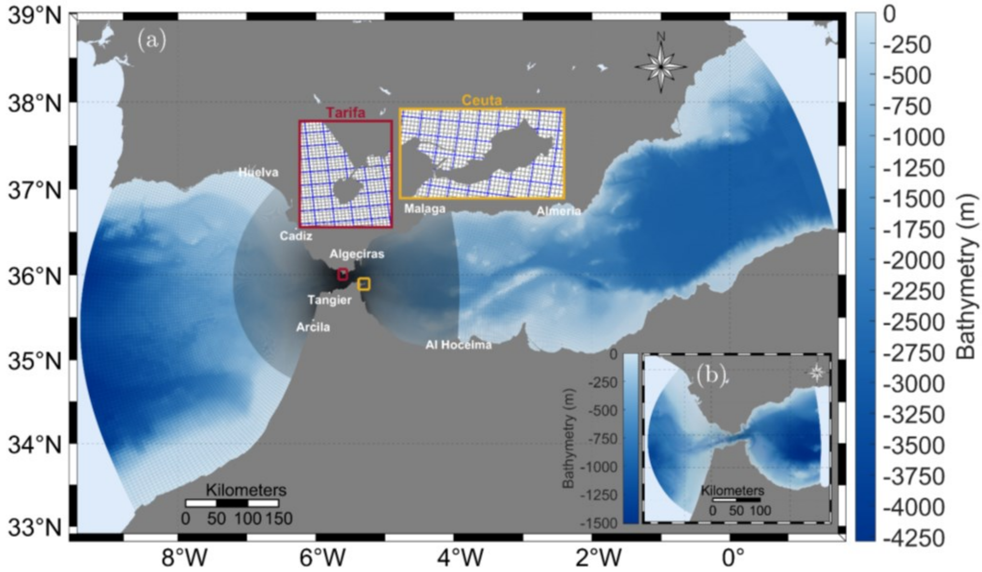


Figure 6.2. Computational grid and bottom topography of the two nested domains, where the regional model (a), of larger extent and less horizontal resolution, embeds the local model (a, b), of less spatial extent and higher horizontal resolution. In the

insets, a zoomed-in view of the outer (blue lines) and inner (grey lines) grids in Tarifa (maroon box) and Ceuta (yellow box) are displayed.

The regional model simulation run from late 2020 to the end of 2021, and it is fed with imposed initial and boundary conditions. The approach is based on a one-way nesting scheme, whereby the model variables at the open boundaries are relaxed within a sponge layer by interpolating the outputs from larger-scale models (Spall & Robinson, 1989). At the two lateral open boundaries, the Mediterranean Sea Physics Analysis and Forecast System (CMEMS MED-Currents, EAS6 system; Clementi et al., 2021) provides the hourly baroclinic (density-varying) fields of temperature, salinity, and zonal (u) and meridional (v) components of velocity. The operational storm surge NIVMAR model (Álvarez-Fanjul et al., 2001) provides meteorologically-driven barotropic velocities to account for the remote effect of the atmospheric forcing over the Mediterranean basin. The MOG2D-G High Resolution barotropic model (Carrère & Lyard, 2003), developed by Legos/CNRS, contributes the tidal harmonics necessary for the calculation of the barotropic tidal velocity forcing, namely, M_2, S_2, N_2, K_2, K_1, O_1, Q_1 and P_1. The atmospheric forcing at the sea surface, including wind stress, humidity, air temperature, and shortwave and longwave radiation, is computed using data from the ECMWF ERA5 atmospheric reanalysis (Hersbach et al., 2023). Conversely, the inner domain simulation is run from March 1 to March 15, 2021, due to the achieved high-resolution and the computational effort required for a longer simulation. The baroclinic fields of the initial and boundary conditions are provided by the lower resolution model results, while the atmospheric forcing from the ECMWF ERA5 atmospheric reanalysis is interpolated to the grid's surface resolution.

6.4.2 Model validation

Previous studies have satisfactorily validated the regional model at tidal and subinertial timescales using diverse observational data sources, including a set of mooring lines deployed in the Algeciras Bay during the SAMPA project (Sammartino, Sánchez-Garrido, et al., 2014; Sánchez-Garrido et al., 2014), and a network of Lagrangian drifting buoys released in the SoG as part of the MEDESS-4MS project (Sotillo et al., 2016). Therefore, revalidation of the regional model output used in this study is not necessary, and only a brief description of the local model performance is provided here. It has been evaluated by directly comparing its current velocity outputs with measured velocities from an Acoustic Doppler Current Profiler (ADCP) deployed at the main sill of Camarinal (CS, ~290 m depth; refer to Figure 6.1c) in years 2020-2021. The dataset was already used by García-Lafuente et al. (2023) to assess the cross-strait transport of *R. okamurae*, and their work should be consulted for details on the experimental setup. Figure 6.3 presents the result of the time-series comparison.

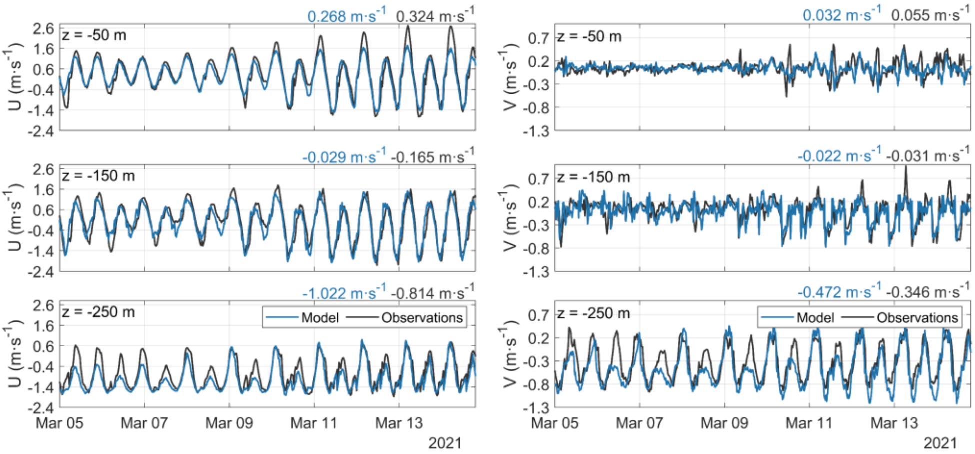


Figure 6.3. Observed (black line) and modeled (blue line) time series of zonal (U) and meridional (V) velocity obtained in the Camarinal Sill (CS) at the representative depths of the Atlantic inflow (50 m), the interface between inflow and outflow (150 m), and the Mediterranean outflow (250 m). Mean values of each time series are shown at the top of each panel in the corresponding color code.

The comparison shows a satisfactory agreement between the model and observations for the three analyzed horizontal layers, although some minor discrepancies must be noted. These mainly concern the differences in the mean value of the time series, which are particularly noticeable in the case of the prevailing zonal component at a depth of 250 m, where the mean modelled velocity exceeds the observed value by 0.2 m·s^{-1}. The discrepancy can be partially attributed to the fine features of the bottom topography, which are not yet accurately represented by the model. Even so, the model hindcast matches well with the amplitude and periodicity of the fluctuations, both at the fortnightly period of the spring-neap tidal cycle and also at the diurnal frequency (diurnal inequality), resulting in correlations of 0.9 and a RMSE below 30 $cm \cdot s^{-1}$ for the zonal component. The meridional component exhibits a more irregular pattern which yields poorer correlation and RMSE values, but still agreeably, at above 0.7 and below 0.2 $m \cdot s^{-1}$, respectively. The results are satisfactory enough to justify the use of the model as a tool for particle advection experiments.

6.5 Lagrangian setup

The particle advection experiments were carried out using OpenDrift (version 1.10.6, Dagestad et al., 2018), an open-source framework designed to simulate the trajectories and fate of objects or substances drifting in the ocean. Particles in this application represented healthy fragments or spores of *Rugulopteryx okamurae*. The algorithm was coupled with the nested MITgcm models which provided the three-dimensional fields of zonal (u), meridional (v), and vertical (w) components of velocity for the year 2021 and March 2021 for the regional and local model, respectively. Supplementary Figure S6.1 displays the monthly averaged surface velocity data provided by the regional model for the simulated months (January to February 2021).

Dispersal simulations were conducted within the first 40 meters of the water column, which is the depth where the macroalga has been most frequently observed (García-Gómez et al., 2018, 2020). To calculate particle trajectories, a fourth order Runge-Kutta integration scheme was utilized, which bilinearly interpolated the simulated eastward (u), northward (v), and upward (w) components of current velocity. Wind drift, expressed as a percentage of the wind speed, is a critical parameter in predicting particle transport. Studies using the OpenDrift model suggest that a 10% wind drift factor yields the most accurate results when comparing predicted trajectories with observations and, therefore, this value was incorporated into the experiments.

Considering the detections of *Rugulopteryx okamurae* spotted in Figure 6.1 and the uncertainty in the precise timing and location of their discharge, the initial experiment assumed a random distribution of 6,000 particles in the SoG from 5.95°W to 5.25°W and from 35.8°N to 36.2°N (Figure 6.4a), released hourly for a 12-hour tidal cycle every six tidal cycles (approximately every 3 days) during the year 2021. Particles were then tracked over a 30-day period, as there is no consensus on the time algae spend freely drifting healthily. The possible combinations added up to 108 different release scenarios, four of which are shown in Figure 6.4b,c where the zonal and meridional components of the winds and sea level at Tarifa, a representative location of the central SoG, are shown for a fraction of the simulated period.

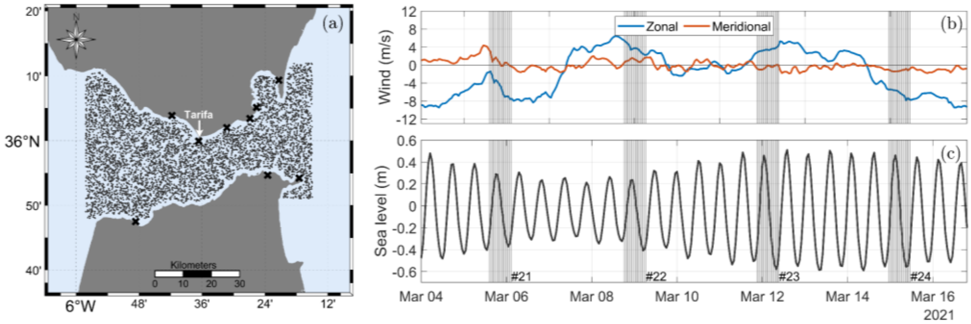


Figure 6.4. (a) Initial positions of particle release in the SoG, with crosses marking the locations where *Rugulopteryx okamurae* has been detected (Figure 6.1). (b) Zonal (blue) and meridional (orange) wind components extracted from the ECMWF ERA5 reanalysis model at Tarifa in a fraction of the month of March 2021. (c) Simulated sea level extracted at the node closest to the Tarifa tide gauge in the same fraction of the month of March. The particle release times are indicated by grey vertical lines, with each group of lines representing a single scenario.

In addition to the spatio-temporal conditions established in the simulations, a sensitivity analysis was conducted on particle buoyancy, as it is anticipated that this factor will influence the distribution of algae. The terminal settling velocity, which is the steady-state vertical velocity due to positive or negative buoyant individual behavior, is typically neglected in particle advection studies, especially in areas where vertical advection by currents is much lower than horizontal advection, such as the area under study, or when simulating positively buoyant elements, as certain macroplastic debris (Lebreton et al., 2019), angiosperm fruits (Pastor et al., 2023), or fish eggs (Nadal et al., 2022). Recent studies on *R. okamurae* sinking have found, nonetheless, non-zero sedimentation velocities (García-Lafuente et al., 2023), ranging from 1 to 4 cm·s^{-1} in experimental conditions and from 1 to 6 cm·s^{-1} in controlled scenarios, for which it is worth testing their influence on model results.

Shorelines are among the areas most affected by the invasion, and it is therefore essential to accurately assess the extent of algal accumulation (Altamirano-Jeschke et al., 2022; García-Gómez et al., 2018, 2020, 2021; Muñoz et al., 2019). To estimate these beaching rates along the coastal zone, the shoreline was divided into 630 segments (n), each ~1000 m in length and ~100 m in width. For each period simulated, the accumulation per segment (A_n) and the total accumulation for all segments ($A_T = \sum_1^n A_n$) were obtained. The accumulation ratios for each region were then calculated by dividing the amount of settled particles in each segment by the total accumulation in all segments as $\frac{A_n}{A_T} \times 100$.

To illustrate the spatial distribution of *Rugulopteryx okamurae* across the studied coastlines and, thereby, differentiate between low and high accumulation zones, the percentiles P20, P40, P60 and P80 were calculated with respect to the maximum accumulation of all segments. These percentiles were then used to determine the accumulation thresholds for identifying minimal (zero values), low (below the 20th percentile), medium-low (between the 20th and 40th percentiles), medium (between the 40th and 60th percentiles), medium-high (between the 60th and 80th percentiles), and high (above the 80th percentile) levels of risk.

6.6 Results and discussion

The spatial distribution of algal accumulation averaged over all simulations for the year 2021 and discretized by the percentile thresholds is shown in Figure 6.5.

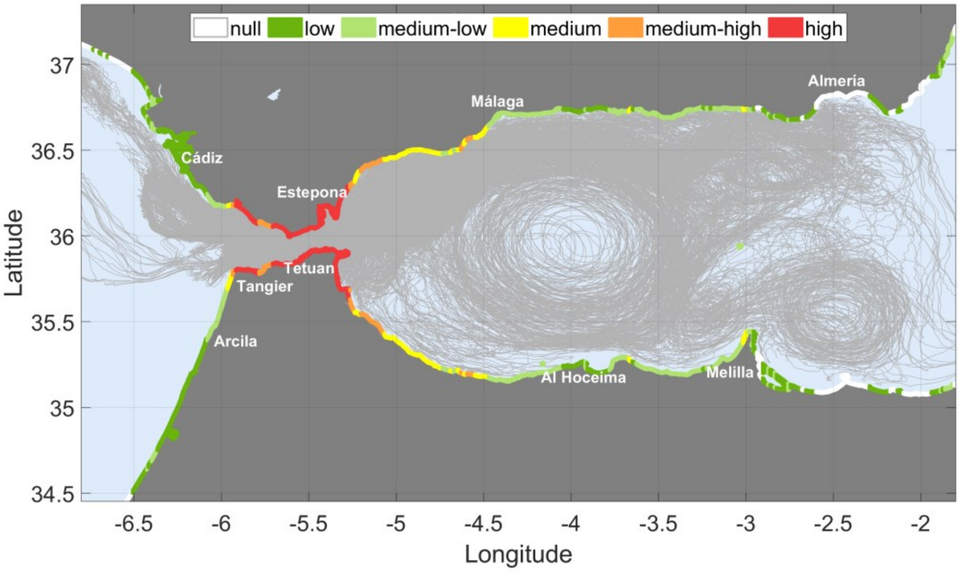


Figure 6.5. Accumulation ratios (A_n/A_T) at the end of the tracking period (30 days) averaged over all the 108 simulations described in section 6.5. The classification "null" corresponds to zero accumulation values; "low" corresponds to accumulation values below P20; "medium-low", between P20 and P40; "medium", between P40 and P60; "medium-high", between P60 and P80; and "high", above P80. A set of particle trajectories extracted from one of the 108 simulations is shown as an example.

The primary spatial pattern that is evident in Figure 6.5 is the role of the eastward-flowing AJ, which is responsible for the almost direct propagation of algal particles from the SoG towards the Alboran Sea, with a markedly reduced transport of particles towards the Atlantic side. As expected, the number of accumulated particles increases in areas most exposed to high dynamic environmental conditions. In particular, the accumulation is highest in the Strait, with an annual mean accumulation of no less than P60, which means that algal particles are registered in these coastlines for at least 60% of the tracked time, a finding that justifies, in the medium to long term, the reported large accumulation of algal biomass in both shores of the SoG (Aamri et al., 2018; García-Gómez et al., 2018; Ocaña Vicente et al., 2016).

Yet inside the Alboran Sea, the map illustrates two clearly defined accumulation zones, identified by the segments with medium (yellow, P40-P60) and medium-high (orange, P60-P80) to high (red, >P80) levels of risk

(Figure 6.5). The first accumulation hotspot is identified in the northwestern Alboran Sea, off the coast of Estepona, whereas the second is in the southwestern Alboran Sea, off Tetuan. The accumulation pattern in the northern zone is again consistent with the AJ flowing into the Alboran Sea, which advects a significant fraction of particles released from the SoG northeastward. Conversely, the accumulation in the southern zone, which stands out from the path of this stream, is attributed to the existence of a small cyclonic eddy between the African coast and the WAG, faintly visible in the background trajectories displayed in Figure 6.5. The central inner region of the Alboran Sea displays an average accumulation value below P40, indicating a low, though not negligible, level of risk in these areas. Conversely, more sheltered areas such as the Gulf of Almería in the north and eastwards Melilla in the south, exhibit the lowest particle accumulation percentages (<P20).

The resulting distribution shown in Figure 6.5 provides insight into the influence of general hydrodynamics on accumulation patterns in the mid- to long-term. The results are consistent with those reported in observational studies (refer to Figure 6.1d), which confirms the predictive capability of the model in preliminarily forecasting the dispersal of the species. It is, however, worth identifying the specific conditions that may lead to lower or higher accumulation on the coasts, as these results may provide valuable information for the early detection and management of the alien algae under these conditions. This can be estimated by directly comparing the total accumulated amounts of virtual algae over time for each release, along with the times at which these accumulations occur on average, with the time series of wind and sea level, as potential causes of accumulation variability. These have been divided into the northern (Iberian Peninsula) and southern (African) coasts, which have shown preliminary indications of high concentrations of particles and variability over time.

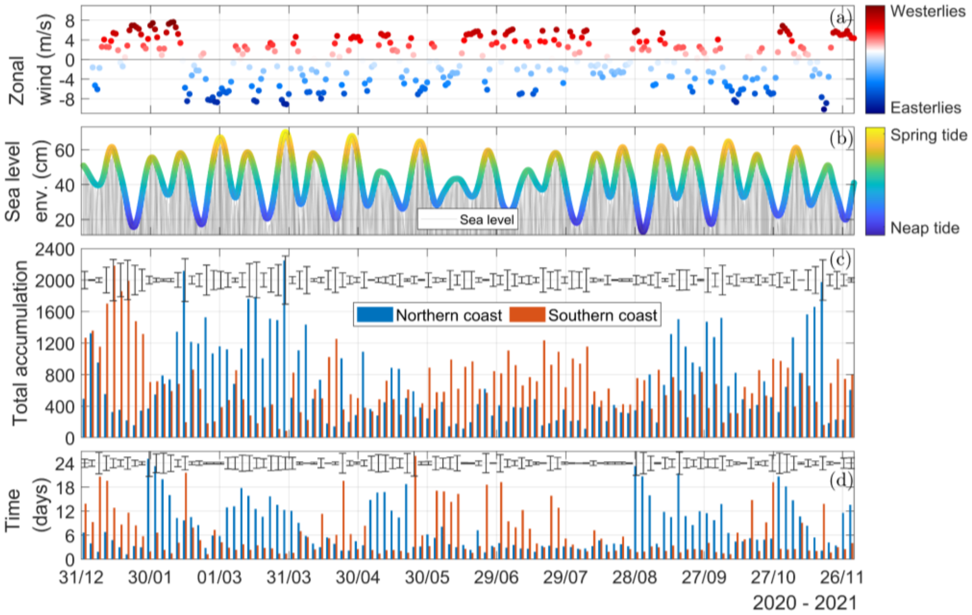


Figure 6.6. (a) Zonal component of the wind (m·s^{-1}) extracted from the ERA5 dataset at Tarifa. (b) Upper envelope of the sea level amplitude extracted from the regional model at the closest node to the Tarifa tide gauge. (c) Total accumulations along with their corresponding standard deviations for the year 2021, for the northern (blue) and southern (orange) coasts. (d) Same as (c) for the times at which accumulations occur on average for the northern (blue) and southern (orange) coasts.

Spring tides in the SoG typically entail increased surface velocities, which might intuitively lead to diminished particle retention in coastal areas. However, Figure 6.6c illustrates that spring tides (yellowish line in Figure 6.6b) actually result in higher particle accumulation on both the northern and southern coast compared to neap tides (bluish line in Figure 6.6b) throughout the year 2021. Specifically, the accounted accumulation is ~8% and ~20% higher in spring than in neap tides for the north and south coasts, respectively. This notable difference can be attributed to the fact that spring tides not only generate stronger currents and inject more energy into the Alboran Sea, but also induce greater variability, which leads to increased particle scattering and consequently increased beaching rates throughout the basin. The difference between tidal conditions is particularly noticeable during the first and last bimester of 2021, when spring tides imply almost 40% more beaching than neap tides. This is likely due to the increase in the amplitude of the spring tidal excursion associated with the increased atmospheric variability during the winter, which is expected to result in a more dispersed pattern across the basin during this period.

The effect of wind on particle accumulation is subtler, but still worth considering. The role of the local coastline orientation appears to be a critical parameter. On the northern coast, strong episodes of easterly winds contribute to a significant increase in accumulation in 2021. This is particularly noticeable in the period from mid-February to mid-April, where the clear dominance of easterlies (on average 5 $m \cdot s^{-1}$ and up to ~9 $m \cdot s^{-1}$) over westerlies (on average 2 $m \cdot s^{-1}$ and up to ~5 $m \cdot s^{-1}$) contributes to a mean particle deposition that is 40% higher on the north coast than on the south coast. On the south coast, however, it is the westerlies that generally cause relatively higher deposition than the easterlies, with only the easterlies in May causing a slight increase in particle stranding. This is particularly noticeable in the period from mid-June to mid-August, when the prolonged dominance of westerlies (on average 4 $m \cdot s^{-1}$ and up to ~8 $m \cdot s^{-1}$) over easterlies (on average 2 $m \cdot s^{-1}$ and up to ~7 $m \cdot s^{-1}$) causes 25% more accumulation in the south than in the north. This can be partially related to the fluctuations in the AJ as a function of wind direction (García Lafuente, Alvarez Fanjul, et al., 2002). In this regard, easterly winds have been demonstrated to diminish the inflow and divert the primary stream towards the north, while westerly winds strengthen the inflow and deflect the flow towards the south (García Lafuente & Delgado, 2004; Sarhan et al., 2000). Consequently, it can be assumed that during easterly (westerly) winds, the AJ leads to higher dispersion and a slight increase in particle accumulation over the northern (southern) coasts.

The main factor accounting for the variability in the times of accumulation Figure 6.6 is the geographic location of the coastlines (north vs. south coast). In the northern coastline, the arrival of particles is faster during spring tides than during neap tides. This phenomenon is attributed to the stronger AJ during spring tides, which is responsible for the direct transport of particles to the northern coasts. It is even further helped by easterly winds, which, as already mentioned, deflect the AJ to the north, thus favoring the fast accumulation of particles in the north. The influence of the mainstream is less discernible on the southern coast, where the main advection mechanism is wind. In this instance, it is the westerly wind that typically drives an AJ deflection to the south, which is the mechanism that presumably causes the fastest times of accumulation under these conditions. Conversely, accumulation on the southern coast is delayed under easterly wind conditions, which favor higher accumulation to the north.

The scenario-averaged values reflect the prevailing role of the main dynamic structures of the SoG-Alboran Sea system on the accumulation patterns, although the large uncertainties associated with these values reveal high variability attributed to the spatial variability of the receiving regions. These issues are addressed next for a particular case study.

6.6.1 March 2021 as a case of study

In addition to the already commented tidal and wind variability inferred from the Figure 6.6, this section addresses an illustrative case to differentiate the impact that diverse environmental conditions have on accumulation ratios at different coastal locations. In particular, it examines the simulated month of March as an example, when the combination of the two prevailing wind components (westerly and easterly) and the fortnightly tidal cycle (spring and neap tide) occur for a fraction of the month (Figure 6.4b,c). Figure 6.7 depicts the outcome of algal accumulation under these four conditions: spring-easterly (a), spring-westerly (b), neap-easterly (c), and neap-westerly (d).

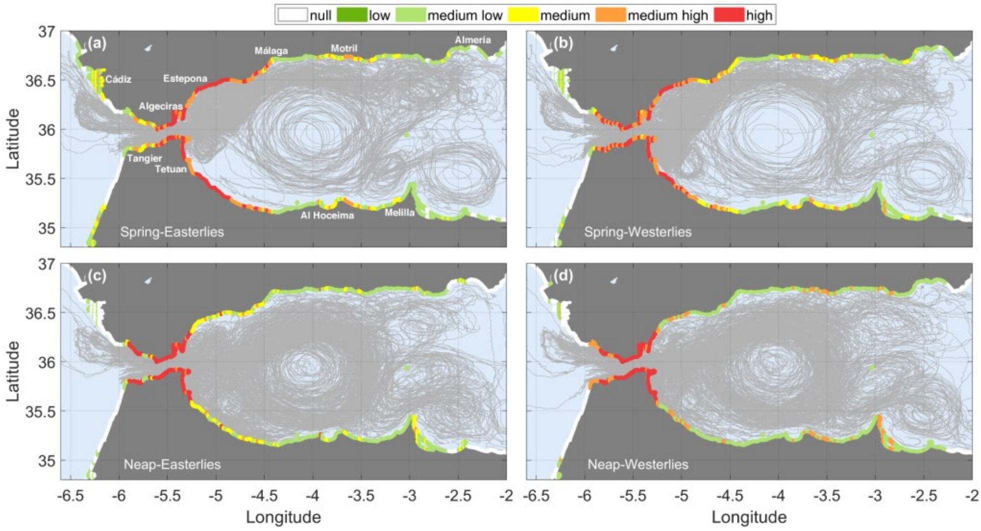


Figure 6.7. Accumulation ratios in the SoG and the Alboran Sea coastlines at the middle of the tracking period (15 days) for the four scenarios illustrated in Figure 6.4: a) an easterly wind during spring tide on March 14, 2021 [#24 in Figure 6.4c], b) a westerly wind during spring tide on March 11, 2021 [#23 in Figure 6.4c], c) an easterly wind during neap tide on March 5, 2021 [#21 in Figure 6.4c], d) a westerly wind during neap tide on March 8, 2021 [#22 in Figure 6.4c]. Particle trajectories are displayed for each scenario. Some relevant locations are displayed in map (a).

The advection of particles is significantly greater during spring (Figure 6.7a,b) than during neap tide (Figure 6.7c,d) due to the higher energy injected into the basing during the former tidal condition. This increased transport is not only apparent in the Alboran Sea, but also within the SoG itself, which reveals greater dispersion and thus lower accumulation of particles during the spring tide (P60-P80 on average) compared to the neap tide (>P80). It is also evident on the Atlantic side, which shows an average low to medium accumulation during spring tide, but low or zero accumulation during neap tide. Upon entering the Alboran Sea, the enhanced advection during spring tides (see trajectories in Figure 6.7a, b), leads to higher scattering throughout the basin, which causes slightly higher accumulation rates along the northern coastlines, as it was preliminarily indicated by Figure 6.6c.

Specifically, accumulation rates are highest (>P80) along the coast of Estepona during easterly winds, extending up with medium-high (P60-P80) values to the bay Malaga. These rates then decrease (P20-P40) towards

Almería, with a notable peak (P60-P80) in Motril. The pattern of accumulation in the northern region is mirrored in the southern region, with high concentrations in Tetuan, followed by a decrease towards Oran, and a peak in Al Hoceima.

During neap tides (Figure 6.7c, d), trajectories reveal a prevalence of gyre circulation, which results in more stable pattern over the entire Alboran Sea. This process is slower and generally results in lower coastal accumulation rates along the coasts. However, certain areas exhibit higher accumulations, which are worthy of note. Coastal regions in proximity to the SoG, such as Estepona and Tetuan, exhibit the most pronounced accumulations, although the values remain below the P40-P60 range observed during spring tides. The least conducive scenario for particle accumulation across both the northern and southern Alboran coasts is provided by the neap-westerly one

Wind plays a secondary role in particle accumulation, and its influence is almost indiscernible from the maps (Figure 6.7). A comprehensive analysis of wind intensity for a given wind direction cannot be accurately achieved using our set of realistic scenarios, due to the concomitant influence of other factors that can mask the potential effects of wind variability, such as tidal strength and tidal phase.

6.6.2 Sinking velocity dependence

The impact of the terminal settling velocity of *Ruguloperyx okamurae* on their distribution throughout the basin was further assessed by conducting additional simulations in which a constant sedimentation velocity of 1, 2, and 3 $cm\cdot s^{-1}$ was applied to the released particles[1]. Although the sedimentation velocities are relatively small, the particles sink at the very beginning of the experiments, with this sinking being generally greater as the imposed

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[1] It is important to clarify that these velocities are lower than those obtained in laboratory experiments (García-Lafuente et al., 2023) and should not be considered a realistic representation of the *Rugulopteryx okamurae* sedimentation behavior, but rather an approximation of the possible evolution of particles in the vertical dimension.

sedimentation velocity increases. As a result, some of the particles, especially those released in shallow areas, remain in the same place where they were released because they are stuck to the seafloor. This is particularly evident in the case of 3 cm·s^{-1}, where nearly 20% of the total particles sink to the bottom within a few instants after release, while in the 1 cm·s^{-1} and 2 cm·s^{-1} scenarios, only the 8% and 15% of total particles sink, respectively.

The key point to note is that nearly 7% of the total released particles were able to sink, and if vertical flow velocity or bathymetry permitted, rise to the upper layers. An illustrative example of this is shown by the trajectories in Figure 6.8, released under the three settling velocity scenarios.

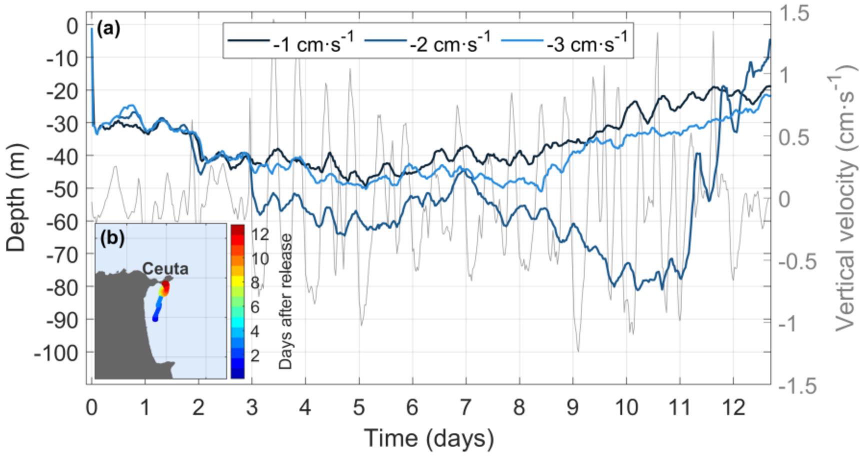

Figure 6.8. (a) Depth time-series of a particle released at surface with a sedimentation velocity of 1 (dark blue), 2 (blue) and 3 (light blue) cm·s^{-1}, superimposed on the vertical velocities encountered by the 2 cm·s^{-1} particle during the first 15 days after the release. (b) Particle trajectory from the 2 cm-s^{-1} sedimentation velocity simulation. The trajectories followed by the 1 cm·s^{-1} and 3 cm·s^{-1} particles diverge only slightly from the 2 cm·s^{-1} trajectories, and are not shown for clarity.

Figure 6.8 demonstrates that the initial settling velocity of the particles exerts a significant influence on their trajectories and ultimate fate within the short to mid-term. This is apparent in the similar dispersion patterns of particles with initial velocities of 1 cm·s^{-1} and 3 cm·s^{-1}, but different from those with an initial velocity of 2 cm·s^{-1}. For instance, particles with 1 cm·s^{-1} and 3 cm·s^{-1} show an initial sinking, after which the particles gradually rise to the surface with little vertical fluctuations, whereas the trajectory of particles with an initial velocity of 2 cm·s^{-1} shows significant vertical displacements before finally rising to the surface and settling. In both instances, the upwelling is facilitated by the proximity of the trajectories to the continental shelf off the coast of Ceuta, although it is also enhanced by the notable vertical fluctuations of the current in this location. In the case of 2 cm·s^{-1}, the algae would be transported to the area in question after spending several days in low-light or no-light conditions. The success of colonization in the settled environment would thus depend on whether the algae arrive in good reproductive condition after this period.

6.6.3 Implications of the results for invasion management

The results have demonstrated the usefulness of numerical models in elucidating the spread of a non-native and range-expanding species in response to changing environmental conditions. In particular, the model has facilitated the identification of high-risk areas, which, when combined with information about biological traits, may incentivate targeted monitoring, early detection, and management strategies for such species under certain favorable conditions.

For instance, the confluence of spring tides and easterly winds results in elevated and accelerated rates of accumulation along the northern Alboran coast, according to the present study (Figure 6.7a, b). It is particularly true in the vicinity of the SoG, and the expectable beaching risk should be considered for early action in the affected coastal regions. It is interesting to note that the scenario depicted in Figure 6.8c is consistent with the massive beaching that took place in the Algeciras Bay shores on that date reported by a local newspaper (https://www.europasur.es/algeciras/alga-invasora-cubre-nuevo-Getares-Algeciras_3_1554174568.html accessed 01 June 2024). As a matter of fact, easterlies have been repeatedly reported by the newspapers as a wind associated with important beaching events, an association that is corroborated by the model results, providing reliability to this study. The most favorable scenario for no coastal beaching, on the other hand, is neap tides occurring simultaneously with westerly winds, which have shown the lesser extent of accumulation on the coasts (Figure 6.7c,d). However, this situation leaves a good proportion of algal particles freely drifting in the Alboran area, which can have consequences in the fishing sector.

6.7 Final remarks

Since its initial detection on the coast of the SoG in 2015, the exotic brown alga *Rugulopteryx okamurae* has spread explosively over a large part of the Atlantic and Mediterranean coasts, producing severe impacts on previously established benthic communities, and causing massive accumulations along the shorelines, affecting fisheries and tourism. The impact and adaptability of the algae in the Mediterranean environment has recently been the subject of extensive research, but crucial aspects of the invasion, including its distribution and the underlying causes of its success, still remain unknown. To gain insight into the spreading and establishment of the species, two nested high-resolution and three-dimensional hydrodynamic models coupled with a Lagrangian particle tracking algorithm have been used, with virtual tracers representing free spores, thalli fragments or detached mats of *Rugulopteryx okamurae*.

The work has focused on the SoG and its adjacent basins, the Gulf of Cadiz and the Alboran Sea, which have been significantly affected by the algal invasion. The hindcast of the passive spreading of the algae in 2021 indicated a mainly eastward direction, with transport by the AJ entering the Alboran Sea being the most influential physical mechanism. Tides near the SoG are an influential process. The variability due to tidal forcing is particularly noticeable in terms of fortnightly modulation and gives rise to two different outputs: Spring tides tend to favor accumulation by direct advection promoted by the increased energy of the currents. On the contrary, neap tides favor a higher dispersal pattern over the whole Alboran Sea, with consequently slower and generally lower coastal accumulation rates along the coasts. Wind plays a minor role in particle accumulation, although its influence is still not negligible. The role of the local coastline orientation seems to be a critical parameter: on the north coast, easterly winds contribute to a slight increase in particles, whereas on the south coast, it is the westerly winds that generally cause a relatively higher accumulation compared to the easterly winds. This has been related to the variability of the Atlantic inflow and its own jet as a function of wind direction.

The interpretation and implications of the results presented in this study are valuable for different stakeholders, as it provides insights into the invasion pathways, high risk areas, and managing guidance. Further research is required to ascertain the role of other important biological traits not included in this study, which may help decision-makers to establish effective management strategies. Overall, improving our knowledge on the interaction of this species with its physical environment is a key issue in the efforts towards preventing and managing the invasion, preserving the integrity of ecosystems and minimizing the ecological and economic impacts. This would not only benefit the control of *Rugulopteryx okamurae*, but also serve as a valuable framework for managing the introduction of future invasive species through the Strait of Gibraltar, ultimately minimizing the ecological damage that these introduced species may cause.

6.8 Supplementary material

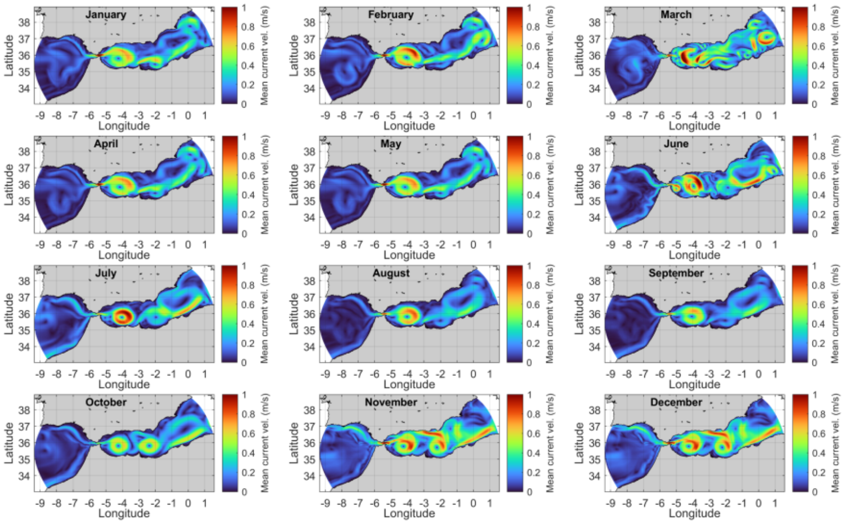

Figure S6.1. Monthly averages of surface velocity data for the year 2021.

7 Integrated discussion and conclusion

7.1 Thesis synthesis: patterns of connectivity

Two themes have recurrently emerged throughout this thesis. First, oceanographic features play a significant role in shaping population connectivity and dispersal, especially in highly dynamic environments influenced by tidal and wind-driven currents, such as the regions under study. Second, Lagrangian particle tracking has proven to be a valuable and effective technique among the available methods for investigating these complex dynamics. This research has specifically evaluated connectivity and dispersal patterns for populations or population groups in the Alboran and Adriatic Seas. A notable focus has been put on coastal fish populations, including the blackspot seabream population in the Alboran Sea (Chapter 3) and an analysis of key egg and larval fish groups in the Adriatic (Chapter 4). This has been mainly motivated by two main factors: the vulnerability of these species to overfishing, and their crucial role in maintaining the ecological balance of coastal ecosystems. Another major topic addressed in this thesis is the identification of alien species transfer, highlighted by the recent and concerning case of *Rugulopteryx okamurae* in the Strait of Gibraltar (Chapters 5 and 6). Analyzing the findings presented thus far allows for the identification of general connectivity patterns for each region. A summary of these patterns follows.

7.1.1 Alboran Sea

Figure 7.1 depicts some general connectivity patterns of the Strait of Gibraltar and Alboran Sea system interpreted in Chapter 3. From a hydrodynamic perspective, the mean circulation patterns favor the zonal (west-to-east) connectivity: the northern coast of the Strait is well-connected to the northern margin of the Alboran Sea, as a result of the direct connection between the AJ and the northern edge of the WAG, whereas the southern coast of the Strait, diverging from the mainstream, is connected to the southern margin of the Alboran basin.

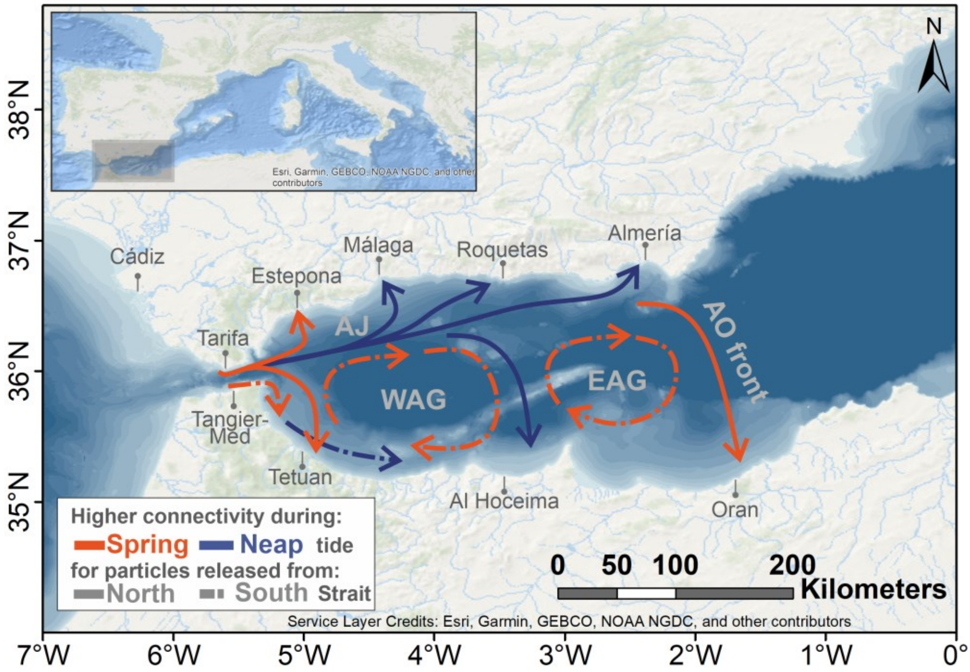

Figure 7.1. Sketch of the main connectivity patterns of particles released from the northern (solid line) and southern (dashed line) Strait under conditions of spring (orange) and neap (blue) tide, based on the information described in Chapter 3.

Dispersal patterns are contingent upon tidal conditions, the tidal strength being more influential than tidal phase. Spreading of particles released from the northern Strait is typically enhanced by spring tides, which facilitate that particles reach nearer coastal areas directly (Figure 7.1, solid lines). This pattern is demonstrated in the case of the study of the Tarifa box and the Estepona and Malaga landings on the north coast in Chapter 3 (see Figure 3.8) and, interestingly, is further confirmed by the patterns of algal accumulation observed in Chapter 6 (Figure 6.7a,b), which shows the highest accumulation in Estepona during the spring tide. The remaining northern coast of Alboran is more efficiently connected under neap tides, which facilitate a steadier and slower dispersal pattern, and result in a greater distance reached by particles, as displayed in Chapters 3 and 6, respectively.

Upon reaching its eastern edge, the WAG bifurcates into two main paths. Most part flows eastwards, feeding the rest of the structures of the basin (the EAG and the Almeria-Oran front), whereas another part flows southwards closing the gyre and veering westwards. Eastward connectivity is enhanced under spring tides, while southward is mostly fostered by neap tides. During spring tides, the greater spread of the AJ at its exit facilitates the formation of a southern coastal gyre, which directly feeds the southern coast and gives rise to a much faster and more efficient connection of the northern Strait to the African coast. Conversely, during neap tides, the prevailing direction of particle movement along the southern coast is westward. In both scenarios, the time required for particles to be received from the northern Strait and distributed throughout the southern Alboran region is considerable, as particles arrive after completing at least one WAG turn around.

Conversely, the primary mechanism affecting particles released from the southern margin of the Strait (Figure 7.1, dashed lines) is the incorporation into a coastal gyre that forms at the far southern exit of the Strait, off Tetuan. Then, almost independently of the tidal modulation, the particles are quickly swept southward to flow along the African coast with a more eastward connectivity. When the coastal gyre is wide and strong, as is the case during spring tides, there is a greater likelihood that a significant fraction will break off and flow northeastwards as part of the WAG pathway. This allows particles initially destined for the African coast to be dispersed along the northern coast, favoring delayed south-north connectivity. This is observed in Chapter 3 and is further supported by the slightly increased accumulation ratios observed on the northern coast during spring tides in Figure 6.7a,b, compared to the lower accumulation observed in this area during the neap tide.

Although the scheme is generally applicable to most situations, it is important to note that depth and subinertial variability, particularly of meteorological nature, can significantly impact the outcome. For instance, in a hypothetical scenario where the release occurs at a greater depth in the Strait of Gibraltar, below the interface between the upper Atlantic and the lower Mediterranean layers, the mean circulation would favor east-to-west connectivity, as revealed by the sensitivity analysis. In this context, another point of interest is the existence of sustained periods of enlarged cross-strait velocity near the interface between Atlantic and Mediterranean waters, that provides opportunities for connectivity not only in the along-strait direction, but also in a cross-strait (north-to-south/south-to-north) scenario.

This possibility, though remote, was considered in Chapter 5 for *Rugulopteryx okamurae* in an attempt to determine the potential origin pathways of the alien algae in the strait and the probable reason for this spread from the initially settled shore to the algae-free shore on the opposite side. The mechanisms responsible for the spread of algae are likely to be multiple and varied. The most plausible of these is linked to human-mediated vectors, with algae attached to ship hulls or fishing nets representing a significant risk. An alternative hypothesis, however, is that the algae managed to cross the SoG taking advantage of hydrodynamic processes without human intervention. Meteorologically induced fluctuations are key processes in that possibility. Northward flow within the intermediate layer would increase under high pressure over the western Mediterranean basin and local winds from the southwest. If these specific conditions occur during neap tides, optimal conditions for south-to-north connectivity would be generated. The north-to-south connection is less achievable, as it would be conversely favored in either the upper or deeper layer, where the strong zonal currents would impede the meridional connection. These patterns are consistent again with the connectivity patterns observed for the blackspot seabream (Chapter 3) and the alien alga (Chapter 6) which, being released in the upper layer of that exchange, exhibit a significant eastward advection of particles, with only a few particles (i.e. those released below the interface in Chapter 3 or those that hypothetically reached that depth by their own means in Chapter 5) being displaced in the westward direction. In both applications, it cannot be excluded that particles may be transported from one shore to another across the interface, which interestingly could potentially give rise to patterns of connectivity that are at first glance unexpected in both cases.

7.1.2 Adriatic Sea

As in the previous region, some general connectivity patterns can be extracted from the analysis of population dynamics in the Adriatic Sea discussed in Chapter 4. These are displayed in Figure 7.2.

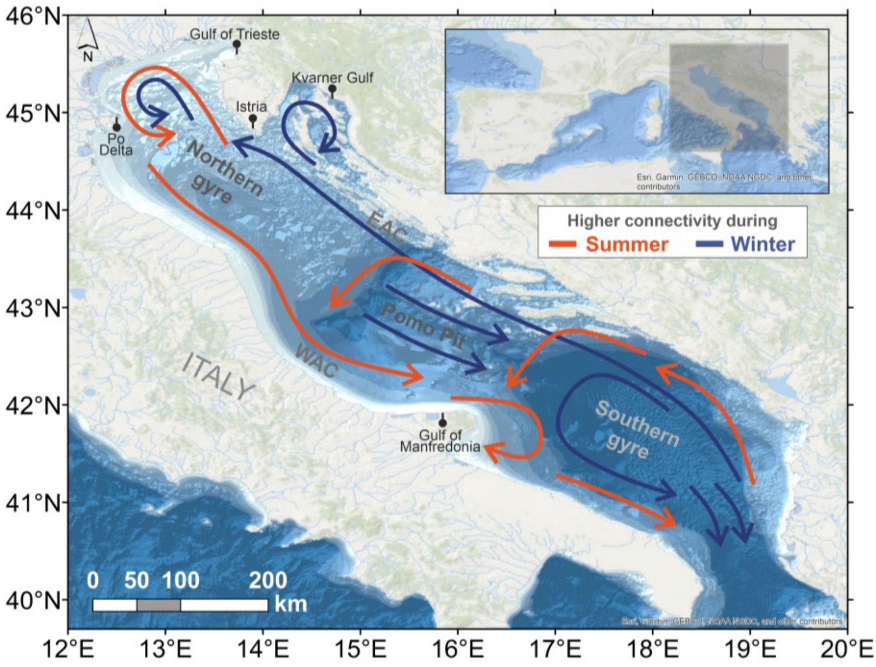

Figure 7.2. Sketch of the main connectivity patterns of particles released throughout the Adriatic Sea during summer (orange) and winter (blue), based on the information described in Chapter 4.

Particles released throughout the Adriatic Sea shown a preferential advection of particles along the coastlines, with the EAC being the primary mechanism for this advection process along the Balkan Peninsula during the winter season, and the WAC being the main advection process responsible for transporting particles along the Italian shelf during the summer. Seasonality is also reflected in the retentive characteristics of the diverse regions studied within the Adriatic basin. During winter, the prevailing currents over the Adriatic Sea and the more variable atmospheric forcing inject more energy in the basin, leading to a significantly wider dispersal of particles that increases the export of particles to the Ionian Sea. The scattered connections in winter contrast with the much more unidirectional connectivity pathways in summer, which favors generally slower and steadier dispersal patterns in this period and promotes a higher number of retentive areas, curiously resembling the pattern observed in the case of neap against spring tides in the previous region discussion.

Areas distributed along the Italian shelf are identified as essential nursery grounds, particularly when the region's productivity is influenced by wind-induced upwelling and river discharges, creating favorable environmental conditions for larvae. During the summer, when the velocity is reduced, retention is promoted, coinciding with the spawning period of anchovy, Mediterranean horse mackerel, and hake. The observed variability during winter provides advantageous opportunities for marine species with longer pelagic larval durations and spawning periods concentrated in winter, such as sardines and common soles. Specifically, most retentive areas arise in the Kvarner Gulf in winter, which, despite the extremely complex rocky coastline, shows the highest connectivity receptions. Similarly, the Gulf of Manfredonia during summer also shows consistent connectivity with the main path of the prevailing WAC during this period. From a more evolutionary point of view, these dispersal timescales could be associated with typical residence times of coastal waters in order to balance auto-recruitment and larval export/import

7.2 Applicability of results and obstacles on current connectivity applications

To date, connectivity studies have addressed a variety of demands emerging from multiple fields, including fisheries (Botsford et al., 2009; Fogarty & Botsford, 2007; Fuller et al., 2017), ecosystem management (Hidalgo et al., 2017), marine pollution (Fifani et al., 2021; Martínez et al., 2024) and climate change (Abernathey et al., 2022; Jönsson & Watson, 2016).

In the context of population connectivity studies aiming to provide insights into the dynamics of such systems, such as those provided in this memory, this need in turn has increased the relevance and applicability of research to marine resource management, ultimately leading to a more comprehensive understanding of all taxa and of controlling processes that influence ecosystem functioning (Pineda et al., 2007).

In particular, the relevance of population connectivity in the design and management of marine protected areas has recently gained increasing attention in the field of marine conservation (Bastari et al., 2016; Batista et al., 2011; Rossi et al., 2014). In fisheries, for instance, estimates of dispersal and connectivity are crucial for understanding the dynamics of target fish populations and for the eventual proper conservation of potentially harvested stocks. The incorporation of such information in this sector is anticipated to be accomplished through the definition of restricted fishing areas, in which both dispersal and retention patterns can provide data regarding the optimal dimensions, distances, and closure periods. In this regard, marine protected areas within a network are more likely to support the persistence and recovery of harvested populations from external disturbances, whereas isolated areas (i.e., not connected by dispersal) are more susceptible to local extinctions due to the lack of natural replenishment (Deudero et al., 2017; Gaines et al., 2010).

In both regions studied, hydrodynamics plays a key role in shaping the dispersal patterns of propagules, with the fortnightly tidal cycle (spring vs. neap tides) in the Alboran Sea and seasonal shifts (winter vs. summer) in the Adriatic Sea acting as dominant forces. While some retention areas are present, the results indicate a high number of spawner migrations, underscoring the role of these basins as a network of interconnected populations. Interestingly, this finding aligns with genetic connectivity studies, which report a homogeneous distribution of genetic components across the two basins for several fish species (Di Franco et al., 2012; Angiulli et al., 2016), including the blackspot seabream (Ferrari et al., 2023).

A network of effective and self-sustaining marine protected areas in both regions could therefore provide enormous benefits for both conservation and fisheries production (Deudero et al., 2017; Di Franco et al., 2012). However, the evaluation of the ecological and economic implications of such regions is still in its early stages and, in practice, information on connectivity has thus far rarely been considered nor incorporated into their design and development (Berkström et al., 2022). Indeed, most marine conservation laws and regulations globally do not explicitly recognize connectivity as a fundamental component of ecosystem management (Estradivari et al., 2022; Lausche et al., 2013). There is therefore a prior urgent need to raise awareness of the importance of marine connectivity, both within and outside protected areas, in order to improve the ecological services they provide (Rossi et al., 2014).

Despite the boundaries that are still in place, there is a growing consensus that the results of ocean connectivity research will increasingly be incorporated into these fields (Andrello et al., 2013; Batista et al., 2011; Crochelet et al., 2016; Demmer et al., 2022). To achieve this, future research should concentrate on improving the integration of functional connectivity at both small and large spatial and temporal scales (Hidalgo et al., 2017). One of the most important challenges will then be to identify the anthropogenic impacts on natural connectivity pathways, as the significant and accelerating pressures of human activities on the marine environment, including habitat alteration, fishing pressure, coastal population growth, introduction of invasive species, climate change, and water quality degradation, are expected to have (and are already having) enormous impacts (Hidalgo et al., 2017). Climate change, in particular, is anticipated to have important consequences on the dispersal and connectivity of marine populations (Gerber et al., 2014), with increasing temperature expectedly affecting community structure through changes in spawning phenology, prey-predator distributions, and larval transport, behavior and mortality (Andrello et al., 2013; Lett et al., 2010; O'Connor et al., 2007).

However, even for models operating under present-day conditions, there is still a significant gap between the ability to simulate larval dispersal and the ability to measure actual connectivity (Lett et al., 2010). A challenge for the future will be to compare real (observed) and virtual (modeled) drifters to validate the physical transport predicted by biophysical models (G. P. Jones et al., 2009; Levin, 2006). In addition, there are several other limitations that can be pursued within the field of physical oceanography, some of which are described below.

7.3 Modelling limitations and future paths

The difficulties associated with direct measurement of larval dispersal in the marine environment have led to a significant increase in the use of alternative methods to quantify larval transport, of which biophysical models have emerged as a relatively affordable and highly effective approach for studying and predicting dispersal patterns at different temporal and spatial scales (Monroy et al., 2017). However, despite their undeniable usefulness in elucidating such dynamics, some of which have been explored in this thesis, models are still limited tools in their ability to provide a fully realistic representation of the complete natural process (Calò et al., 2013).

The predictive performance of biophysical models in simulating larval transport is contingent upon the accuracy and veracity of the input parameters, whether pertaining to hydrodynamic or biological data. In the first case, refinement of models have progressively increased the spatial scale at which they can be applied, thus offering a more complete view of small-scale larval dynamics (Alcaraz & Estrada, 2022; Fuchs et al., 2015, 2017; G. P. Jones et al., 2009). However, parameterization and resolution are limited by the fact that the fine-scale nearshore circulation is still largely unknown, and these models can only be as accurate as the parameters estimated in the field (Metaxas & Saunders, 2009). In the second, knowledge of key biological traits such as spawning areas, larval duration, behavior or mortality rates is still poor (Simons et al., 2013). In our research, this has been no exception, and the limited knowledge of the biology of the species studied has led to uncertain configurations with little or no information, and unavoidable simplifications.

A relevant aspect to note in this regard is the assumption that the larvae are passive (non-swimming) particles during the pelagic larval duration. In a few cases, models have incorporated somewhat more complex biological parameters, such as the swimming speed of larvae, with not entirely consistent, but certainly not null, effects on connectivity patterns (Savina et al., 2010). Other studies suggest that even for actively mobile life stages, dynamics play a key role in regulating the spatial distribution of environmental variables and planktonic food (D'Ortenzio & Ribera d'Alcalà, 2009), thus controlling the location, timing and success of spawning, dispersal and settlement (P. Mariani et al., 2010; Monroy et al., 2017). In practice, the behavior of most species remains largely uncertain, and the ability to actively swim can vary widely among larval stages, with swimming capacities generally expected to increase at more advanced developmental stages. However, the short periods during which the highest connectivity rates occur in the Alboran Sea (less than 20 days in most cases, due to fast travel times, and in certain areas of the Adriatic Sea (less than 30 days in the majority of the basin during summer, owing to favorable retention conditions, may lead to consider the simplification of movements as a reasonable assumption.

Another simplification in our approach on propagules dispersion studies (Chapters 3, 4) has been to disregard vertical displacement. Most particle advection studies similarly overlook the vertical behaviors of buoyant individuals, particularly in regions like our study area, where horizontal advection dominates over vertical currents. This assumption is further supported by considerable uncertainties around the vertical displacement mechanisms of propagules, which include diel migration cycles, food availability patterns, buoyancy fluctuations due to changing egg lipid content, thermocline variability, and small-scale eddy turbulence, all factors beyond the resolution of our model. Consequently, accurately estimating vertical motion remains a remarkable challenge, and in some cases, even the direction of movement (upward or downward) is indeterminate. Given these complexities, focusing solely on horizontal transport processes provides a more reliable approach for this analysis.

Despite these assumptions, knowledge of the impact of different parameter settings on connectivity estimates and their variability is unclear, and most progress in this regard should be made by re-running Lagrangian analyses with updated biological information, which is still under investigation for the two main species (or group of species) assessed in this thesis. In the case of the blackspot seabream (Chapter 3), this includes key information on egg buoyancy, larval drifting duration, number of spawners, and vertical behavior, among others (Gil Herrera, 2010). This is also the case for the alien alga (Chapters 5, 6), whose specific parameters, such as thermal tolerance, particle size, or sedimentation rates under different environmental conditions, is still undetermined (Mateo-Ramírez et al., 2023). In both cases, the knowledge and inclusion of these parameters is crucial for obtaining results that can be applied effectively for the conservation, in the first case, or for the control, in the second case, of such populations. In this respect, it is also important to note that the adjustment of specific biological and hydrological parameters implicitly entails that these results are only valid for the species and region of interest, and that similar studies should be carried out on a larger number of species with different life history characteristics (life stages, reproductive strategies, etc.) in order to gain further insight into other population dynamics in specific regions.

Ultimately, further research is needed to gain a deeper and more comprehensive understanding of the mechanisms of connectivity. When information on specific parameter values for the species of interest is available, end-to-end ecosystem approaches can be valuable tools. The end-to-end models typically combine a regional circulation, a lower trophic level nutrient-phytoplankton-zooplankton network, and a multispecies individual-based model for the fish species of interest (Sánchez-Garrido et al., 2020). The basic principle of the individual model is that a population or system consists of discrete individuals that have a set of characteristics and can be distinguished from other individuals by life history traits such as fecundity, life span, offspring size, reproductive strategy, biotic interactions, and abundance of its predators, among many others (Deangelis & Mooij, 2005; Megrey, 2001; Mims & Olden, 2012; Sánchez-Garrido et al., 2020). By filling the aforementioned gaps in biological information, these models can therefore be used to capture individual variation in greater detail than previous modeling approaches and to simulate the biophysical interactions between individuals and their environment. In the near future, the additional knowledge gained from our efforts to understand the functioning and dynamics of those populations will help to develop new perspectives on marine ecological awareness and to implement appropriate adaptive management strategies.

7.4 Concluding remarks

The principal findings and conclusions that can be derived from the chapters of this dissertation are as follows:

Chapter 1: General Introduction

- Oceanographic features exert a significant influence on the extent of separation between individuals within and between local populations. An understanding of these dynamics is essential for the study of marine ecosystems, the management of fishery resources, the regulation of invasive species, and the design of marine protected areas.
- Recent efforts have been made to gain a deeper understanding of population dynamics. Several methodologies exist for this purpose, of which hydrodynamical models coupled with Lagrangian particle tracking algorithms are relatively affordable and extremely powerful tools for studying and predicting dispersal patterns at different temporal and spatial scales.
- In the nearshore environment, where several physical processes act at different spatio-temporal scales, connectivity is of particular importance. Two examples of this complexity are provided by:
    - The Strait of Gibraltar and the Alboran Sea.
    - The Strait of Otranto and the Adriatic Sea.

Chapter 2: Methodology

- Numerical models are effective tools for reproducing complex geophysical processes occurring in a given domain. A variety of applications have been developed to represent such oceanic flows, and the use of an existing model is considered a reasonable choice over the development of a new one.
- Lagrangian algorithms involve the analysis of sets of virtual particles representing fluid parcels, tracers, or passively drifting individuals. Their primary goal is to estimate the probability distribution of spatial dispersal, providing valuable information about the origins and trajectories of dispersing individuals within populations.
- A key quantitative measure of connectivity is the so-called connectivity matrix, where each cell represents the number of particles released from a given source and collected in a given destination at a given time. Alternative definitions can be adopted by quantifying the maximum percentage of particles in each target region over a given time, or by tracking the temporal changes in source-sink dynamics.

Chapter 3: Hydrodynamic connectivity and dispersal patterns of a transboundary species (Pagellus bogaraveo) in the Strait of Gibraltar and adjacent basins

- The dynamics of the Strait of Gibraltar play a key role in regulating the dispersal and connectivity patterns of early life stages of blackspot seabream in the Alboran Sea.
- The main differences in connectivity patterns are caused by the geographic location of the spawning areas (north vs. south). The northern strait is mostly connected to the northern basin of Alboran, while the southern Strait is mostly connected to the southern basin of Alboran.
- Tides are an influential phenomenon. The variability is particularly noticeable in terms of fortnightly modulation. Spring tides tend to favor connectivity by direct advection promoted by the increased

energy of the currents. In neap tides, connectivity is achieved by the mean circulation of the Alboran.

- The different depths of spawning create distinct patterns of connectivity. At the surface, particles are more actively scattered by the energetic current, while in deeper layers the circulation weakens, allowing particles to move less chaotically and travel farther.

Chapter 4: Spatio-temporal connectivity and dispersal seasonal patterns in the Adriatic Sea using a retention clock approach

- Understanding how species interact with the physical processes occurring in the Adriatic Sea is essential for managing vulnerable populations and identifying areas that require effective conservation efforts for the generic marine organisms inhabiting the region.
- The temporal component of connectivity is highlighted using a previously developed retention clock matrix over different larval durations.
- Seasonality is a critical factor in dispersal, with greater variability and reduced efficiency in winter compared to summer.

Chapter 5: Could secondary flows have made possible the cross-strait transport and explosive invasion of Rugulopteryx okamurae algae in the Strait of Gibraltar?

- The simultaneous occurrence of *Rugulopteryx okamurae* on both shores of the SoG is highly unlikely. A more plausible scenario is that the algae first colonized one shore and then spread to the opposite shore. A hydrodynamically-based spreading is assessed, even if highly improbable. This possibility is examined using current meter observations, which show layers with no zero velocity in the cross-strait direction.
- The depth range for cross-strait transport is 100-150 m, where the interface of zero velocity along the Strait is located. Layers of weak southward and northward currents are identified above and below the interface, respectively.
- High pressure over the western Mediterranean and local southwesterly winds associated with neap tides provide the best

conditions for south-to-north connectivity. Conversely, low pressure and local northeasterly spring tides reduce the chances for such transport.

Chapter 6: Modeling spread of an alien alga under different temporal scenarios in the Strait of Gibraltar and adjacent basins

- The impact and adaptability of *Rugulopteryx okamurae* in the Mediterranean environment has recently been the subject of extensive research, but crucial aspects of the invasion, including its distribution and the underlying causes of its success, remain unknown.
- The prediction of the passive dispersal of the algae in 2021 indicated a predominantly eastward spread, with transport by the Atlantic jet leaving the Strait being the most influential process.
- Tides depict two different mechanisms: spring tides tend to favor accumulation by direct advection favored by the increased energy of the currents, while neap tides favor a higher dispersion with consequently slower and generally lower accumulation rates along the coasts.

Resumen en español

Es una realidad evidente que los océanos se encuentran en perpetuo movimiento. Los sistemas costeros, en particular, son entornos altamente dinámicos y sensibles, afectados por diversos procesos a diferentes escalas espaciotemporales que interactúan de forma no lineal. Tal entorno ofrece múltiples vías que, en mayor o menor medida, condicionan el transporte, distribución, conexión o separación de individuos o conjuntos de individuos de un determinado ecosistema. Comprender los procesos que controlan tales movimientos es un desafío crucial en la predicción de la distribución biogeográfica de las especies y la viabilidad de las medidas de conservación en una determinada región, pues estas interacciones biofísicas regulan y determinan ulteriormente la dinámica poblacional.

Dispersión y conectividad son dos términos que emergen al abordar las interacciones entre los individuos y su entorno. El primer término describe el mecanismo empleado para dispersar individuos, mayoritariamente en los primeros estadios vitales del ciclo biológico (esporas, huevos, larvas para especies bentónicas o pelágicas, y también juveniles para las pelágicas) y tiene como objetivo maximizar la distribución de las especies en el área de distribución geográfica. La dispersión de los propágulos está condicionada por la dinámica ambiental, en la que la turbulencia, la advección y la difusión actuando a diferentes escalas determinan las conexiones o la separación de diferentes conjuntos de individuos. Tales patrones de conexión o aislamiento, que determinan el propio desarrollo y abundancia de ciertas especies en determinadas zonas, se resumen bajo el concepto de conectividad. La conectividad es, de hecho, el resultado de la interacción del ciclo biológico de una especie con las condiciones dinámicas del medio marino. En términos más generales, la conectividad puede resumirse como el grado en el que el intercambio de individuos, tratados como partículas pasivas, se produce entre distintas áreas. Por lo tanto, la conectividad puede estimarse no sólo para analizar las interacciones entre individuos dentro de una población, sino también para estimar los flujos de momento y calor en el océano, y los intercambios de otras partículas inertes en suspensión, incluidos los sedimentos, microplásticos y otras partículas contaminantes.

Debido a su amplia definición y a su creciente relevancia, el término "conectividad" se ha introducido y aplicado en multitud de campos. De esta forma, existen varias interpretaciones, cuyas principales diferencias radican en la escala de aplicabilidad del estudio. En términos ecológicos, la conectividad se refiere al grado en que poblaciones separadas espacialmente están vinculadas por la dispersión de individuos que forman parte de una metapoblación, definida como un conjunto de poblaciones de la misma especie distribuidas por zonas habitables. La conectividad sedimentaria se refiere al grado en que un sistema controla la transferencia de sedimentos entre diferentes formas del terreno o unidades del paisaje. La conectividad genética se define como el grado en que el flujo de genes influye en los procesos evolutivos de una población. Tales definiciones representan sólo una muestra de la multitud de aplicaciones, siendo aquellas que vinculan la influencia de los procesos de conectividad en la función ecológica y los servicios ecosistémicos las más relevantes, un uso que suele denominarse conectividad funcional.

Dependiendo de la magnitud de los fenómenos ambientales implicados y de otros parámetros biológicos, como el tamaño y la edad de los propágulos, se pueden identificar diversas diferencias espaciales en el intercambio de individuos. Estas van desde niveles muy bajos de conectividad entre poblaciones, en las que la estructura y el tamaño de la población se mantienen únicamente a través de la retención larvaria y posterior auto-reclutamiento, hasta altos niveles de conectividad que se producen a través de una elevada dispersión de larvas entre metapoblaciones. Por lo tanto, conocer en detalle tanto la magnitud como las escalas espaciotemporales en las que ocurren dichas conexiones, es esencial para comprender la estructura de las poblaciones marinas y sus interrelaciones.

Las escalas espaciotemporales de conectividad están mediadas por el éxito en el intercambio entre individuos. Esto es particularmente relevante en las primeras etapas de la vida, cuando las esporas, los huevos y las larvas en desarrollo pueden tratarse, al menos en gran parte, como elementos pasivos. En determinadas especies de peces con fases larvarias pelágicas, la hidrodinámica es fundamental para conectar las poblaciones, condicionando la distribución del plancton a través de procesos de mesoescala y submesoescala que dispersan o retienen partículas vivas e inertes, procesos fundamentales para la supervivencia en las primeras fases de la vida. Ejemplos de estos organismos incluyen la mayoría de las especies pelágicas, algunas de las cuales transitan todo su ciclo de vida (holoplancton), o sólo sus etapas larvarias (meroplancton e ictioplancton) como plancton, aunque también incluyen muchas especies bentónicas, que normalmente se caracterizan por una fase sedentaria precedida por una etapa planctónica, durante la cual se produce la dispersión. Como tal, las distancias de dispersión, y por lo tanto la conectividad, se determinan por el tiempo que los individuos pasan en las etapas de vida planctónicas.

Las escalas temporales y espaciales en las que varía la conectividad durante la fase pelágica aumentan en relación con la fase de desove, cuyo momento y ubicación están a su vez determinados por múltiples factores externos, incluyendo la hidrodinámica del sistema y el comportamiento larvario. Algunas condiciones hidrodinámicas pueden aumentar las distancias de dispersión de las larvas (por ejemplo, las corrientes superficiales gobernadas por el viento y las corrientes de marea), mientras que otras pueden reducirlas (por ejemplo, la turbulencia). Por lo tanto, es razonable esperar variabilidad en los patrones de conectividad no solamente entre especies, sino también entre regiones y periodos de tiempo determinados. En este sentido, las poblaciones marinas que residen en regiones protegidas son menos susceptibles a una fuerte advección, lo que implica una dispersión relativamente limitada, que a su vez podría conducir a una mayor retención local y supervivencia de juveniles, y a una mayor conectividad de la población en de dicha región. Por el contrario, en los entornos expuestos y altamente dinámicos, donde confluyen las mareas, las corrientes impulsadas por el viento y la turbulencia a pequeña escala, la dispersión puede dar lugar a una menor retención de individuos, lo que se traduce en una menor conectividad de la población.

El estudio de la conectividad es, por tanto, esencial para una comprensión integral de la dinámica poblacional de dichas especies, además de una efectiva gestión de recursos pesqueros, control de especies invasoras y diseño de áreas marinas protegidas, entre otros. De hecho, a medida que ha surgido la conciencia de que la conectividad es un componente clave para comprender y gestionar determinadas poblaciones marinas, se ha invertido un esfuerzo considerable en el desarrollo y la aplicación de diversos métodos para obtener información sobre la dinámica de las poblaciones. En el entorno cercano a la costa, los enfoques más utilizados son los análisis moleculares, de otolitos y numéricos, todos con el objetivo común de elucidar los patrones de dispersión. En este sentido, las herramientas de modelación son un buen ejemplo, ya que proporcionan un análisis integral del origen y las trayectorias de individuos. Un método común para aplicar estos resultados numéricos es el análisis Lagrangiano, que implica estudiar conjuntos de partículas virtuales que representan parcelas fluidas, trazadores o individuos que se desplazan pasivamente, para identificar sus rutas, escalas temporales asociadas y transportes entre distintas regiones oceánicas.

Sin embargo, aun habiéndose desarrollado múltiples herramientas para su estimación, los conocimientos sobre la conectividad de especies marinas concretas y regiones geográficas específicas siguen siendo escasos. Esto es ciertamente observable en el Mar Mediterráneo, a pesar de ser considerado un "laboratorio" para tales estudios debido a sus patrones oceanográficos bien estudiados. Sin embargo, la importancia del entorno mediterráneo como punto caliente de biodiversidad y las amenazas humanas acumulativas a las que se enfrentan continuamente las poblaciones marinas, hacen que la investigación de la conectividad sea una tarea urgente.

Ciertas regiones del Mediterráneo proporcionan ejemplos específicos de este hecho. Entre ellos, destaca el mar de Alborán y el mar Adriático, donde los avances en conectividad y dispersión, junto con la orientación sobre cómo integrar esta información en las acciones de gestión, requieren una atención urgente. Sin embargo, las dificultades encontradas para cuantificar la conectividad costera, ya sea mediante métodos observacionales o numéricos, han dado lugar a una falta de comprensión de los vínculos entre la hidrodinámica de esas regiones mediterráneas y las características biológicas de las especies presentes allí.

Con el objetivo de contribuir a una mejor comprensión de estas dinámicas, esta tesis doctoral tiene como objetivo estimar los patrones potenciales de conectividad y dispersión de ciertos grupos poblacionales importantes a diferentes escalas regionales en el Mar Mediterráneo. Se centra en las dos regiones relevantes mencionadas: a) el mar de Alborán, una cuenca de transición entre el mar Mediterráneo y el océano Atlántico fuertemente influenciada por el flujo de agua atlántica a través del el Estrecho de Gibraltar, y b) el mar Adriático, un cuerpo de agua semicerrado caracterizado por una topografía peculiar y una gran cantidad de fuentes de agua dulce. En particular, se han empleado algoritmos Lagrangianos acoplados a modelos numéricos con el fin de determinar las trayectorias y conectividad de partículas virtuales que emulan larvas u otros organismos entre distintas subáreas por la advección de las corrientes. Dichas herramientas numéricas se describen en detalle en el Capítulo 2. En concreto, se han evaluado los patrones de dispersión y conectividad de tres especies (o grupos de especies) diferenciadas, cuyos resultados se detallan en los Capítulos 3, 4, 5 y 6 de la presente tesis. A continuación, se ofrece un resumen desglosado de cada uno de ellos:

Capítulo 3

El voraz (*Pagellus bogaraveo*) es una especie altamente apreciada tanto por su valor económico como gastronómico, que tiene un importante caladero en el Estrecho de Gibraltar. Por esta misma razón, es una de las especies más sobreexplotadas de la zona, lo que ha provocado que las capturas estén descendiendo significativamente a lo largo de los años. Dentro del ámbito científico, existe un consenso que considera que, para optimizar las pesquerías, simultáneamente a dejar de sobre explotar el recurso, es necesario hacer estudios de dinámica poblacional y conectividad. Con el objetivo de conocer mejor la dinámica poblacional de la especie y sus mecanismos de dispersión en el Mar de Alborán, se ha estudiado su conectividad hidrodinámica y patrones de dispersión a partir de un modelo numérico utilizando los estadios de vida temprana (huevos y larvas) como partículas virtuales Lagrangianas.

Para determinar los patrones espaciotemporales de dispersión, se definieron tres zonas de suelta de partículas en el Estrecho de Gibraltar, zona preferencial de desove del voraz, cinco profundidades de liberación desde la superficie hasta los 81 metros, y ocho combinaciones de marea en función de la fase mareal y de la modulación quincenal (marea viva-marea muerta). Para cada uno de estos escenarios mareales iniciales se realizaron simulaciones de 60 días, que es la duración pelágica del voraz, en distintas fechas para estudiar la variabilidad subinercial asociada al forzamiento meteorológico, todo ello en el periodo comprendido entre diciembre de 2004 y abril de 2005. En conjunto se realizaron 480 simulaciones, de cuyo análisis se ha deducido que el transporte hacia el este por el chorro Atlántico que sale del Estrecho de Gibraltar es el proceso más influyente. En cuanto a las fluctuaciones temporales, la modulación quincenal es el factor predominante para la dispersión horizontal, siendo el escenario de marea muerta el que produce una dispersión más baja y velocidad más uniforme de los huevos y larvas. La profundidad del desove en el Estrecho de Gibraltar es una condición crítica, como lo revelan las pruebas de sensibilidad del modelo.

Capítulo 4

Las características hidrodinámicas desempeñan un papel clave en los patrones de dispersión y conectividad de las poblaciones de peces, especialmente en zonas altamente energéticas determinadas por las corrientes, el caudal de los ríos y las fluctuaciones inducidas meteorológicamente. Comprender cómo interactúan las especies con estos procesos físicos es esencial para gestionar las poblaciones vulnerables e identificar las zonas que requieren esfuerzos de conservación eficaces. Este Capítulo examina la hidrodinámica que regula la conectividad en el mar Adriático, una cuenca poco profunda y semicerrada ampliamente reconocida como una de las zonas más importantes del mar Mediterráneo para su protección.

Un modelo hidrodinámico de alta resolución acoplado a un módulo de seguimiento Lagrangiano sirve de herramienta numérica. Las partículas Lagrangianas, que representan huevos y larvas con características biológicas típicas de los organismos marinos genéricos que habitan la región, se liberan por toda la cuenca en diferentes momentos durante un año de prueba para identificar las vías más probables de dispersión. El componente temporal de la conectividad se estima utilizando una matriz de retención, previamente desarrollada, a lo largo de diferentes duraciones larvarias.

Las áreas distribuidas a lo largo de la plataforma italiana se identifican como zonas de retención esenciales, especialmente cuando la productividad de la región se ve influenciada por la surgencia inducida por el viento y las descargas fluviales, creando condiciones ambientales favorables para las larvas. Durante el verano, cuando la velocidad se reduce, se promueve la retención, coincidiendo con el período de desove de la anchoa, y la merluza. La variabilidad observada durante el invierno se atribuye a las fluctuaciones ambientales, específicamente a la presencia de vientos fuertes que afectan significativamente el desplazamiento de las partículas. Este fenómeno brinda oportunidades favorables para las especies marinas con duraciones pelágicas larvarias más largas y períodos de desove concentrados en invierno, como la sardina y el lenguado. Muchas partículas llegan después de someterse a una recirculación, proceso que requiere más tiempo y se traduce en duraciones de llegada extendidas.

Capítulo 5

Actualmente, el Estrecho de Gibraltar está experimentando una invasión sin precedentes del alga exótica *Rugulopteryx okamurae*, originaria del Pacífico Norte. Según la escasa literatura disponible, el alga se asentó primero en la costa sur, probablemente debido a los intercambios comerciales con puertos franceses donde fue introducida accidentalmente junto con ostras japonesas importadas para la maricultura. Sin embargo, no hay certeza de que el alga colonizara primero la costa sur del Estrecho y, desde allí, se extendiera hacia el norte. Podría haber sucedido al revés. Sea como fuere, se extendió por todo el Estrecho y áreas circundantes con una rapidez sorprendente. La intervención humana (algas adheridas a los cascos de los barcos o redes de pesca, por ejemplo) pueden estar detrás de la propagación desde la costa inicialmente colonizada hasta la costa opuesta libre de algas. Pero también podría haber sucedido mediante procesos hidrodinámicos sin intervención humana directa. Esta posibilidad se evalúa en este Capítulo revisando perfiles históricos de corrientes recogidos en el Estrecho de Gibraltar en busca de flujos secundarios a través del Estrecho.

El transporte de las esporas del alga entre ambas costas del Estrecho, consideradas como partículas pasivas advectadas por las corrientes, implica cruzar las intensas corrientes zonales ligadas al intercambio bicapa entre el Atlántico y el Mediterráneo, que desplazarían las esporas más allá de las dimensiones espaciales del Estrecho antes de que éstas alcanzaran la costa opuesta. Sí existe, sin embargo, una posibilidad para este transporte transversal si éste puede realizarse en la profundidad de la interfaz entre ambos flujos, ubicada a 100-150 m, donde la corriente se anula. Si existen corrientes secundarias transversales a esta profundidad, aunque sean débiles, las posibilidades de cruzar con éxito el Estrecho no serían nulas. La hipótesis se evalúa empleando observaciones históricas de velocidad en la zona. En todas las estaciones, los perfiles medios de velocidad presentan una componente no-nula de la componente transversal que sugieren la posibilidad de cruzar el Estrecho meridionalmente. Los perfiles muestran una estructura común, caracterizada por una capa de profundidad media de velocidad transversal positiva, flanqueada por una parte negativa, tanto en superficie como en profundidad. De esta forma, la conexión de la costa sur a la norte sería posible en la capa intermedia, mientras que el transporte de norte a sur tendría lugar en las capas superficiales y profundas de la columna de agua. Los valores de velocidad transversal son de unos 5 $cm \cdot s^{-1}$ por lo que las algas requerirían unos 4 días al menos para atravesar el Estrecho por su parte más estrecha (~14 km). Incluso para un valor medio moderado de 40 $cm \cdot s^{-1}$ para la velocidad longitudinal, en 4 días las partículas serían desplazadas zonalmente unos 150 km, mucho más que las dimensiones del Estrecho, por lo que no alcanzarían la orilla opuesta. Sólo evitando las capas de mayor velocidad y permaneciendo cerca de la interfaz, las algas podrían tener posibilidades de cruzar el Estrecho meridionalmente.

Aun considerando estas condiciones, el éxito del transporte transversal depende de una cadena de eventos circunstanciales. Las algas deben ser arrancadas y resuspendidas del fondo (por redes de arrastre u otros agentes) en la zona iluminada donde se establece. Sus propágulos o esporas deben ser desplazados mar adentro en la horizontal y hasta la profundidad de la interfaz en la vertical. Luego, deberían ser transportados a través del Estrecho hasta alcanzar el talud continental opuesto, llevados a la superficie y desplazados hacia la costa y, finalmente, asentarse y prosperar en el nuevo entorno. Este proceso lleva de días a semanas, gran parte de cuyo tiempo el alga estaría en condiciones de oscuridad. La factibilidad de esta posibilidad sólo puede comprobarse con la ayuda de esquemas de advección acoplados a modelos numéricos tridimensionales de alta resolución.

Capítulo 6

Desde su detección inicial en la costa del Estrecho de Gibraltar en 2015, el alga parda exótica *Rugulopteryx okamurae* se ha extendido de forma explosiva por gran parte de las costas Atlántica y Mediterránea, produciendo graves impactos en comunidades bentónicas previamente establecidas y provocando acumulaciones masivas a lo largo de las costas, afectando a la pesca y al turismo. Su extraordinariamente elevado potencial de conectividad (es decir, la conexión efectiva entre las fuentes de liberación del alga y las costas de recepción), se ve facilitada por su dispersión a través de talos flotantes a la deriva a prácticamente cualquier profundidad en la columna de agua, la propagación por esporas y la supervivencia en condiciones ambientales adversas, como la escasa o nula luminosidad y las amplias variaciones térmicas. El impacto y la adaptabilidad del alga en el entorno mediterráneo han sido objeto recientemente de numerosas investigaciones, pero aspectos cruciales de la invasión, como su distribución y las causas subyacentes de su éxito, aún se desconocen.

Para comprender mejor la propagación y el asentamiento de la especie, se han empleado dos modelos hidrodinámicos anidados de alta resolución acoplados a un algoritmo Lagrangiano de seguimiento de partículas, con trazadores virtuales que representaban esporas libres, fragmentos de talos de *Rugulopteryx okamurae*. El trabajo se centra en el Estrecho de Gibraltar y sus cuencas adyacentes, el Golfo de Cádiz y el Mar de Alborán, que hasta el momento se han visto significativamente afectadas por la invasión de dicha alga. Las simulaciones de la dispersión de larvas a partir de una introducción en el Estrecho indican que los propágulos de algas se propagaron primero hacia el este antes de extenderse hacia el oeste, siendo el transporte por el chorro atlántico que sale del Estrecho de Gibraltar el proceso más influyente. El ciclo de marea, seguido de los vientos, es un agente dominante, siendo las mareas vivas y los vientos de levante los que generalmente promueven una mayor acumulación de partículas dentro de la cuenca de Alborán. La velocidad de sedimentación terminal de las partículas es una condición crítica, tal como revela una prueba de sensibilidad del modelo.

Bibliography

Aamri, F. E., Idhalla, M., & Tamsouri, M. N. (2018). Occurrence of the invasive brown seaweed *Rugulopteryx okamurae* (E.Y.Dawson) I.K.Hwang, W.J.Lee & H.S.Kim (Dictyotales, Phaeophyta) in Morocco (Mediterranean Sea). *Mediterranean Fisheries and Aquaculture Research*, *1*(2), 92–96.

Abaunza, P., Gordo, L., Karlou-Riga, C., Murta, A., Zimmermann, C., Hammer, C., Lucio, P., Iversen, S. A., Molloy, J., & Gallo, E. (2003). *Growth and reproduction of horse mackerel,* Trachurus trachurus *(carangidae).*

Abernathey, R., Bladwell, C., Froyland, G., & Sakellariou, K. (2022). Deep Lagrangian Connectivity in the Global Ocean Inferred from Argo Floats. *Journal of Physical Oceanography*, *52*(5), 951–963. https://doi.org/10.1175/JPO-D-21-0156.1

Acosta Yepes, Juan, Rivera Martínez, Jesús, & Hidalgo Bravo, Jesús. (2006). *Submarine Topobathymetric Relief Map of the Alboran Sea and the Strait of Gibraltar—How is the seabed and its geology in the Alboran Sea.*

Albérola, C., Rousseau, S., Millot, C., Astraldi, M., Font, J., García-Lafuente, J., Gasparini, G. P., Send, U., & Vangriesheim, A. (1995). *Tidal currents in the western Mediterranean Sea*. https://digital.csic.es/handle/10261/194257

Alcaraz, M., & Estrada, M. (2022). *Turbulence and plankton dynamics in a warmer ocean*. Consejo Superior de Investigaciones Científicas (España). https://digital.csic.es/handle/10261/255537

Altamirano Jeschke, M., Rosa Álamos, J. C. de la, Martínez Gil, F. J., & Muñoz Gallego, A. R. (2017). Prolifera en el Estrecho un alga nunca citada en nuestro litoral: De origen asiático, “Rugulopteryx okamurae” ocupa ya una gran extensión. *Quercus*, *374*, 32–33.

Altamirano-Jeschke, M., De la Rosa Álamos, J., & Martínez Medina, F. J. (2016). *Arribazones de la especia exótica* Rugulopteryx okamurae *(E.Y. Dawson) en el Estrecho de Gibraltar*. Sesión Científica de la Sociedad Española de Ficología, Madrid, Spain. https://riuma.uma.es/xmlui/handle/10630/12433

Altamirano-Jeschke, M., Rosa, J. de la, Carmona-Fernández, R., Kawai, H., Hanyuda, T., Gómez, A., Rull, J., Zanolla-Balbuena, M. F., Rosas-Guerrero, J., Blasco, C., & Muñoz-Gallego, A. R. (2022). *Arguments to consider* Rugulopteryx okamurae *(Dictyotales, Ochrophyta) the potential first seaweed species to be included in the lists of invasive species of European*

Union concern. 22nd International Conference on Aquatic Invasive Species, Oostende, Belgium. https://riuma.uma.es/xmlui/handle/10630/23989

Álvarez Fanjul, E., Pérez Gómez, B., & Rodríguez Sánchez Arévalo, I. (2001). Nivmar: A storm surge forecasting system for Spanish waters. *Scientia Marina*, *65*(S1), 145–154. https://doi.org/10.3989/scimar.2001.65s1145

Alvarez, P., Fives, J., Motos, L., & Santos, M. (2004). Distribution and abundance of European hake *Merluccius merluccius* (L.), eggs and larvae in the North East Atlantic waters in 1995 and 1998 in relation to hydrographic conditions. *Journal of Plankton Research*, *26*(7), 811–826. https://doi.org/10.1093/plankt/fbh074

Amoroso, P. P., Aguilar, F. J., Parente, C., & Aguilar, M. A. (2023). Statistical Assessment of Some Interpolation Methods for Building Grid Format Digital Bathymetric Models. *Remote Sensing*, *15*(8), Article 8. https://doi.org/10.3390/rs15082072

Andrello, M., Mouillot, D., Beuvier, J., Albouy, C., Thuiller, W., & Manel, S. (2013). Low Connectivity between Mediterranean Marine Protected Areas: A Biophysical Modeling Approach for the Dusky Grouper *Epinephelus marginatus*. *PLoS ONE*, *8*(7). https://doi.org/10.1371/journal.pone.0068564

Angiulli, E., Sola, L., Ardizzone, G., Fassatoui, C., & Rossi, A. R. (2016). Phylogeography of the common pandora *Pagellus erythrinus* in the central Mediterranean Sea: Sympatric mitochondrial lineages and genetic homogeneity. *Marine Biology Research*, *12*(1), 4–15. https://doi.org/10.1080/17451000.2015.1069355

Antell, G. T., Kiessling, W., Aberhan, M., & Saupe, E. E. (2020). Marine Biodiversity and Geographic Distributions Are Independent on Large Scales. *Current Biology*, *30*(1), 115-121.e5. https://doi.org/10.1016/j.cub.2019.10.065

Arneri, E., & Morales-Nin, B. (2000). Aspects of the early life history of European hake from the central Adriatic. *Journal of Fish Biology*, *56*(6), 1368–1380. https://doi.org/10.1111/j.1095-8649.2000.tb02149.x

Ashton, G., Zabin, C., Davidson, I., & Ruiz, G. (2022). Recreational boats routinely transfer organisms and promote marine bioinvasions. *Biological Invasions*, *24*, 1–14. https://doi.org/10.1007/s10530-021-02699-x

Assis, J., Zupan, M., Nicastro, K. R., Zardi, G. I., McQuaid, C. D., & Serrão, E. A. (2015). Oceanographic Conditions Limit the Spread of a Marine

Invader along Southern African Shores. *PLoS ONE*, *10*(6), e0128124. https://doi.org/10.1371/journal.pone.0128124

Ayata, S. D., Lazure, P., & Thiébaut, É. (2010). How does the connectivity between populations mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of Biscay and the English Channel (North-East Atlantic). *Progress in Oceanography*, *87*(1–4), 18–36. https://doi.org/10.1016/j.pocean.2010.09.022

Báez, J. C., Camiñas, J. A., Aguilera, R., Castro-Gutiérrez, J., & Real, R. (2023). When non-target wildlife species and alien species both affect negatively to an artisanal fishery: The case of trammel net in the Alboran Sea. *Reviews in Fish Biology and Fisheries*, *33*(3), 785–799. https://doi.org/10.1007/s11160-023-09759-6

Báez, J. C., Macías, D., & De Castro, M. (2014). Assessing the response of exploited marine populations in a context of rapid climate change: The case of blackspot seabream from the Strait of Gibraltar. In *Animal Biodiversity and Conservation* (Vol. 37).

Bajo, M., Ferrarin, C., Dinu, I., Umgiesser, G., & Stanica, A. (2014). The water circulation near the Danube Delta and the Romanian coast modelled with finite elements. *Continental Shelf Research*, *78*, 62–74. https://doi.org/10.1016/j.csr.2014.02.006

Barton, E. D. (2001). Canary And Portugal Currents. In *Encyclopedia of Ocean Sciences* (pp. 380–389). Academic Press. https://doi.org/10.1006/rwos.2001.0360

Baschek, B., Send, U., García Lafuente, J., & Candela, J. (2001). Transport estimates in the Strait of Gibraltar with a tidal inverse model. *Journal of Geophysical Research: Oceans*, *106*(C12), 31033–31044. https://doi.org/10.1029/2000JC000458

Basilone, G., Ferreri, R., Aronica, S., Mazzola, S., Bonanno, A., Gargano, A., Pulizzi, M., Fontana, I., Giacalone, G., Calandrino, P., Genovese, S., & Barra, M. (2021). Reproduction and Sexual Maturity of European Sardine (*Sardina pilchardus*) in the Central Mediterranean Sea. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.715846

Basilone, G., Guisande, C., Patti, B., Mazzola, S., Cuttitta, A., Bonanno, A., Vergara, A. r., & Maneiro, I. (2006). Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. *Fisheries Oceanography*, *15*(4), 271–280. https://doi.org/10.1111/j.1365-2419.2005.00391.x

Bastari, A., Micheli, F., Ferretti, F., Pusceddu, A., & Cerrano, C. (2016). Large marine protected areas (LMPAs) in the Mediterranean Sea: The opportunity of the Adriatic Sea. *Marine Policy*, *68*, 165–177. https://doi.org/10.1016/j.marpol.2016.03.010

Batista, M. I., Baeta, F., Costa, M. J., & Cabral, H. N. (2011). MPA as management tools for small-scale fisheries: The case study of Arrábida Marine Protected Area (Portugal). *Ocean & Coastal Management*, *54*(2), 137–147. https://doi.org/10.1016/j.ocecoaman.2010.10.032

Beca-Carretero, P., Winters, G., Teichberg, M., Procaccini, G., Schneekloth, F., Zambrano, R. H., Chiquillo, K., & Reuter, H. (2024). Climate change and the presence of invasive species will threaten the persistence of the Mediterranean seagrass community. *Science of The Total Environment*, *910*, 168675. https://doi.org/10.1016/j.scitotenv.2023.168675

Bellafiore, D., & Umgiesser, G. (2010). Hydrodynamic coastal processes in the North Adriatic investigated with a 3D finite element model. *Ocean Dynamics*, *60*(2), 255–273. https://doi.org/10.1007/s10236-009-0254-x

Bellissimo, G., Altamirano Jeschke, M., Muñoz, A.-R., De la Rosa, J., Hung, T. H., Rizzuto, G., Vizzini, S., & Tomasello, A. (2023). The invasive brown seaweed *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) continues to expand: First record in Italy. *BioInvasions Records*, *13*(2), 385–401. https://doi.org/10.1101/2023.09.23.559131

Berkström, C., Wennerström, L., & Bergström, U. (2022). Ecological connectivity of the marine protected area network in the Baltic Sea, Kattegat and Skagerrak: Current knowledge and management needs. *Ambio*, *51*(6), 1485–1503. https://doi.org/10.1007/s13280-021-01684-x

Bethoux, J. P. (1979). Budgets of the mediterranean sea—Their dependance on the local climate and on the characteristics of the atlantic waters. *Oceanologica Acta*, *2*(2), 157–163.

Bethoux, J. P., Gentili, B., Morin, P., Nicolas, E., Pierre, C., & Ruiz-Pino, D. (1999). The Mediterranean Sea: A miniature ocean for climatic and environmental studies and a key for the climatic functioning of the North Atlantic. *Progress in Oceanography*, *44*(1), 131–146. https://doi.org/10.1016/S0079-6611(99)00023-3

Beudin, A., Ganju, N. K., Defne, Z., & Aretxabaleta, A. L. (2017). Physical response of a back-barrier estuary to a post-tropical cyclone. *Journal of Geophysical Research: Oceans*, *122*(7), 5888–5904. https://doi.org/10.1002/2016JC012344

Biagi, F., Gambaccini, S., & Zazzetta, M. (1998). Settlement and recruitment in fishes: The role of coastal areas. *Italian Journal of Zoology*, *65*(sup1), 269–274. https://doi.org/10.1080/11250009809386831

Bignami, F., Sciarra, R., Carniel, S., & Santoleri, R. (2007). Variability of Adriatic Sea coastal turbid waters from SeaWiFS imagery. *Journal of Geophysical Research*, *112*, C03S10. https://doi.org/10.1029/2006JC003518

Bomers, A., Schielen, R. M. J., & Hulscher, S. J. M. H. (2019). The influence of grid shape and grid size on hydraulic river modelling performance. *Environmental Fluid Mechanics*, *19*(5), 1273–1294. https://doi.org/10.1007/s10652-019-09670-4

Bonnin, L., Lett, C., Dagorn, L., Filmalter, J. D., Forget, F., Verley, P., & Capello, M. (2021). Can drifting objects drive the movements of a vulnerable pelagic shark? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*(1), 74–82. https://doi.org/10.1002/aqc.3420

Boog, C., Pietrzak, J., Dijkstra, H., Brüggemann, N., Westen, R., James, R., Bouma, T., Riva, R., Slobbe, D., Klees, R., Zijlema, M., & Katsman, C. (2019). The impact of upwelling on the intensification of anticyclonic ocean eddies in the Caribbean Sea. *Ocean Science*, *15*, 1419–1437. https://doi.org/10.5194/os-15-1419-2019

Book, J. W., Signell, R. P., & Perkins, H. (2007). Measurements of storm and nonstorm circulation in the northern Adriatic: October 2002 Through April 2003. *Journal of Geophysical Research: Oceans*, *112*(C11). https://doi.org/10.1029/2006JC003556

Boon, J. D. (2004). *Secrets of the Tide: Tide and Tidal Current Analysis and Predictions, Storm Surges and Sea Level Trends*. Horwood Publishing.

Botsford, L., Brumbaugh, D., Grimes, C., Kellner, J., Largier, J., O'Farrell, M., Ralston, S., Soulanille, E., & Wespestad, V. (2009). Connectivity, sustainability, and yield: Bridging the gap between conventional fisheries management and marine protected areas. *Reviews in Fish Biology and Fisheries*, *19*, 69–95. https://doi.org/10.1007/s11160-008-9092-z

Boutov, D., Peliz, Á., Miranda, P. M. A., Soares, P. M. M., Cardoso, R. M., Prieto, L., Ruiz, J., & García-Lafuente, J. (2014). Inter-annual variability and long term predictability of exchanges through the Strait of Gibraltar. *Global and Planetary Change*, *114*, 23–37. https://doi.org/10.1016/j.gloplacha.2013.12.009

Bracken, L., Turnbull, L., Wainwright, J., & Bogaart, P. (2015). Sediment connectivity: A framework for understanding sediment transfer at multiple scales. *Earth Surface Processes and Landforms, 40*. https://doi.org/10.1002/esp.3635

Bradford, R., Griffin, D., & Bruce, B. (2015). Estimating the duration of the pelagic phyllosoma phase of the southern rock lobster, *Jasus edwardsii* (Hutton). *Marine and Freshwater Research, 66,* 213–219. https://doi.org/10.1071/MF14065)

Bray, L., Kassis, D., & Hall-Spencer, J. M. (2017). Assessing larval connectivity for marine spatial planning in the Adriatic. *Marine Environmental Research*, *125*, 73–81. https://doi.org/10.1016/j.marenvres.2017.01.006

Brown, C. J., Harborne, A. R., Paris, C. B., & Mumby, P. J. (2016). Uniting paradigms of connectivity in marine ecology. *Ecology*, *97*(9), 2447–2457.

Brünnich, M. T. (1768). *Ichthyologia Massiliensis, sistens piscium descriptiones eorumque apud incolas nomina. Accedunt Spolia Maris Adriatici. Hafniae et Lipsiae. I-xvi + 1-110. [In 2 parts; first as i-xvi + 1-84; 2nd as Spolia e Mari Adriatica reportata: 85-110.].*

Bryden, H. L., Candela, J., & Kinder, T. H. (1994). Exchange through the Strait of Gibraltar. *Progress in Oceanography*, *33*, 201–248. https://doi.org/10.1016/0079-6611(94)90028-0

Burgos, C., Gil, J., & Olmo, L. (2013). The Spanish blackspot seabream (*Pagellus bogaraveo*) fishery in the Strait of Gibraltar: Spatial distribution and fishing effort derived from a small-scale GPRS/GSM based fisheries vessel monitoring system. *Aquatic Living Resources*, *26*, 399–407. https://doi.org/10.1051/alr/2013068

Calò, A., Félix-Hackradt, F. C., Garcia, J., Hackradt, C. W., Rocklin, D., Treviño Otón, J., & Charton, J. A. G. (2013). A review of methods to assess connectivity and dispersal between fish populations in the Mediterranean Sea. *Advances in Oceanography and Limnology*, *4*(2), 150–175. https://doi.org/10.1080/19475721.2013.840680

Calò, A., Lett, C., Mourre, B., Pérez-Ruzafa, Á., & García-Charton, J. A. (2018). Use of Lagrangian simulations to hindcast the geographical position of propagule release zones in a Mediterranean coastal fish. *Marine Environmental Research*, *134*, 16–27. https://doi.org/10.1016/j.marenvres.2017.12.011

Campana, S. (1999). Chemistry and composition of fish otoliths: Pathways, mechanisms and applications. *Marine Ecology-Progress Series - MAR ECOL-PROGR SER*, *188*, 263–297. https://doi.org/10.3354/meps188263

Candela, J., Winant, C. D., & Bryden, H. L. (1989). Meteorologically forced subinertial flows through the Strait of Gibraltar. *Journal of Geophysical*

Research: Oceans, *94*(C9), 12667–12679. https://doi.org/10.1029/JC094iC09p12667

Candelma, M., Marisaldi, L., Daniela, B., Radaelli, G., Gioacchini, G., Santojanni, A., Colella, S., & Carnevali, O. (2021). Aspects of Reproductive Biology of the European Hake (*Merluccius merluccius*) in the Northern and Central Adriatic Sea (GSA 17-Central Mediterranean Sea). *Journal of Marine Science and Engineering*, *9*, 389. https://doi.org/10.3390/jmse9040389

Carbonara, P., Intini, S., Modugno, E., Maradonna, F., Spedicato, M. T., Lembo, G., Zupa, W., & Carnevali, O. (2015). Reproductive biology characteristics of red mullet (*Mullus barbatus* L., 1758) in Southern Adriatic Sea and management implications. *Aquat. Living Resour.*, *28*, 21–31. https://doi.org/10.1051/alr/2015005

Carney, L., & Edwards, M. (2006). Cryptic Processes in the Sea: A Review of Delayed Development in theMicroscopic Life Stages of Marine Macroalgae. *ALGAE*, *21*. https://doi.org/10.4490/ALGAE.2006.21.2.161

Carrère, L., & Lyard, F. (2003). Modeling the barotropic response of the global ocean to atmospheric wind and pressure forcing—Comparisons with observations. *Geophysical Research Letters*, *30*(6). https://doi.org/10.1029/2002GL016473

Carrere, L., Lyard, F., Cancet, M., Guillot, A., & Roblou, L. (2013). *FES 2012: A New Global Tidal Model Taking Advantage of Nearly 20 Years of Altimetry*. *710*, 13. 20 Years of Progress in Radar Altimatry.

Cavraro, F., Anelli Monti, M., Matić-Skoko, S., Caccin, A., & Pranovi, F. (2023). Vulnerability of the Small-Scale Fishery to Climate Changes in the Northern-Central Adriatic Sea (Mediterranean Sea). *Fishes*, *8*(1), Article 1. https://doi.org/10.3390/fishes8010009

Chassignet, E. P., Hurlburt, H. E., Metzger, E. J., Smedstad, O. M., Cummings, J. A., Halliwell, G. R., Bleck, R., Baraille, R., Wallcraft, A. J., Lozano, C., Tolman, H. L., Srinivasan, A., Hankin, S., Cornillon, P., Weisberg, R., Barth, A., He, R., Werner, F., & Wilkin, J. (2009). US GODAE: Global Ocean Prediction with the HYbrid Coordinate Ocean Model (HYCOM). *Oceanography*, *22*(2), 64–75.

Ciannelli, L., Bailey, K., & Olsen, E. M. (2015). Evolutionary and ecological constraints of fish spawning habitats. *ICES Journal of Marine Science*, *72*(2), 285–296. https://doi.org/10.1093/icesjms/fsu145

Civitarese, G., Gačić, M., Vetrano, A., Boldrin, A., Bregant, D., Rabitti, S., & Souvermezoglou, E. (1998). Biogeochemical fluxes through the Strait of Otranto (Eastern Mediterranean). *Continental Shelf Research*, *18*(7), 773–789. https://doi.org/10.1016/S0278-4343(98)00016-8

Clementi, E., Aydogdu, A., Goglio, A. C., Pistoia, J., Escudier, R., Drudi, M., Grandi, A., Mariani, A., Lyubartsev, V., Lecci, R, Cretí, S., Coppini, G., Masina, S., & Pinardi, N. (2021). *Mediterranean Sea Physical Analysis and Forecast (CMEMS MED-Currents, EAS6 system) (Version 1) [Data set].* [Dataset]. Copernicus Monitoring Environment Marine Service (CMEMS). https://doi.org/10.25423/CMCC/MEDSEA_ANALYSISFORECAST_PHY_006_013_EAS6

Coll, M., Santojanni, A., Palomera, I., & Arneri, E. (2010). Ecosystem assessment of the North-Central Adriatic Sea: Towards a multivariate reference framework. *Marine Ecology Progress Series*, *417*, 193–210. https://doi.org/10.3354/meps08800

Commission Implementing Regulation (EU) 2016/1141 of 13 July 2016 Adopting a List of Invasive Alien Species of Union Concern Pursuant to Regulation (EU) No 1143/2014 of the European Parliament and of the Council (2022). http://data.europa.eu/eli/reg_impl/2016/1141/2022-08-02/eng

CopeMed II. (2017). *Report of the CopeMed II Workshop on methodologies for the identification of stock units in the Alboran Sea* (CopeMed II Technical Documents Technical Documents N°46; (GCP/INT/028/SPA - GCP/INT/270/EC), p. 58). Food and Agriculture Organization of the United Nations (FAO).

CopeMed II. (2019). *Report of the Mid-Term Workshop on TRANSBORAN project, "Transboundary population structure of sardine, European hake and blackspot seabream in the Alboran Sea and adjacent waters: A multidisciplinary approach"* (CopeMed II Technical Documents Technical Documents N°52; (GCP/INT/028/SPA - GCP/INT/270/EC), p. 33). Food and Agriculture Organization of the United Nations (FAO).

Costa, A. M. (2013). Somatic Condition, Growth and Reproduction of Hake, *Merluccius merluccius* L., in the Portuguese Coast. *Open Journal of Marine Science*, *13*, 12–30. https://doi.org/10.4236/ojms.2013.31002

Costello, M. J., & Chaudhary, C. (2017). Marine Biodiversity, Biogeography, Deep-Sea Gradients, and Conservation. *Current Biology*, *27*(11), R511–R527. https://doi.org/10.1016/j.cub.2017.04.060

Cowen, R. K., Gawarkiewicz, G., Pineda, J., Thorrold, S. R., & Werner, F. E. (2007). Population connectivity in marine systems: An overview.

Oceanography, *20*(SPL.ISS. 3), 14–21. https://doi.org/10.5670/oceanog.2007.26

Cowen, R. K., Lwiza, K. M., Sponaugle, S., Paris, C. B., & Olson, D. B. (2000). Connectivity of marine populations: Open or closed? *Science (New York, N.Y.)*, *287*(5454), 857–859. https://doi.org/10.1126/science.287.5454.857

Cowen, R. K., Paris, C. B., & Srinivasan, A. (2006). Scaling of connectivity in marine populations. *Science (New York, N.Y.)*, *311*(5760), 522–527. https://doi.org/10.1126/science.1122039

Cowen, R. K., & Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, *1*, 443–466. https://doi.org/10.1146/annurev.marine.010908.163757

Cozzi, S., & Giani, M. (2011). River water and nutrient discharges in the Northern Adriatic Sea: Current importance and long term changes. *Continental Shelf Research*, *31*(18), 1881–1893. https://doi.org/10.1016/j.csr.2011.08.010

Criado-Aldeanueva, F., Soto-Navarro, F. J., & García-Lafuente, J. (2012). Seasonal and interannual variability of surface heat and freshwater fluxes in the Mediterranean Sea: Budgets and exchange through the Strait of Gibraltar. *International Journal of Climatology*, *32*(2), 286–302. https://doi.org/10.1002/joc.2268

Crivellaro, M. S., Candido, D. V., Silveira, T. C. L., Fonseca, A. C., & Segal, B. (2022). A tool for a race against time: Dispersal simulations to support ongoing monitoring program of the invasive coral *Tubastraea coccinea*. *Marine Pollution Bulletin*, *185*(Pt B), 114354. https://doi.org/10.1016/j.marpolbul.2022.114354

Crochelet, E., Roberts, J., Lagabrielle, E., Obura, D., Petit, M., & Chabanet, P. (2016). A model-based assessment of reef larvae dispersal in the Western Indian Ocean reveals regional connectivity patterns- Potential implications for conservation policies. *Regional Studies in Marine Science*, *7*. https://doi.org/10.1016/j.rsma.2016.06.007

Cushman-Roisin, B., & Beckers, J.-M. (2006). *Introduction to Geophysical Fluid Dynamics: Physical and Numerical Aspects*. Academic Press.

Cushman-Roisin, B., Gacic, M., Poulain, P.-M., & Artegiani, A. (2001). *Physical Oceanography of the Adriatic Sea: Past, Present and Future*. https://doi.org/10.1007/978-94-015-9819-4

Da Ros, Z., Fanelli, E., Cassatella, S., Biagiotti, I., Canduci, G., Menicucci, S., De Felice, A., Malavolti, S., & Leonori, I. (2023). Resource Partitioning among “Ancillary” Pelagic Fishes (*Scomber* spp., *Trachurus* spp.) in the

Adriatic Sea. *Biology*, *12*(2), Article 2. https://doi.org/10.3390/biology12020272

Dagestad, K.-F., Röhrs, J., Breivik, Ø., & Ådlandsvik, B. (2018). OpenDrift v1.0: A generic framework for trajectory modelling. *Geoscientific Model Development*, *11*(4), 1405–1420. https://doi.org/10.5194/gmd-11-1405-2018

D'Agostini, A., Gherardi, D. F. M., & Pezzi, L. P. (2015). Connectivity of Marine Protected Areas and Its Relation with Total Kinetic Energy. *PLOS ONE*, *10*(10), e0139601. https://doi.org/10.1371/journal.pone.0139601

D'Aloia, C. C., Bogdanowicz, S. M., Francis, R. K., Majoris, J. E., Harrison, R. G., & Buston, P. M. (2015). Patterns, causes, and consequences of marine larval dispersal. *Proceedings of the National Academy of Sciences*, *112*(45), 13940–13945. https://doi.org/10.1073/pnas.1513754112

Darnaude, A., Arnaud-Haond, S., Hunter, E., Gaggiotti, O., Sturrock, A., Beger, M., Volckaert, F., Pérez-Ruzafa, A., López-López, L., Tanner, S. E., Turan, C., Doğdu, S. A., Katsanevakis, S., & Costantini, F. (2022). Unifying approaches to Functional Marine Connectivity for improved marine resource management: The European SEA-UNICORN COST Action. *Research Ideas and Outcomes*, *8*, e80223. https://doi.org/10.3897/rio.8.e80223

Daskalaki, E., Koufalis, E., Dimarchopoulou, D., & Tsikliras, A. C. (2022). Scientific progress made towards bridging the knowledge gap in the biology of Mediterranean marine fishes. *PloS One*, *17*(11), e0277383. https://doi.org/10.1371/journal.pone.0277383

Daud, N. R., Akhir, M. F., & Muslim, A. M. (2019). Dynamic of ENSO towards upwelling and thermal front zone in the east coast of Peninsular Malaysia. *Acta Oceanologica Sinica*, *38*(1), 48–60. https://doi.org/10.1007/s13131-019-1369-7

De la Lama-Calvente, D., Mancilla-Leytón, J. M., Borja, R., & Fernández-Rodríguez, M. J. (2024). Use of anaerobic digestate as biofertilizer: Another step forward in the valorisation of the invasive brown macroalgae *Rugulopteryx okamurae*. *Scientia Horticulturae*, *325*, 112638. https://doi.org/10.1016/j.scienta.2023.112638

De Pascalis, F., Pérez-Ruzafa, A., Gilabert, J., Marcos, C., & Umgiesser, G. (2012). Climate change response of the Mar Menor coastal lagoon (Spain) using a hydrodynamic finite element model. *Estuarine, Coastal and Shelf Science*, *114*, 118–129. https://doi.org/10.1016/j.ecss.2011.12.002

Deangelis, D., & Mooij, W. (2005). Individual-Based Modeling of Ecological and Evolutionary Processes 1. *Annu. Rev. Ecol. Evol. Syst*, *36*, 147–168. https://doi.org/10.1146/annurev.ecolsys.36.102003.152644

Defne, Z., Ganju, N. K., & Aretxabaleta, A. (2016). Estimating time-dependent connectivity in marine systems. *Geophysical Research Letters*, *43*(3), 1193–1201. https://doi.org/10.1002/2015GL066888

Demmer, J., Neill, S. P., Andres, O., Malham, S. K., Jones, T., & Robins, P. (2022). Larval dispersal from an energetic tidal channel and implications for blue mussel (*Mytilus edulis*) shellfisheries. *Aquaculture International*, *30*(6), 2969–2995. https://doi.org/10.1007/s10499-022-00948-x

Desbrosses, P. (1932). La dorade commune (*Pagellus centrodontus* Delaroche) et sa pêche. *Revue Du Travail de L'Office Des Pêches Maritime*, *5*(18), 167-222.

Deudero, S., Arnaud-Haond, S., Di Franco, A., Fromentin, J.-M., Gucu, A. C., Hilário, A., Mariani, P., Panigada, S., Pascual, M., Rossi, V., Soldo, A., Villamor, A., Zalota, A., & Briand, F. (2017). Marine connectivity: Migration and larval dispersal - An overview. *CIESM Workshop Monographs*, *48*, 5–18.

Di Franco, A., Coppini, G., Pujolar, J. M., Leo, G. A. D., Gatto, M., Lyubartsev, V., Melià, P., Zane, L., & Guidetti, P. (2012). Assessing Dispersal Patterns of Fish Propagules from an Effective Mediterranean Marine Protected Area. *PLOS ONE*, *7*(12), e52108. https://doi.org/10.1371/journal.pone.0052108

Dickey, T. (2001). The Role of New Technology in Advancing Ocean Biogeochemical Research. *Oceanography*, *14*(4), 108–120. https://doi.org/10.5670/oceanog.2001.11

Dominique, P. (2011). INDICATORS – Constructing and validating indicators of the effectiveness of marine protected areas. In *Marine Protected Areas: A Multidisciplinary Approach* (pp. 247–266). https://doi.org/10.1017/CBO9781139049382.014

Döös, K., Kjellsson, J., & Jönsson, B. (2013). TRACMASS—A Lagrangian Trajectory Model. In T. Soomere & E. Quak (Eds.), *Preventive Methods for Coastal Protection: Towards the Use of Ocean Dynamics for Pollution Control* (pp. 225–249). Springer International Publishing. https://doi.org/10.1007/978-3-319-00440-2_7

Dorostkar, A., Boegman, L., Schweitzer, S., & Pollard, A. (2022). Three-dimensional numerical simulation of basin-scale internal waves in a long narrow lake. *Environmental Fluid Mechanics*, *23*. https://doi.org/10.1007/s10652-022-09868-z

D'Ortenzio, F., & Ribera d'Alcalà, M. (2009). On the trophic regimes of the Mediterranean Sea: A satellite analysis. *Biogeosciences*, *6*(2), 139–148. https://doi.org/10.5194/bg-6-139-2009

Dubois, M., Rossi, V., Ser-Giacomi, E., Arnaud-Haond, S., López, C., & Hernández-García, E. (2016). Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems. *Global Ecology and Biogeography*, *25*(5), 503–515. https://doi.org/10.1111/geb.12431

Echevarría, F., García Lafuente, J., Bruno, M., Gorsky, G., Goutx, M., González, N., García, C. M., Gómez, F., Vargas, J. M., Picheral, M., Striby, L., Varela, M., Alonso, J. J., Reul, A., Cózar, A., Prieto, L., Sarhan, T., Plaza, F., & Jiménez-Gómez, F. (2002). Physical–biological coupling in the Strait of Gibraltar. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*(19), 4115–4130. https://doi.org/10.1016/S0967-0645(02)00145-5

Edson, J., Jampana, V., Weller, R., Bigorre, S., Plueddemann, A., Fairall, C., Miller, S., Mahrt, L., Vickers, D., & Hersbach, H. (2013). On the Exchange of Momentum over the Open Ocean. *Journal of Physical Oceanography*, *43*, 1589–1610. https://doi.org/10.1175/JPO-D-12-0173.1

EMODnet Bathymetry Consortium. (2018). *European Marine Observation and Data Network (EMODnet)* [Map]. Energy, Climate change, Environment. European Commission. 10.12770/18ff0d48-b203-4a65-94a9-5fd8b0ec35f6

Esposito, G., Donnet, S., Berta, M., Shcherbina, A. Y., Freilich, M., Centurioni, L., D'Asaro, E. A., Farrar, J. T., Johnston, T. M. S., Mahadevan, A., Özgökmen, T., Pascual, A., Poulain, P., Ruiz, S., Tarry, D. R., & Griffa, A. (2023). Inertial Oscillations and Frontal Processes in an Alboran Sea Jet: Effects on Divergence and Vertical Transport. *Journal of Geophysical Research: Oceans*, *128*(3), e2022JC019004. https://doi.org/10.1029/2022JC019004

Estévez, R., Palacios, M., Cervera, J., & González-Duarte, M. (2022). Expansion of the invasive alga *Rugulopteryx okamurae* (Dictyotaceae, Ochrophyta) in the Mediterranean Sea: First evidence as epiphyte of the cold-water coral *Dendrophyllia ramea* (Cnidaria: Scleractinia). *BioInvasions Records*, *11*(4), 925–936. https://doi.org/10.3391/bir.2022.11.4.11

Estradivari, Agung, Muh. F., Adhuri, D. S., Ferse, S. C. A., Sualia, I., Andradi-Brown, D. A., Campbell, S. J., Iqbal, M., Jonas, H. D., Lazuardi, M. E., Nanlohy, H., Pakiding, F., Pusparini, N. K. S., Ramadhana, H. C., Ruchimat, T., Santiadji, I. W. V., Timisela, N. R., Veverka, L., & Ahmadia, G. N. (2022). Marine conservation beyond MPAs: Towards the recognition of other effective area-based conservation measures (OECMs) in Indonesia. *Marine Policy*, *137*, 104939. https://doi.org/10.1016/j.marpol.2021.104939

Faillettaz, R., Paris, C. B., & Irisson, J. O. (2018). Larval fish swimming behavior alters dispersal patterns from marine protected areas in the North-Western Mediterranean Sea. *Frontiers in Marine Science*, *5*(MAR). https://doi.org/10.3389/fmars.2018.00097

Fanelli, E., Da Ros, Z., Menicucci, S., Malavolti, S., Biagiotti, I., Canduci, G., De Felice, A., & Leonori, I. (2023). The pelagic food web of the Western Adriatic Sea: A focus on the role of small pelagics. *Scientific Reports*, *13*(1), 14554. https://doi.org/10.1038/s41598-023-40665-w

Fanelli, E., Principato, E., Monfardini, E., Da Ros, Z., Scarcella, G., Santojanni, A., & Colella, S. (2022). Seasonal Trophic Ecology and Diet Shift in the Common Sole *Solea solea* in the Central Adriatic Sea. *Animals*, *12*(23), Article 23. https://doi.org/10.3390/ani12233369

Fanjul, E. Á., Gómez, B. P., & Arévalo, I. R. S. (2001). Nivmar: A storm surge forecasting system for Spanish waters. *Scientia Marina*, *65*(S1), Article S1. https://doi.org/10.3989/scimar.2001.65s1145

Faria, J., Prestes, A. C. L., Moreu, I., Cacabelos, E., & Martins, G. M. (2022). Dramatic changes in the structure of shallow-water marine benthic communities following the invasion by *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in Azores (NE Atlantic). *Marine Pollution Bulletin*, *175*, 113358. https://doi.org/10.1016/j.marpolbul.2022.113358

Farmer, D. M., Armi, L., Armi, L., & Farmer, D. M. (1988). The flow of Atlantic water through the Strait of Gibraltar. *Progress in Oceanography*, *21*(1), 1–103. https://doi.org/10.1016/0079-6611(88)90055-9

Federico, I., Pinardi, N., Coppini, G., Oddo, P., Lecci, R., & Mossa, M. (2017). Coastal ocean forecasting with an unstructured grid model in the southern Adriatic and northern Ionian seas. *Natural Hazards and Earth System Sciences*, *17*(1), 45–59. https://doi.org/10.5194/nhess-17-45-2017

Féral, J.-P. (2002). How useful are the genetic markers in attempts to understand and manage marine biodiversity? *Journal of Experimental Marine Biology and Ecology*, *268*(2), 121–145. https://doi.org/10.1016/S0022-0981(01)00382-3

Ferrari, A., Spiga, M., Rodriguez, M. D., Fiorentino, F., Gil-Herrera, J., Hernandez, P., Hidalgo, M., Johnstone, C., Khemiri, S., Mokhtar-Jamaï, K., Nadal, I., Pérez, M., Sammartino, S., Vasconcellos, M., & Cariani, A. (2023). Matching an Old Marine Paradigm: Limitless Connectivity in a Deep-Water Fish over a Large Distance. *Animals*, *13*(17), Article 17. https://doi.org/10.3390/ani13172691

Ferrarin, C., Cucco, A., Umgiesser, G., Bellafiore, D., & Amos, C. L. (2010). Modelling fluxes of water and sediment between Venice Lagoon and the sea. *Continental Shelf Research*, *30*(8), 904–914. https://doi.org/10.1016/j.csr.2009.08.014

Ferrarin, C., Davolio, S., Bellafiore, D., Ghezzo, M., Maicu, F., Mc Kiver, W., Drofa, O., Umgiesser, G., Bajo, M., De Pascalis, F., Malguzzi, P., Zaggia, L., Lorenzetti, G., & Manfè, G. (2019). Cross-scale operational oceanography in the Adriatic Sea. *Journal of Operational Oceanography*, *12*(2), 86–103. https://doi.org/10.1080/1755876X.2019.1576275

Ferrarin, C., Maicu, F., & Umgiesser, G. (2017). The effect of lagoons on Adriatic Sea tidal dynamics. *Ocean Modelling*, *119*, 57–71. https://doi.org/10.1016/j.ocemod.2017.09.009

Ferrarin, C., Umgiesser, G., Cucco, A., Hsu, T.-W., Roland, A., & Amos, C. L. (2008). Development and validation of a finite element morphological model for shallow water basins. *Coastal Engineering*, *55*(9), 716–731. https://doi.org/10.1016/j.coastaleng.2008.02.016

Ferrarin, C., Umgiesser, G., Roland, A., Bajo, M., De Pascalis, F., Ghezzo, M., & Scroccaro, I. (2016). Sediment dynamics and budget in a microtidal lagoon—A numerical investigation. *Marine Geology*, *381*, 163–174. https://doi.org/10.1016/j.margeo.2016.09.006

Ferraro, G., & Failler, P. (2022). Bringing nature into decision-making and policy design: Experiences from overseas Europe. *Policy Design and Practice*, *5*(2), 226–244. https://doi.org/10.1080/25741292.2021.1885797

Ferreira-Anta, T., Flórez-Fernández, N., Torres, M. D., Mazón, J., & Dominguez, H. (2023). Microwave-Assisted Hydrothermal Processing of *Rugulopteryx okamurae*. *Marine Drugs*, *21*(6), 319. https://doi.org/10.3390/md21060319

Fifani, G., Baudena, A., Fakhri, M., Baaklini, G., Faugère, Y., Morrow, R., Mortier, L., & d'Ovidio, F. (2021). Drifting Speed of Lagrangian Fronts and Oil Spill Dispersal at the Ocean Surface. *Remote Sensing*, *13*(22), Article 22. https://doi.org/10.3390/rs13224499

Figueroa, F. L., Vega, J., Valderrama, M., Korbee, N., Mercado, J., Bañares España, E., & Flores-Moya, A. (2020). Invasión de la especie exótica

Rugulopteryx okamurae en Andalucía I: Estudios preliminares de la actividad fotosintética. *Algas*, *56*, 35–46.

Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F., & Huse, G. (2007). Linking behavioural ecology and oceanography: Larval behaviour determines growth, mortality and dispersal. *Marine Ecology Progress Series*, *347*, 195–205. https://doi.org/10.3354/meps06978

Flexas, M. M., Gomis, D., Ruiz, S., Pascual, A., & León, P. (2006). In situ and satellite observations of the eastward migration of the Western Alboran Sea Gyre. *Progress in Oceanography*, *70*(2–4), 486–509. https://doi.org/10.1016/j.pocean.2006.03.017

Florido, M., Megina, C., & García, J. (2023). Coexistiendo con una invasora en el estrecho de Gibraltar: La integración de *Rugulopteryx okamurae* en la fauna y flora residente. *Almoraima. Revista de Estudios Campogibraltareños*, *58*.

Fogarty, M., & Botsford, L. (2007). Population Connectivity and Spatial Management of Marine Fisheries. *Oceanography*, *20*(3), 112–123. https://doi.org/10.5670/oceanog.2007.34

Fortič, A., Alshikh Rasheed, R., Almagid, Z., Badreddine, A., Báez, J., Belmonte-Gallegos, Á., Bettoso, N., Borme, D., Camisa, F., Caracciolo, D., Çinar, M., Crocetta, F., Ćetković, I., Doğan, A., Galiya, M., huertos, alvaro, Grech, D., Guallart, J., Gündeğer, G., & Virgili, R. (2023). New records of introduced species in the Mediterranean Sea (April 2023). *Mediterranean Marine Science*, *24*, 182–202. https://doi.org/10.12681/mms.34016

Fox-Kemper, B., & Menemenlis, D. (2008). Can Large Eddy Simulation Techniques Improve Mesoscale Rich Ocean Models? In *Ocean Modeling in an Eddying Regime* (pp. 319–337). American Geophysical Union (AGU). https://doi.org/10.1029/177GM19

Fredj, E., Carlson, D. F., Amitai, Y., Gozolchiani, A., & Gildor, H. (2016). The particle tracking and analysis toolbox (PaTATO) for Matlab. *Limnology and Oceanography: Methods*, *14*(9), 586–599. https://doi.org/10.1002/lom3.10114

Fuchs, H. L., Gerbi, G. P., Hunter, E. J., Christman, A. J., & Diez, F. J. (2015). Hydrodynamic sensing and behavior by oyster larvae in turbulence and waves. *Journal of Experimental Biology*, *218*(9), 1419–1432. https://doi.org/10.1242/jeb.118562

Fuchs, H. L., Specht, J. A., Adams, D. K., & Christman, A. J. (2017). Turbulence induces metabolically costly behaviors and inhibits food capture in oyster larvae, causing net energy loss. *Journal of Experimental Biology*, *220*(19), 3419–3431. https://doi.org/10.1242/jeb.161125

Fuller, E., Samhouri, J., Stoll, J., Levin, S., & Watson, J. (2017). Characterizing fisheries connectivity in marine social– ecological systems. *ICES Journal of Marine Science*, *74*. https://doi.org/10.1093/icesjms/fsx128

Fumagalli, M. (2013). Assessing the effect of sequencing depth and sample size in population genetics inferences. *PloS One*, *8*(11), e79667. https://doi.org/10.1371/journal.pone.0079667

Gaide, S., Bender, M., & Wintersteller, P. (2018). Gridded EM122 multibeam-echosounder bathymetry of cruise MSM36—Gulf of Cadiz [Dataset]. In *MARUM - Center for Marine Environmental Sciences, University Bremen*. PANGAEA. https://doi.org/10.1594/PANGAEA.893200

Gaines, S., Gaylord, B., Gerber, L., Hastings, A., & Kinlan, B. (2007). Connecting Places: The Ecological Consequences of Dispersal in the Sea. *Oceanography*, *20*(3), 90–99. https://doi.org/10.5670/oceanog.2007.32

Gaines, S., White, C., Carr, M., & Palumbi, S. (2010). Designing Marine Reserve Networks for Both Conservation and Fisheries Management. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 18286–18293. https://doi.org/10.1073/pnas.0906473107

Galland, J.-C., Goutal, N., & Hervouet, J.-M. (1991). TELEMAC: A new numerical model for solving shallow water equations. *Advances in Water Resources*, *14*(3), 138–148. https://doi.org/10.1016/0309-1708(91)90006-A

Gamoyo, M., Obura, D., & Reason, C. J. C. (2019). Estimating Connectivity Through Larval Dispersal in the Western Indian Ocean. *Journal of Geophysical Research: Biogeosciences*, *124*(8), 2446–2459. https://doi.org/10.1029/2019JG005128

García Lafuente, J., Alvarez Fanjul, E., Vargas, J., & Ratsimandresy, A. (2002). Subinertial variability in the flow through the Strait of Gibraltar. *Journal of Geophysical Research*, *107*. https://doi.org/10.1029/2001JC001104

García Lafuente, J., Bruque Pozas, E., Sánchez Garrido, J. C., Sannino, G., & Sammartino, S. (2013). The interface mixing layer and the tidal dynamics at the eastern part of the Strait of Gibraltar. *Journal of Marine Systems*, *117*, 31–42. https://doi.org/10.1016/j.jmarsys.2013.02.014

García Lafuente, J., Cano, N., Vargas, M., Rubín, J. P., & Hernández-Guerra, A. (1998). Evolution of the Alboran Sea hydrographic structures during July 1993. *Deep Sea Research Part I: Oceanographic Research Papers*, *45*(1), 39–65. https://doi.org/10.1016/S0967-0637(97)00216-1

García Lafuente, J., & Delgado, J. (2004). The Meandering Path of a Drifter around the Western Alboran Gyre. *Journal of Physical Oceanography*, *34*(3), 685–692. https://doi.org/10.1175/3516.1

García Lafuente, J., Delgado, J., & Criado, F. (2002). Inflow interruption by meteorological forcing in the Strait of Gibraltar. *Geophysical Research Letters*, *29*(19), 20-1-20–24. https://doi.org/10.1029/2002GL015446

García Lafuente, J., Sammartino, S., Sánchez Garrido, J. C., & Naranjo, C. (2019). On the role of the Bay of Algeciras in the exchange across the Strait of Gibraltar. *Regional Studies in Marine Science*, *29*, 100620. https://doi.org/10.1016/j.rsma.2019.100620

García-Gómez, J. C., Florido, M., Olaya-Ponzone, L., Rey Díaz de Rada, J., Donázar-Aramendía, I., Chacón, M., Quintero, J. J., Magariño, S., & Megina, C. (2021). Monitoring Extreme Impacts of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in El Estrecho Natural Park (Biosphere Reserve). Showing Radical Changes in the Underwater Seascape. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.639161

García-Gómez, J. C., Sempere-Valverde, J., González, A. R., Martínez-Chacón, M., Olaya-Ponzone, L., Sánchez-Moyano, E., Ostalé-Valriberas, E., & Megina, C. (2020). From exotic to invasive in record time: The extreme impact of *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) in the Strait of Gibraltar. *Science of The Total Environment*, *704*, 135408. https://doi.org/10.1016/j.scitotenv.2019.135408

García-Gómez, J. C., Sempere-Valverde, J., Ostalé-Valriberas, E., Martínez, M., González, A. R., Espinosa, F., Sánchez-Moyano, E., Megina, C., & Parada, A. (2018). *RUGULOPTERYX OKAMURAE* (E.Y. DAWSON) I.K. HWANG, W. J. LEE & H.S. KIM (DICTYOTALES, OCHROPHYTA), ALGA EXÓTICA “EXPLOSIVA” EN EL ESTRECHO DE GIBRALTAR. OBSERVACIONES PRELIMINARES DE SU DISTRIBUCIÓN E IMPACTO. *Almoraima. Revista de Estudios Campogibraltareños*.

García-Lafuente, J., Delgado, J., Sánchez Román, A., Soto, J., Carracedo, L., & Díaz del Río, G. (2009). Interannual variability of the Mediterranean outflow observed in Espartel sill, western Strait of Gibraltar. *Journal of Geophysical Research: Oceans*, *114*(C10). https://doi.org/10.1029/2009JC005496

García-Lafuente, J., Nadal, I., Sammartino, S., Korbee, N., & Figueroa, F. L. (2023). Could secondary flows have made possible the cross-strait transport and explosive invasion of *Rugulopteryx okamurae* algae in the Strait of Gibraltar? *PLOS ONE*, *18*(5), e0285470. https://doi.org/10.1371/journal.pone.0285470

García-Lafuente, J., Naranjo, C., Sammartino, S., Sánchez-Garrido, J. C., & Delgado, J. (2017). The Mediterranean outflow in the Strait of Gibraltar and its connection with upstream conditions in the Alborán Sea. *Ocean Science*, *13*(2), 195–207. https://doi.org/10.5194/os-13-195-2017

García-Lafuente, J., Sammartino, S., Huertas, I. E., Flecha, S., Sánchez-Leal, R. F., Naranjo, C., Nadal, I., & Bellanco, M. J. (2021). Hotter and Weaker Mediterranean Outflow as a Response to Basin-Wide Alterations. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.613444

García-Lafuente, J., Sammartino, S., Sánchez-Garrido, J. C., & Naranjo, C. (2018). Asymmetric Baroclinic Response to Tidal Forcing Along the Main Sill of the Strait of Gibraltar Inferred from Mooring Observations. In M. G. Velarde, R. Yu. Tarakanov, & A. V. Marchenko (Eds.), *The Ocean in Motion: Circulation, Waves, Polar Oceanography* (pp. 193–210). Springer International Publishing. https://doi.org/10.1007/978-3-319-71934-4_14

García-Lafuente, J., Sánchez Román, A., Díaz del Río, G., Sannino, G., & Sánchez Garrido, J. C. (2007). Recent observations of seasonal variability of the Mediterranean outflow in the Strait of Gibraltar. *Journal of Geophysical Research: Oceans*, *112*(C10). https://doi.org/10.1029/2006JC003992

García-Lafuente, J., Sanchez-Garrido, J. C., Garcia, A., Hidalgo, M., Sammartino, S., & Laiz, R. (2021). Biophysical Processes Determining the Connectivity of the Alboran Sea Fish Populations. In J. C. Báez, J.-T. Vázquez, J. A. Camiñas, & M. Malouli Idrissi (Eds.), *Alboran Sea—Ecosystems and Marine Resources* (pp. 459–487). Springer International Publishing. https://doi.org/10.1007/978-3-030-65516-7_12

García-Lafuente, J., Vargas, J. M., Plaza, F., Sarhan, T., Candela, J., & Bascheck, B. (2000). Tide at the eastern section of the Strait of Gibraltar. *Journal of Geophysical Research: Oceans*, *105*(C6), 14197–14213. https://doi.org/10.1029/2000JC900007

Garrett, C. (2004). Frictional processes in straits. *Deep Sea Research Part II: Topical Studies in Oceanography*, *51*(4), 393–410. https://doi.org/10.1016/j.dsr2.2003.10.005

Garrett, C., Maccready, P., & Rhines, P. (1993). Boundary Mixing and Arrested Ekman Layers: Rotating Stratified Flow Near a Sloping Boundary. *Annu. Rev. Fluid Mech.*, *25*, 291–323. https://doi.org/10.1146/annurev.fl.25.010193.001451

Gerber, L. R., Mancha-Cisneros, M. D. M., O'Connor, M. I., & Selig, E. R. (2014). Climate change impacts on connectivity in the ocean: Implications for conservation. *Ecosphere*, *5*(3), art33. https://doi.org/10.1890/ES13-00336.1

GFCM. (2009). *Resolution GFCM/33/2009/2 on the establishment of geographical subareas in the GFCM area of application, amending Resolution GFCM/31/2007/2.*

GFCM. (2021a). *Recommendation GFCM/44/2021/2 on the establishment of a fisheries restricted area in the Jabuka/Pomo Pit in the Adriatic Sea (geographical subarea 17), amending Recommendation GFCM/41/2017/3.*

GFCM. (2021b). *Report of the Working Group on Stock Assessment of Demersal species (WGSAD). General Fisheries Commission for the Mediterranean. Online, 18–30 January 2021.*

Ghezzo, M., De Pascalis, F., Umgiesser, G., Zemlys, P., Sigovini, M., Marcos, C., & Pérez-Ruzafa, A. (2015). Connectivity in Three European Coastal Lagoons. *Estuaries and Coasts*, *38*(5), 1764–1781. https://doi.org/10.1007/s12237-014-9908-0

Ghezzo, M., Pellizzato, M., De Pascalis, F., Silvestri, S., & Umgiesser, G. (2018). Natural resources and climate change: A study of the potential impact on Manila clam in the Venice lagoon. *Science of the Total Environment*, *645*, 419–430. https://doi.org/10.1016/j.scitotenv.2018.07.060

Ghezzo, M., Sarretta, A., Sigovini, M., Guerzoni, S., Tagliapietra, D., & Umgiesser, G. (2011). Modeling the inter-annual variability of salinity in the lagoon of Venice in relation to the water framework directive typologies. *Ocean & Coastal Management*, *54*(9), 706–719. https://doi.org/10.1016/j.ocecoaman.2011.06.007

Gil Herrera, J. (2006). *Biología y pesca del voraz [*Pagellus bogaraveo *(Brünnich, 1768)] en el Estrecho de Gibraltar* [PhD thesis]. Universidad de Cádiz. Cadiz, Spain.

Gil Herrera, J. (2010). *SPANISH INFORMATION ABOUT THE RED SEABREAM (*PAGELLUS BOGARAVEO*) FISHERY IN THE STRAIT*

OF GIBRALTAR REGION CopeMed II Occasional Paper Nº 2 (GCP/INT/028/SPA-GCP/INT/006/EC). www.faocopemed.org

Gil, J., Silva, L., & Sobrino, I. (2001). Results of two tagging survey of red seabream *Pagellus bogaraveo*, (Brunnich, 1768) in the Spanish south Mediterranen region. *Thalassas: An International Journal of Marine Sciences*, *17*(2), 43–46.

Gil-Herrera, J., Gutiérrez-Estrada, J. C., Benchoucha, S., Pérez-Gil, J. L., Sanz-Fernández, V., el Arraf, S., Burgos, C., Malouli Idrissi, M., & Farias, C. (2021). The Blackspot Seabream Fishery in the Strait of Gibraltar: Lessons and Future Perspectives of Shared Marine Resource. In J. C. Báez, J.-T. Vázquez, J. A. Camiñas, & M. Malouli Idrissi (Eds.), *Alboran Sea—Ecosystems and Marine Resources* (pp. 629–657). Springer International Publishing. https://doi.org/10.1007/978-3-030-65516-7_19

Gill, A. E. (1982). *Atmosphere-Ocean Dynamics*. Academic Press.

Goethel, D. R., & Berger, A. M. (2017). Accounting for spatial complexities in the calculation of biological reference points: Effects of misdiagnosing population structure for stock status indicators. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(11), 1878–1894. https://doi.org/10.1139/cjfas-2016-0290

Goodwin, J. D., Munroe, D. M., Defne, Z., Ganju, N. K., & Vasslides, J. (2019). Estimating Connectivity of Hard Clam (Mercenaria mercenaria) and Eastern Oyster (Crassostrea virginica) Larvae in Barnegat Bay. *Journal of Marine Science and Engineering*, *7*(6), Article 6. https://doi.org/10.3390/jmse7060167

Gordillo, F. J. L., Carmona, R., & Jiménez, C. (2022). A Warmer Arctic Compromises Winter Survival of Habitat-Forming Seaweeds. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.750209

Graham, J., Watson, J., García-García, L., Bradley, K., Bradley, R., Brown, M., Ciotti, B., Goodwin, D., Nash, R., Roche, W., Wogerbauer, C., & Hyder, K. (2023). Pelagic connectivity of European sea bass between spawning and nursery grounds. *Frontiers in Marine Science*. https://doi.org/10.3389/fmars.2022.1046585

Grati, F., Aladžuz, A., Azzurro, E., Bolognini, L., Carbonara, P., Çobani, M., Domenichetti, F., Dragičević, B., Dulčić, J., Durović, M., Ikica, Z., Joksimović, A., Kolitari, J., Marčeta, B., Matić-Skoko, S., Vrdoljak, D., Lembo, G., Santojanni, A., Spedicato, M. T., … Milone, N. (2018). Seasonal dynamics of small-scale fisheries in the Adriatic Sea.

Mediterranean Marine Science, *19*(1), 21–35. https://doi.org/10.12681/mms.2153

Greenberg, D., Dupont, F., Lyard, F., Lynch, D., & Werner, F. (2007). Resolution issues in numerical models of oceanic and coastal circulation. *Continental Shelf Research*, *27*, 1317–1343. https://doi.org/10.1016/j.csr.2007.01.023

Griffies, S. M., & Adcroft, A. J. (2008). Formulating the equations of ocean models. In M. W. Hecht & H. Hasumi (Eds.), *Geophysical Monograph Series* (Vol. 177, pp. 281–317). American Geophysical Union. https://doi.org/10.1029/177GM18

Guidetti, P., & Claudet, J. (2010). Comanagement practices enhance fisheries in marine protected areas. *Conservation Biology: The Journal of the Society for Conservation Biology*, *24*(1), 312–318. https://doi.org/10.1111/j.1523-1739.2009.01358.x

Hansen, F., Pastor-Rollan, A., Christensen, A., & Stuer-Lauridsen, F. (2024). Using biophysical modelling and marine connectivity to assess the risk of natural dispersal of non-indigenous species to comply with the Ballast Water Management Convention. *Biological Invasions*, 1–22. https://doi.org/10.1007/s10530-024-03327-0

Hariri, S., Meier, H. E. M., & Väli, G. (2024). Investigating the influence of sub-mesoscale current structures on Baltic Sea connectivity through a Lagrangian analysis. *Frontiers in Marine Science*, *11*. https://doi.org/10.3389/fmars.2024.1340291

Hauser, L., & Ward, R. (1998). Population identification in pelagic fish: The limits of molecular markers. In *Advances in Molecular Ecology* (pp. 191–224).

Hedgecock, D., Barber, P., & Edmands, S. (2007). Genetic Approaches to Measuring Connectivity. *Oceanography (Washington D.C.)*, *20*, 70–79. https://doi.org/10.5670/oceanog.2007.30

Hersbach, H., Bell, B., Berrisford, P., Biavati, G., Horányi, A., Muñoz Sabater, J., Nicolas, J., Peubey, C., Radu, R., Rozum, I., Schepers, D., Simmons, A., Soci, C., Dee, D., Thépaut, J-N. (2023). *ERA5 hourly data on single levels from 1940 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS)* [Dataset]. https://doi.org/10.24381/cds.adbb2d47

Hidalgo, M., Kaplan, D. M., Kerr, L. A., Watson, J. R., Paris, C. B., & Browman, H. I. (2017). Advancing the link between ocean connectivity, ecological function and management challenges. *Ices Journal Of*

Marine Science, *74*(6), 1702–1707. https://doi.org/10.1093/icesjms/fsx112

Hidalgo, M., Ligas, A., Bellido, J. M., Bitetto, I., Carbonara, P., Carlucci, R., Guijarro, B., Jadaud, A., Lembo, G., Manfredi, C., Esteban, A., Garofalo, G., Ikica, Z., García, C., de Sola, L. G., Kavadas, S., Maina, I., Sion, L., Vittori, S., & Vrgoc, N. (2019). Size-dependent survival of european hake juveniles in the Mediterranean sea. *Scientia Marina*, *83*(S1), 207–221. https://doi.org/10.3989/scimar.04857.16A

Hidalgo, M., Rossi, V., Monroy, P., Ser-Giacomi, E., Hernández-García, E., Guijarro, B., Massutí, E., Alemany, F., Jadaud, A., Perez, J. L., & Reglero, P. (2019). Accounting for ocean connectivity and hydroclimate in fish recruitment fluctuations within transboundary metapopulations. *Ecological Applications*, *29*(5). https://doi.org/10.1002/eap.1913

Hsu, P.-C., Ho, C.-Y., Lee, H.-J., Lu, C.-Y., & Ho, C.-R. (2020). Temporal Variation and Spatial Structure of The Kuroshio-Induced Submesoscale Island Vortices Observed from GCOM-C and Himawari-8 Data. *Remote Sensing*, *12*, 883. https://doi.org/10.3390/rs12050883

Huang, Z. G. (1994). *Marine Species and Their Distributions in China's Seas.* China Ocean Press.

Hwang, I.-K., Lee, W., Kim, H.-S., & Clerck, O. (2009). Taxonomic Reappraisal of *Dilophus okamurae* (Dictyotales, Phaeophyta) from The Western Pacific Ocean. *Phycologia*, *48*, 1–12. https://doi.org/10.2216/07-68.1

Hyun, B., Shin, K., Jang, M.-C., Jang, P.-G., Lee, W.-J., Park, C., & Choi, K.-H. (2015). Potential invasions of phytoplankton in ship ballast water at South Korean ports. *Marine and Freshwater Research*, *67*. https://doi.org/10.1071/MF15170

Iacono, R., Napolitano, E., Palma, M., & Sannino, G. (2021). The Tyrrhenian Sea Circulation: A Review of Recent Work. *Sustainability*, *13*(11), Article 11. https://doi.org/10.3390/su13116371

Ibáñez-Tejero, L., Ladah, L. B., Sánchez-Velasco, L., Barton, E. D., & Jiménez-Rosenberg, S. P. A. (2019). Vertical distribution and abundance of copepod nauplii and ichthyoplankton in northern Baja California during strong internal tidal forcing. *Journal of Plankton Research*, *41*(2), 177–187. https://doi.org/10.1093/plankt/fbz007

Jalón-Rojas, I., Wang, X. H., & Fredj, E. (2019). A 3D numerical model to Track Marine Plastic Debris (TrackMPD): Sensitivity of microplastic trajectories and fates to particle dynamical properties and physical processes. *Marine Pollution Bulletin*, *141*, 256–272. https://doi.org/10.1016/j.marpolbul.2019.02.052

Jardas, I., Šantić, M., & Pallaoro, A. (2004). Diet composition and feeding intensity of horse mackerel, *Trachurus trachurus* (Osteichthyes: Carangidae) in the eastern Adriatic. *Marine Biology*, *144*(6), 1051–1056. https://doi.org/10.1007/s00227-003-1281-7

Jensen, M., Nisancioglu, K., & Spall, M. (2018). Large Changes in Sea Ice Triggered by Small Changes in Atlantic Water Temperature. *Journal of Climate*, *31*. https://doi.org/10.1175/JCLI-D-17-0802.1

Johnson, G. C., & Ohlsen, D. R. (1994). Frictionally Modified Rotating Hydraulic Channel Exchange and Ocean Outflows. *Journal of Physical Oceanography*, *24*(1), 66–78. https://doi.org/10.1175/1520-0485(1994)024<0066:FMRHCE>2.0.CO;2

Jones, B. (2014). Nemo: A parallelized Lagrangian particle-tracking model. *Computer Science, Environmental Science*.

Jones, G. P., Almany, G. R., Russ, G. R., Sale, P. F., Steneck, R. S., Van Oppen, M. J. H., & Willis, B. L. (2009). Larval retention and connectivity among populations of corals and reef fishes: History, advances and challenges. *Coral Reefs*, *28*(2), 307–325. https://doi.org/10.1007/s00338-009-0469-9

Jönsson, B. F., & Watson, J. R. (2016). The timescales of global surface-ocean connectivity. *Nature Communications*, *7*, 11239. https://doi.org/10.1038/ncomms11239

Jungclaus, J. H., Fischer, N., Haak, H., Lohmann, K., Marotzke, J., Matei, D., Mikolajewicz, U., Notz, D., & von Storch, J. S. (2013). Characteristics of the ocean simulations in the Max Planck Institute Ocean Model (MPIOM) the ocean component of the MPI-Earth system model. *Journal of Advances in Modeling Earth Systems*, *5*(2), 422–446. https://doi.org/10.1002/jame.20023

Juza, M., Renault, L., Ruiz, S., & Tintoré, J. (2013). Origin and pathways of Winter Intermediate Water in the Northwestern Mediterranean Sea using observations and numerical simulation. *Journal of Geophysical Research: Oceans*, *118*(12), 6621–6633. https://doi.org/10.1002/2013JC009231

Kadoya, T. (2009). Assessing functional connectivity using empirical data. *Population Ecology*, *51*(1), 5–15. https://doi.org/10.1007/s10144-008-0120-6

Kasapidis, P., & Magoulas, A. (2008). Development and application of microsatellite markers to address the population structure of the horse mackerel *Trachurus trachurus*. *Fisheries Research*, *89*(2), 132–135. https://doi.org/10.1016/j.fishres.2007.09.015

Katsanevakis, S., Poursanidis, D., Hoffmann, R., Rizgalla, J., Rothman, S. B.-S., Levitt-Barmats, Y., & Espinosa Torre, F. (2020). *Unpublished Mediterranean records of marine alien and cryptogenic species*. https://doi.org/10.3391/bir.2020.9.2.01

Kendrick, G. A., Orth, R. J., Statton, J., Hovey, R., Ruiz Montoya, L., Lowe, R. J., Krauss, S. L., & Sinclair, E. A. (2017). Demographic and genetic connectivity: The role and consequences of reproduction, dispersal and recruitment in seagrasses. *Biological Reviews*, *92*(2), 921–938. https://doi.org/10.1111/brv.12261

Khoufi, W., Ferreri, R., Jaziri, H., El Fehri, S., Gargano, A., Mangano, S., Ben Meriem, S., Romdhane, M. S., Bonanno, A., Aronica, S., Genovese, S., Mazzola, S., & Basilone, G. (2014). Reproductive traits and seasonal variability of *Merluccius merluccius* from the Tunisian coast. *Journal of the Marine Biological Association of the United Kingdom*, *94*, 1545–1556. https://doi.org/10.1017/S0025315414000356

Kinder, T. H., & Bryden, H. L. (1990). Aspiration of Deep Waters through Straits. In L. J. Pratt (Ed.), *The Physical Oceanography of Sea Straits* (pp. 295–319). Springer Netherlands. https://doi.org/10.1007/978-94-009-0677-8_14

Kowalik, Z., & Murty, T. S. (1993). *Numerical Modeling Of Ocean Dynamics*. World Scientific.

Krueck, N. C., Treml, E. A., Innes, D. J., & Ovenden, J. R. (2020). Ocean currents and the population genetic signature of fish migrations. *Ecology*, *101*(3), e02967. https://doi.org/10.1002/ecy.2967

Krug, H. M. (1994). *Biologia e avaliaçao do stock Açoreano de goraz,* Pagellus bogaraveo. [PhD thesis]. Universidade dos Açores. Azores, Portugal.

Kundu, P. K., Cohen, I. M., & Dowling, D. R. (Eds.). (2012). Chapter 4—Conservation Laws. In *Fluid Mechanics (Fifth Edition)* (pp. 95–169). Academic Press. https://doi.org/10.1016/B978-0-12-382100-3.10004-6

Kuzmić, M., Janeković, I., Book, J. W., Martin, P. J., & Doyle, J. D. (2006). Modeling the northern Adriatic double-gyre response to intense bora wind: A revisit. *Journal of Geophysical Research: Oceans*, *111*(C3). https://doi.org/10.1029/2005JC003377

Kwon, K., Choi, B.-J., Kim, K. Y., Kim, K., Kwon, K., Choi, B.-J., Kim, K. Y., & Kim, K. (2019). Tracing the trajectory of pelagic *Sargassum* using satellite monitoring and Lagrangian transport simulations in the East

China Sea and Yellow Sea. *Algae*, *34*(4), 315–326. https://doi.org/10.4490/algae.2019.34.12.11

LaCasce, J. H. (2008). Statistics from Lagrangian observations. *Progress in Oceanography*, *77*(1), 1–29. https://doi.org/10.1016/j.pocean.2008.02.002

Lacour, T., Morin, P.-I., Sciandra, T., Donaher, N., Campbell, D. A., Ferland, J., & Babin, M. (2019). Decoupling light harvesting, electron transport and carbon fixation during prolonged darkness supports rapid recovery upon re-illumination in the Arctic diatom *Chaetoceros neogracilis*. *Polar Biology*, *42*(10), 1787–1799. https://doi.org/10.1007/s00300-019-02507-2

Lalire, M., & Gaspar, P. (2019). Modeling the active dispersal of juvenile leatherback turtles in the North Atlantic Ocean. *Movement Ecology*, *7*(1), 7. https://doi.org/10.1186/s40462-019-0149-5

Lange, M., & Van Sebille, E. (2017). *Parcels v0.9: Prototyping a Lagrangian Ocean Analysis frameworkfor the petascale age*. Oceanography. https://doi.org/10.5194/gmd-2017-167

Lanoix, F. (1974). *Projet Alboran, Etude hydrologique et dynamique de la Mer d'Alboran, Tech. Lep.* (66; p. 39).

Largier, J. (2003). Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications - ECOL APPL*, *13*, 71–89. https://doi.org/10.1890/1051-0761(2003)013[0071:CIELDD]2.0.CO;2

Lausche, B., Farrier, D., Verschuuren, J., Viña, A., Trouwborst, A., Born, C.-H., & Aug, L. (2013). *The Legal Aspects of Connectivity Conservation: A Concept Paper* (Vol. 1). IUCN.

Le Corre, N., Guichard, F., & Johnson, L. (2012). *Connectivity as a Management Tool for Coastal Ecosystems in Changing Oceans*. https://doi.org/10.5772/27704

Lebreton, L., Egger, M., & Slat, B. (2019). A global mass budget for positively buoyant macroplastic debris in the ocean. *Scientific Reports*, *9*(1), 12922. https://doi.org/10.1038/s41598-019-49413-5

Lee, S., Kim, J. K., Zheng, X., Ho, Q., Gibson, G. A., & Xing, E. P. (2014). On Model Parallelization and Scheduling Strategies for Distributed Machine Learning. *Advances in Neural Information Processing Systems*, *27*.

Legrand, T., Chenuil, A., Ser-Giacomi, E., Arnaud-Haond, S., Bierne, N., & Rossi, V. (2022). Spatial coalescent connectivity through multi-generation dispersal modelling predicts gene flow across marine phyla. *Nature Communications*, *13*(1), Article 1. https://doi.org/10.1038/s41467-022-33499-z

Legrand, T., Di Franco, A., Ser-Giacomi, E., Caló, A., & Rossi, V. (2019). A multidisciplinary analytical framework to delineate spawning areas and quantify larval dispersal in coastal fish. *Marine Environmental Research*, *151*, 104761. https://doi.org/10.1016/j.marenvres.2019.104761

Leon, L. F., Antenucci, J. P., Rao, Y. R., & McCrimmon, C. (2012). Summary performance of the Estuary and Lake Computer Model (ELCOM): Application in the Laurentian and other Great Lakes. *Water Quality Research Journal*, *47*(3–4), 252–267. https://doi.org/10.2166/wqrjc.2012.022

Lester, S. E., Ruttenberg, B. I., Gaines, S. D., & Kinlan, B. P. (2007). The relationship between dispersal ability and geographic range size. *Ecology Letters*, *10*(8), 745–758. https://doi.org/10.1111/j.1461-0248.2007.01070.x

Lett, C., Ayata, S.-D., Huret, M., & Irisson, J.-O. (2010). Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress in Oceanography*, *87*(1), 106–113. https://doi.org/10.1016/j.pocean.2010.09.005

Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., & Blanke, B. (2008). A Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling & Software*, *23*(9), 1210–1214. https://doi.org/10.1016/j.envsoft.2008.02.005

Leukart, P., & Lüning, K. (1994). Minimum spectral light requirements and maximum light levels for long-term germling growth of several red algae from different water depths and a green alga. *European Journal of Phycology*, *29*, 103–112. https://doi.org/10.1080/09670269400650551

Levin, L. (2006). Recent progress in understanding larval dispersal: New directions and digressions. *Integrative and Comparative Biology*, *46*, 282–297. https://doi.org/10.1093/icb/icj024

Li, H., Scheschonk, L., Heinrich, S., Valentin, K., Harms, L., Glöckner, G., Corre, E., & Bischof, K. (2020). Transcriptomic Responses to Darkness and the Survival Strategy of the Kelp *Saccharina latissima* in the Early Polar Night. *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.592033

Ličer, M., Estival, S., Reyes-Suarez, C., Deponte, D., & Fettich, A. (2020). Lagrangian modelling of a person lost at sea during the Adriatic scirocco storm of 29 October 2018. *Natural Hazards and Earth System Sciences*, *20*(8), 2335–2349. https://doi.org/10.5194/nhess-20-2335-2020

Lipcius, R. N., Eggleston, D. B., Fodrie, F. J., van der Meer, J., Rose, K. A., Vasconcelos, R. P., & van de Wolfshaar, K. E. (2019). Modeling

Quantitative Value of Habitats for Marine and Estuarine Populations. *Frontiers in Marine Science*, *6*. https://doi.org/10.3389/fmars.2019.00280

Lipizer, M., Partescano, E., Rabitti, A., Giorgetti, A., & Crise, A. (2014). Qualified temperature, salinity and dissolved oxygen climatologies in a changing Adriatic Sea. *Ocean Science*, *10*(5), 771–797. https://doi.org/10.5194/os-10-771-2014

Liulea, S., Serrão, E. A., & Santos, R. (2023). *Spread and Impact of the Invasive Brown Algae* Rugulopteryx okamurae *On The Algarve Coast, Southern Portugal (Ne Atlantic)* (SSRN Scholarly Paper 4446622). https://doi.org/10.2139/ssrn.4446622

López-Márquez, V., Templado, J., Buckley, D., Marino, I., Boscari, E., Micu, D., Zane, L., & Machordom, A. (2019). Connectivity Among Populations of the Top Shell *Gibbula divaricata* in the Adriatic Sea. *Frontiers in Genetics*, *10*, 177. https://doi.org/10.3389/fgene.2019.00177

López-Parages, J., Rodríguez-Fonseca, B., & Terray, L. (2015). A mechanism for the multidecadal modulation of ENSO teleconnection with Europe. *Climate Dynamics*, *45*(3), 867–880. https://doi.org/10.1007/s00382-014-2319-x

Lorance, P. (2011). History and dynamics of the overexploitation of the blackspot sea bream (*Pagellus bogaraveo*) in the Bay of Biscay. *ICES Journal of Marine Science*, *68*(2), 290–301. https://doi.org/10.1093/icesjms/fsq072

Loseille, A. (2017). Chapter 10—Unstructured Mesh Generation and Adaptation. In R. Abgrall & C.-W. Shu (Eds.), *Handbook of Numerical Analysis* (Vol. 18, pp. 263–302). Elsevier. https://doi.org/10.1016/bs.hna.2016.10.004

Maicu, F., De Pascalis, F., Ferrarin, C., & Umgiesser, G. (2018). Hydrodynamics of the Po River-Delta-Sea System. *Journal of Geophysical Research: Oceans*, *123*(9), 6349–6372. https://doi.org/10.1029/2017JC013601

Malanotte-Rizzoli, P., Robinson, A. R., Roether, W., Manca, B., Bergamasco, A., Brenner, S., Civitarese, G., Georgopoulos, D., Haley, P. J., Kioroglou, S., Kontoyannis, H., Kress, N., Latif, M. A., Leslie, W. G., Ozsoy, E., d'Alcala, M. R., Salihoglu, I., Sansone, E., & Theocharis, A. (1996). Experiment in eastern Mediterranean probes origin of deep water masses. *Eos, Transactions American Geophysical Union*, *77*(32), 305–311. https://doi.org/10.1029/96EO00212

Mannino, A. M., Borfecchia, F., & Micheli, C. (2021). Tracking Marine Alien Macroalgae in the Mediterranean Sea: The Contribution of Citizen

Science and Remote Sensing. *Journal of Marine Science and Engineering*, *9*(3), Article 3. https://doi.org/10.3390/jmse9030288

Marandel, F., Lorance, P., Andrello, M., Charrier, G., Le Cam, S., Lehuta, S., & Trenkel, V. M. (2018). Insights from genetic and demographic connectivity for the management of rays and skates. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(8), 1291–1302. https://doi.org/10.1139/cjfas-2017-0291

Marcos, C., Díaz, D., Fietz, K., Forcada, A., Ford, A., García-Charton, J. A., Goñi, R., Lenfant, P., Mallol, S., Mouillot, D., Pérez-Marcos, M., Puebla, O., Manel, S., & Pérez-Ruzafa, A. (2021). Reviewing the Ecosystem Services, Societal Goods, and Benefits of Marine Protected Areas. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.613819

Margalef López, R. (1997). Turbulence and marine life. *Scientia Marina*, *61*(Extra 1), 109–123.

Mariani, P., Mackenzie, B., Iudicone, D., & Bozec, A. (2010). Modelling retention and dispersion mechanisms of bluefin tuna eggs and larvae in the northwest Mediterranean Sea. *Progress in Oceanography*, *86*, 45–58. https://doi.org/10.1016/j.pocean.2010.04.027

Mariani, S., Casaioli, M., Coraci, E., & Malguzzi, P. (2015). A new high-resolution BOLAM-MOLOCH suite for the SIMM forecasting system: Assessment over two HyMeX intense observation periods. *Natural Hazards and Earth System Science*, *15*, 1–24. https://doi.org/10.5194/nhess-15-1-2015

Mariano, A. J., Kourafalou, V. H., Srinivasan, A., Kang, H., Halliwell, G. R., Ryan, E. H., & Roffer, M. (2011). On the modeling of the 2010 Gulf of Mexico Oil Spill. *Dynamics of Atmospheres and Oceans*, *52*(1), 322–340. https://doi.org/10.1016/j.dynatmoce.2011.06.001

Marshall, J., Adcroft, A., Hill, C., Perelman, L., & Heisey, C. (1997). A finite-volume, incompressible Navier Stokes model for studies of the ocean on parallel computers. *Journal of Geophysical Research: Oceans*, *102*(C3), 5753–5766. https://doi.org/10.1029/96JC02775

Marshall, J., Hill, C., Perelman, L., & Adcroft, A. (1997). Hydrostatic, quasi-hydrostatic, and nonhydrostatic ocean modeling. *Journal of Geophysical Research: Oceans*, *102*(C3), 5733–5752. https://doi.org/10.1029/96JC02776

Martin, P. J., Book, J. W., Burrage, D. M., Rowley, C. D., & Tudor, M. (2009). Comparison of model-simulated and observed currents in the central

Adriatic during DART. *Journal of Geophysical Research: Oceans*, *114*(C2). https://doi.org/10.1029/2008JC004842

Martínez, A., Abascal, A. J., García, A., Aragón, G., & Medina, R. (2024). Lagrangian modelling of oil concentrations at sea: A sensitivity analysis to the grid resolution and number of Lagrangian elements. *Marine Pollution Bulletin*, *198*, 115787. https://doi.org/10.1016/j.marpolbul.2023.115787

Mason, E., Ruiz, S., Bourdalle-Badie, R., Reffray, G., Garcia-Sotillo, M., & Pascual, A. (2019). Copernicus (CMEMS) operational model intercomparison in the western Mediterranean Sea: Insights from an eddy tracker. *Ocean Science Discussions*, 1–32. https://doi.org/10.5194/os-2018-169

Mateo-Ramírez, Á., Iñiguez, C., Fernández-Salas, L. M., Sánchez-Leal, R. F., Farias, C., Bellanco, M. J., Gil, J., & Rueda, J. L. (2023). Healthy thalli of the invasive seaweed *Rugulopteryx okamurae* (Phaeophyceae) being massively dragged into deep-sea bottoms by the Mediterranean Outflow Water. *Phycologia*, *62*(2), 99–108. https://doi.org/10.1080/00318884.2023.2177057

Mayorga-Adame, C., Polton, J., Fox, A., & Henry, L. (2022). Spatiotemporal scales of larval dispersal and connectivity among oil and gas structures in the North Sea. *Marine Ecology Progress Series*, *685*, 49–67. https://doi.org/10.3354/meps13970

McKiver, W. J., Sannino, G., Braga, F., & Bellafiore, D. (2016). Investigation of model capability in capturing vertical hydrodynamic coastal processes: A case study in the north Adriatic Sea. *Ocean Science*, *12*(1), 51–69. https://doi.org/10.5194/os-12-51-2016

McWilliams, J. C. (2006). *Fundamentals of Geophysical Fluid Dynamics*. Cambridge University Press.

Medvedev, I. P., Vilibić, I., & Rabinovich, A. B. (2020). Tidal Resonance in the Adriatic Sea: Observational Evidence. *Journal of Geophysical Research: Oceans*, *125*(8), e2020JC016168. https://doi.org/10.1029/2020JC016168

Meer, M., Berumen, M., Hobbs, J.-P., & Herwerden, L. (2015). Population connectivity and the effectiveness of marine protected areas to protect vulnerable, exploited and endemic coral reef fishes at an endemic hotspot. *The Raffles Bulletin of Zoology*, *34*. https://doi.org/10.1007/s00338-014-1242-2

Megrey, B. (2001). Effect of turbulence on feeding of larval fishes: A sensitivity analysis using an individual-based model. *ICES Journal of*

Marine Science, *58*(5), 1015–1029. https://doi.org/10.1006/jmsc.2001.1104

Mercado, J. M., Gómez-Jakobsen, F., Korbee, N., Aviles, A., Bonomi-Barufi, J., Muñoz, M., Reul, A., & Figueroa, F. L. (2022). Analyzing environmental factors that favor the growth of the invasive brown macroalga *Rugulopteryx okamurae* (Ochrophyta): The probable role of the nutrient excess. *Marine Pollution Bulletin*, *174*, 113315. https://doi.org/10.1016/j.marpolbul.2021.113315

Metaxas, A., & Saunders, M. (2009). Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: Advances and pitfalls. *The Biological Bulletin*, *216*(3), 257–272. https://doi.org/10.1086/BBLv216n3p257

Micheli, F., Halpern, B., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., Lewison, R., Nykjaer, L., & Rosenberg, A. (2013). Cumulative Human Impacts on Mediterranean and Black Sea Marine Ecosystems: Assessing Current Pressures and Opportunities. *PloS One*, *8*, e79889. https://doi.org/10.1371/journal.pone.0079889

Miller, J. A., & Shanks, A. (2004). Evidence for limited larval dispersal in black rockfish (Sebastes melanops): Implications for population structure and marine-reserve design. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*, 1723–1735. https://doi.org/10.1139/f04-111

Millot, C. (2013). Levantine Intermediate Water characteristics: An astounding general misunderstanding! *Scientia Marina*, *77*(2), Article 2. https://doi.org/10.3989/scimar.03518.13A

Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, *93*(1), 35–45. https://doi.org/10.1890/11-0370.1

Mogé, M., Russcher, M. J., Emerson, A., & Genseberger, M. (2019). *Scalable Delft3D Flexible Mesh for Efficient Modelling of Shallow Water and Transport Processes*.

Molinaroli, E., Peschiutta, M., & Rizzetto, F. (2023). Long-Term Evolution of an Urban Barrier Island: The Case of Venice Lido (Northern Adriatic Sea, Italy). *Water (Switzerland)*, *15*(10). https://doi.org/10.3390/w15101927

Monismith, S. G., & Fong, D. A. (2004). A note on the potential transport of scalars and organisms by surface waves. *Limnology and Oceanography*, *49*(4), 1214–1217. https://doi.org/10.4319/lo.2004.49.4.1214

Monroy, P., Rossi, V., Ser-Giacomi, E., López, C., & Hernández-García, E. (2017). Sensitivity and robustness of larval connectivity diagnostics obtained from Lagrangian Flow Networks. *ICES Journal of Marine Science*, *74*(6), 1763–1779. https://doi.org/10.1093/icesjms/fsw235

Morales-Nin, B., & Moranta, J. (2004). Recruitment and post-settlement growth of juvenile *Merluccius merluccius* on the western Mediterranean shelf. *Scientia Marina*, *68*(3), Article 3. https://doi.org/10.3989/scimar.2004.68n3399

Morat, F., Letourneur, Y., Dierking, J., Pécheyran, C., Bareille, G., Blamart, D., & Harmelin-Vivien, M. (2014). The Great Melting Pot. Common Sole Population Connectivity Assessed by Otolith and Water Fingerprints. *PLoS ONE*, *9*(1), e86585. https://doi.org/10.1371/journal.pone.0086585

Morello, E. B., & Arneri, E. (2009). Anchovy and Sardine in the Adriatic Sea—An Ecological Review. In *Oceanography and Marine Biology*. CRC Press.

Motos, L. (1996). Reproductive biology and fecundity of the Bay of Biscay Anchovy population (*Engraulis encrasicolus* L.). *Scientia Marina*, *60*.

Muller, H., Blanke, B., Dumas, F., Lekien, F., & Mariette, V. (2009). Estimating the Lagrangian residual circulation in the Iroise Sea. *Journal of Marine Systems*, *78*, S17–S36. https://doi.org/10.1016/j.jmarsys.2009.01.008

Muñoz, A.R., Martín-Taboada, A., De la Rosa, J., Carmona, R., Zanolla, M., & Altamirano, M. (2019). La modelación de la distribución de especies como herramienta en la gestión de invasiones biológicas en el medio marino: El caso de *Rugulopteryx okamurae* (Dictyotaceae, Ochrophyta) en el Mediterráneo. In *Número Especial Boletín de la Sociedad Española de Ficología Diciembre 2019: Gestión de Especies Invasoras Marinas: Construyendo una Propuesta para Andalucía.*

Muñoz, M., Reul, A., Plaza, F., Gómez-Moreno, M.-L., Vargas-Yañez, M., Rodríguez, V., & Rodríguez, J. (2015). Implication of regionalization and connectivity analysis for marine spatial planning and coastal management in the Gulf of Cadiz and Alboran Sea. *Ocean & Coastal Management*, *118*, 60–74. https://doi.org/10.1016/j.ocecoaman.2015.04.011

Muntoni, M. (2015). *A multidisciplinary approach for puzzling over fish connectivity in the Mediterranean Sea: The role of early life history stages of red mullet (*Mullus barbatus*)* [PhD thesis]. Università degli Studi di Cagliari. Cagliari, Italy.

Murua, H., & Motos, L. (2006). Reproductive strategy and spawning activity of the European hake *Merluccius merluccius* (L.) in the Bay of Biscay. *Journal of Fish Biology*, *69*(5), 1288–1303. https://doi.org/10.1111/j.1095-8649.2006.01169.x

Nadal, I., Sammartino, S., García-Lafuente, J., Sánchez Garrido, J. C., Gil-Herrera, J., Hidalgo, M., & Hernández, P. (2022). Hydrodynamic connectivity and dispersal patterns of a transboundary species (*Pagellus bogaraveo*) in the Strait of Gibraltar and adjacent basins. *Fisheries Oceanography*, *31*(4), 384–401. https://doi.org/10.1111/fog.12583

Najafi, S., Dragovich, D., Heckmann, T., & Sadeghi, S. H. (2021). Sediment connectivity concepts and approaches. *CATENA*, *196*, 104880. https://doi.org/10.1016/j.catena.2020.104880

Naranjo, C., Sammartino, S., García-Lafuente, J., Bellanco, M. J., & Taupier-Letage, I. (2015). Mediterranean waters along and across the Strait of Gibraltar, characterization and zonal modification. *Deep Sea Research Part I: Oceanographic Research Papers*, *105*, 41–52. https://doi.org/10.1016/j.dsr.2015.08.003

Nathan, R., & Muller-Landau, H. C. (2000). *Spatial Patterns of Seed Dispersal, Their Determinants and Consequences for Recruitment*. http://repository.si.edu/xmlui/handle/10088/18540

Navarro, G., Gutiérrez, F. J., Díez-Minguito, M., Losada, M. A., & Ruiz, J. (2011). Temporal and spatial variability in the Guadalquivir estuary: A challenge for real-time telemetry. *Ocean Dynamics*, *61*(6), 753–765. https://doi.org/10.1007/s10236-011-0379-6

Navarro-Barranco, C., Muñoz-Gómez, B., Saiz, D., Ros, M., Guerra-García, J. M., Altamirano, M., Ostalé-Valriberas, E., & Moreira, J. (2019). Can invasive habitat-forming species play the same role as native ones? The case of the exotic marine macroalga *Rugulopteryx okamurae* in the Strait of Gibraltar. *Biological Invasions*, *21*(11), 3319–3334. https://doi.org/10.1007/s10530-019-02049-y

Nicolle, A., Dumas, F., Foveau, A., Foucher, E., & Thiébaut, E. (2013). Modelling larval dispersal of the king scallop (Pecten maximus) in the English Channel: Examples from the bay of Saint-Brieuc and the bay of Seine. *Ocean Dynamics*, *63*(6), 661–678. https://doi.org/10.1007/s10236-013-0617-1

Nicolle, A., Moitié, R., Ogor, J., Dumas, F., Foveau, A., Foucher, E., & Thiébaut, E. (2017). Modelling larval dispersal of Pecten maximus in the English Channel: A tool for the spatial management of the stocks. *ICES Journal of Marine Science*, *74*(6), 1812–1825. https://doi.org/10.1093/icesjms/fsw207

Nilsson, H., & Page, M. (2005). OpenFOAM simulation of the flow in the Hölleforsen draft tube model. *Turbine-99 III*, *8*, 6.

Nolasco, R., Gomes, I., Peteiro, L., Albuquerque, R., Luna, T., Dubert, J., Swearer, S. E., & Queiroga, H. (2018). Independent estimates of marine population connectivity are more concordant when accounting for uncertainties in larval origins. *Scientific Reports*, *8*(1), 2641. https://doi.org/10.1038/s41598-018-19833-w

Novi, L., Bracco, A., & Falasca, F. (2021). Uncovering marine connectivity through sea surface temperature. *Scientific Reports*, *11*(1), 8839. https://doi.org/10.1038/s41598-021-87711-z

Ocampo-Torres, F. J. (2001). On the homogeneity of the wave field in coastal areas as determined from ERS-2 and RADARSAT synthetic aperture radar images of the ocean surface. *Scientia Marina*, *65*(S1), Article S1. https://doi.org/10.3989/scimar.2001.65s1215

Ocaña Vicente, O., Afonso-Carrillo, J., & Ballesteros, E. (2016). *Massive proliferation of a dictyotalean species (Phaeophyceae, Ochrophyta) through the Strait of Gibraltar (Research note). Rev Acad Canaria Cienc*. *28*, 165–170.

O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., & Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences*, *104*(4), 1266–1271. https://doi.org/10.1073/pnas.0603422104

Oguz, T., Macias, D., Garcia-Lafuente, J., Pascual, A., & Tintore, J. (2014). Fueling Plankton Production by a Meandering Frontal Jet: A Case Study for the Alboran Sea (Western Mediterranean). *PLOS ONE*, *9*(11), e111482. https://doi.org/10.1371/journal.pone.0111482

Oke, P. R., Proctor, R., Rosebrock, U., Brinkman, R., Cahill, M. L., Coghlan, I., Divakaran, P., Freeman, J., Pattiaratchi, C., Roughan, M., Sandery, P. A., Schaeffer, A., & Wijeratne, S. (2016). The Marine Virtual Laboratory (version 2.1): Enabling efficient ocean model configuration. *Geoscientific Model Development*, *9*(9), 3297–3307. https://doi.org/10.5194/gmd-9-3297-2016

Olivier, R. (1928). Poissons de chalut. La dorade (*Pagellus centrodontus*) (Resume pratique de nos connaissances sur ce poisson). Rev. Trav. De l'Off. Peches Marit., Tome I, fasc. IV. *Revue Des Travaux de l'Institut Des Pêches Maritimes*, *1*(4), 5–32.

OpenStreetMap contributors. (2015). *Map data copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org* [Map].

Orlić, M., Gačić, M., & Laviolette, P. (1992). The currents and circulation of the Adriatic Sea. *Oceanologica Acta*.

https://www.semanticscholar.org/paper/The-currents-and-circulation-of-the-Adriatic-Sea-Orli%C4%87-Ga%C4%8Di%C4%87/0d5b7c22b203a499911d877c6c4dc03ca6058ba9

Orlić, M., Kuzmić, M., & Pasarić, Z. (1994). Response of the Adriatic Sea to the bora and sirocco forcing. *Continental Shelf Research*, *14*(1), 91–116. https://doi.org/10.1016/0278-4343(94)90007-8

Ormerod, S., I., D., Hatton-Ellis, T., Cable, J., Chadwick, E., S., G., Jones, T., Larsen, S., F.L., M., W.O.C., S., Thomas, R., & I.P., V. (2011). Landscape Connectivity of Freshwater Ecosystems: Strategic Review and Recommendations. *Report to the Countryside Council for Wales*.

Palacios-Abrantes, J., Reygondeau, G., Wabnitz, C. C. C., & Cheung, W. W. L. (2020). The transboundary nature of the world's exploited marine species. *Scientific Reports*, *10*(1), 17668. https://doi.org/10.1038/s41598-020-74644-2

Palumbi, S. R. (2003). Population Genetics, Demographic Connectivity, and the Design of Marine Reserves. *Ecological Applications*, *13*(sp1), 146–158. https://doi.org/10.1890/1051-0761(2003)013[0146:PGDCAT]2.0.CO;2

Paoletti, S., Bekaert, K., Barbut, L., Lacroix, G., Volckaert, F. A. M., & Hostens, K. (2021). Validating a biophysical dispersal model with the early life-history traits of common sole (*Solea solea* L.). *PloS One*, *16*(9), e0257709. https://doi.org/10.1371/journal.pone.0257709

Parrilla, G., & Kinder, T. (1987). *The Physical Oceanography of the Alboran Sea* (Vol. 40). Oceanography Group, Division of Applied Sciences.

Pasarić, Z., Belu, D., & Klai, Z. B. (2007). Orographic influences on the Adriatic sirocco wind. *Annales Geophysicae*, *25*(6), 1263–1267. https://doi.org/10.5194/angeo-25-1263-2007

Pasarić, Z., Belušić, D., & Chiggiato, J. (2009). Orographic effects on meteorological fields over the Adriatic from different models. *Journal of Marine Systems*, *78*, S90–S100. https://doi.org/10.1016/j.jmarsys.2009.01.019

Pascual, M., & Macpherson, E. (2016). *Population genetic connectivity among marine species; a matter of dispersal, selection and drift* (CIESM Monograph 48, 172 pages, Publisher: CIESM Publisher, Monaco, Editors: F. Briand, pp. 59–64).

Pastor, A., Catalán, I. A., Terrados, J., Mourre, B., & Ospina-Alvarez, A. (2023). Connectivity-based approach to guide conservation and restoration of seagrass *Posidonia oceanica* in the NW Mediterranean. *Biological Conservation*, *285*, 110248. https://doi.org/10.1016/j.biocon.2023.110248

Patti, B., Torri, M., & Cuttitta, A. (2020). General surface circulation controls the interannual fluctuations of anchovy stock biomass in the Central Mediterranean Sea. *Scientific Reports*, *10*(1), 1554. https://doi.org/10.1038/s41598-020-58028-0

Pawlowicz, R., Pawlowicz, R., Beardsley, R. C., Beardsley, R., Lentz, S., & Lentz, S. (2002). Classical tidal harmonic analysis including error estimates in MATLAB using T_TIDE. *Computers & Geosciences*, *28*(8), 929–937.

Peleteiro-Alonso, J. B., Olmedo-Herrero, M., Gómez-Ceruelo, M. C., & Álvarez-Blázquez, B. (1997). *Study of reproduction in captivity of blackspot sea bream (*Pagellus bogaraveo *B.). Embrionic development and consumption of viteline sac.* ICES 85th Statutory Meeting, Baltimore, USA. http://hdl.handle.net/10261/315570

Peliz, Á., Teles-Machado, A., Marchesiello, P., Dubert, J., & García Lafuente, J. (2009). Filament generation off the Strait of Gibraltar in response to Gap winds. *Dynamics of Atmospheres and Oceans*, *46*(1), 36–45. https://doi.org/10.1016/j.dynatmoce.2008.08.002

Pineda, J. (1991). Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science (New York, N.Y.)*, *253*(5019). https://doi.org/10.1126/science.253.5019.548

Pineda, J., Hare, J., & Sponaugle, S. (2007). Larval Transport and Dispersal in the Coastal Ocean and Consequences for Population Connectivity. *Oceanography*, *20*(3), 22–39. https://doi.org/10.5670/oceanog.2007.27

Pineda, J., & López, M. (2002). Effects of El Niño on Nearshore Stratification and Larval Settlement. *Investigaciones Marinas*, *30*(1), 126–127. https://doi.org/10.4067/S0717-71782002030100036

Pineda, J., Reyns, N., & Lentz, S. J. (2018). Reduced barnacle larval abundance and settlement in response to large-scale oceanic disturbances: Temporal patterns, nearshore thermal stratification, and potential mechanisms. *Limnology and Oceanography*, *63*(6), 2618–2629. https://doi.org/10.1002/lno.10964

Pinho, M., Diogo, H., Carvalho, J., & Pereira, J. G. (2014). Harvesting juveniles of blackspot sea bream (*Pagellus bogaraveo*) in the Azores (Northeast Atlantic): Biological implications, management, and life cycle considerations. *ICES Journal of Marine Science*, *71*(9), 2448–2456. https://doi.org/10.1093/icesjms/fsu089

Pinsky, M. L., Reygondeau, G., Caddell, R., Palacios-Abrantes, J., Spijkers, J., & Cheung, W. W. L. (2018). Preparing ocean governance for species on the move. *Science (New York, N.Y.)*, *360*(6394), 1189–1191. https://doi.org/10.1126/science.aat2360

Planes, S., Jones, G. P., & Thorrold, S. R. (2009). Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences*, *106*(14), 5693–5697. https://doi.org/10.1073/pnas.0808007106

Podda, C., & Porporato, E. M. D. (2023). Marine spatial planning for connectivity and conservation through ecological corridors between marine protected areas and other effective area-based conservation measures. *Frontiers in Marine Science*, *10*. https://doi.org/10.3389/fmars.2023.1271397

Popels, L., & Hutchins, D. (2002). Factors affecting dark survival of the brown tide alga Aureococcus anophagefferens (Pelagophyceae). *Journal of Phycology*, *38*, 738–744. https://doi.org/10.1046/j.1529-8817.2002.01115.x

Popova, E., Vousden, D., Sauer, W. H. H., Mohammed, E. Y., Allain, V., Downey-Breedt, N., Fletcher, R., Gjerde, K. M., Halpin, P. N., Kelly, S., Obura, D., Pecl, G., Roberts, M., Raitsos, D. E., Rogers, A., Samoilys, M., Sumaila, U. R., Tracey, S., & Yool, A. (2019). Ecological connectivity between the areas beyond national jurisdiction and coastal waters: Safeguarding interests of coastal communities in developing countries. *Marine Policy*, *104*, 90–102. https://doi.org/10.1016/j.marpol.2019.02.050

Poulain, P.-M. (2001). Adriatic Sea surface circulation as derived from drifter data between 1990 and 1999. *Journal of Marine Systems*, *29*, 3–32. https://doi.org/10.1016/S0924-7963(01)00007-0

Pratt, L. L. J., & Whitehead, J. A. (2007). *Rotating Hydraulics: Nonlinear Topographic Effects in the Ocean and Atmosphere*. Springer Science & Business Media.

Punt, A. E. (2019). Spatial stock assessment methods: A viewpoint on current issues and assumptions. *Fisheries Research*, *213*, 132–143. https://doi.org/10.1016/j.fishres.2019.01.014

Rahman, R. O. A. (2019). Introductory Chapter: Development of Assessment Models to Support Pollution Preventive and Control Decisions. In *Kinetic Modeling for Environmental Systems*. IntechOpen. https://doi.org/10.5772/intechopen.83822

Reed, D., Kinlan, B., Raimondi, P., Washburn, L., Gaylord, B., & Drake, P. (2006). A Metapopulation Perspective on the Patch Dynamics of Giant

Kelp in Southern California. *Marine Metapopulations*, 353–386. https://doi.org/10.1016/B978-012088781-1/50013-3

Renault, L., Oguz, T., Pascual, A., Vizoso, G., & Tintore, J. (2012). Surface circulation in the Alborán Sea (western Mediterranean) inferred from remotely sensed data. *Journal of Geophysical Research: Oceans*, *117*(C8). https://doi.org/10.1029/2011JC007659

Revelante, N., & Gilmartin, M. (1992). The lateral advection of particulate organic matter from the Po delta region during summer stratification, and its implications for the northern Adriatic. *Estuarine, Coastal and Shelf Science*, *35*(2), 191–212. https://doi.org/10.1016/S0272-7714(05)80113-1

Riha, S. (2017). *Grid generation for numerical ocean models*.

Rodríguez-Díaz, L., & Gómez-Gesteira, M. (2017). Can lagrangian models reproduce the migration time of European eel obtained from otolith analysis? *Journal of Sea Research*, *130*, 17–23. https://doi.org/10.1016/j.seares.2017.06.010

Rodríguez, J. M., Barton, E. D., Eve, L., & Hernández-León, S. (2001). Mesozooplankton and ichthyoplankton distribution around Gran Canaria, an oceanic island in the NE Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers*, *48*(10), 2161–2183. https://doi.org/10.1016/S0967-0637(01)00013-9

Roelvink, J., & Banning, G. V. (1995). Design and development of DELFT3D and application to coastal morphodynamics. *Oceanographic Literature Review*.

Rosas-Guerrero, J., Carmona-Fernández, R., & Altamirano-Jeschke, M. (2021). *Efecto de la temperatura y la irradiancia sobre el crecimiento, la propagación vegetativa y la actividad fotosintética del alga invasora* Rugulopteryx okamurae *(Dictyotales, Ochrophyta).* III JIs del Mar, Granada, Spain. https://riuma.uma.es/xmlui/handle/10630/22870

Rosas-Guerrero, J., Meco, Y. E., & Altamirano, M. (2018). Could *Rugulopteryx okamurae* (Dictyotales, Ochrophyta) have been introduced by ballast waters. *Algas*, *54*(52).

Rossi, V., Ser-Giacomi, E., Lõpez, C., & Hernández-García, E. (2014). Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves. *Geophysical Research Letters*, *41*(8), 2883–2891. https://doi.org/10.1002/2014GL059540

Rueda, J. L., Mena-Torres, A., Gallardo-Núñez, M., González-García, E., Martín-Arjona, A., Valenzuela, J., García-Ruiz, C., González-Aguilar, M., Mateo-Ramírez, Á., García, M., Sayago-Gil, M., & Vázquez, J. T.

(2023). Spatial Distribution and Potential Impact of Drifted Thalli of the Invasive Alga *Rugulopteryx okamurae* in Circalittoral and Bathyal Habitats of the Northern Strait of Gibraltar and the Alboran Sea. *Diversity*, *15*(12), Article 12. https://doi.org/10.3390/d15121206

Rühs, S. (2018). *Lagrangian connectivity of the upper limb of the overturning circulation studied with high-resolution ocean models* [PhD thesis]. Universität Kiel. Kiel, Germany.

Ruitton, S., Blanfuné, A., Boudouresque, C.-F., Guillemain, D., Michotey, V., Roblet, S., Thibault, D., Thibaut, T., & Verlaque, M. (2021). Rapid Spread of the Invasive Brown Alga *Rugulopteryx okamurae* in a National Park in Provence (France, Mediterranean Sea). *Water*, *13*(16), 2306. https://doi.org/10.3390/w13162306

Russo, A., & Artegiani, A. (1996). *Adriatic Sea hydrography* (Vol. 60, Issue 2, pp. 33–43). Scientia Marina.

Ruti, P. M., Somot, S., Giorgi, F., Dubois, C., Flaounas, E., Obermann, A., Dell'Aquila, A., Pisacane, G., Harzallah, A., Lombardi, E., Ahrens, B., Akhtar, N., Alias, A., Arsouze, T., Aznar, R., Bastin, S., Bartholy, J., Béranger, K., Beuvier, J., … Vervatis, V. (2016). Med-CORDEX Initiative for Mediterranean Climate Studies. *Bulletin of the American Meteorological Society*, *97*(7), 1187–1208. https://doi.org/10.1175/BAMS-D-14-00176.1

Ružić, I., Dugonjić Jovančević, S., Benac, Č., & Krvavica, N. (2019). Assessment of the Coastal Vulnerability Index in an Area of Complex Geological Conditions on the Krk Island, Northeast Adriatic Sea. *Geosciences*, *9*(5), Article 5. https://doi.org/10.3390/geosciences9050219

Safin, A., Bouffard, D., Ozdemir, F., Ramón, C. L., Runnalls, J., Georgatos, F., Minaudo, C., & Šukys, J. (2021). *A Bayesian data assimilation framework for lake 3D hydrodynamic models with a physics-preserving particle filtering method using SPUX-MITgcm v1*. https://doi.org/10.5194/gmd-2021-305

Sale, P. F., & Kritzer, J. P. (2003). Determining the extent and spatial scale of population connectivity: Decapods and coral reef fishes compared. *Fisheries Research*, *65*(1), 153–172. https://doi.org/10.1016/j.fishres.2003.09.013

Sammartino, S., García Lafuente, J., Naranjo, C., Sánchez Garrido, J. C., Sánchez Leal, R., & Sánchez Román, A. (2015). Ten years of marine current measurements in Espartel Sill, Strait of Gibraltar. *Journal of Geophysical Research: Oceans*, *120*(9), 6309–6328. https://doi.org/10.1002/2014JC010674

Sammartino, S., García Lafuente, J., Sánchez Garrido, J. C., De los Santos, F. J., Álvarez Fanjul, E., Naranjo, C., Bruno, M., & Calero, C. (2014). A numerical model analysis of the tidal flows in the Bay of Algeciras, Strait of Gibraltar. *Continental Shelf Research*, *72*, 34–46. https://doi.org/10.1016/j.csr.2013.11.002

Sammartino, S., Sanchez, J., Naranjo, C., García Lafuente, J., Rodríguez-Rubio, P., & Sotillo, M. (2017). Water renewal in semi-enclosed basins: A high resolution Lagrangian approach with application to the Bay of Algeciras, Strait of Gibraltar: Water renewal in semi-enclosed basins. *Limnology and Oceanography: Methods*, *16*. https://doi.org/10.1002/lom3.10231

Sammartino, S., Sánchez-Garrido, J. C., Delgado, J., Naranjo, C., Aldeanueva, F., & García Lafuente, J. (2014). Experimental and numerical characterization of harbor oscillations in the port of Málaga, Spain. *Ocean Engineering*, *88*, 110–119. https://doi.org/10.1016/j.oceaneng.2014.06.011

Sánchez, F. (1983). *Biology and fishery of the red sea-bream (*Pagellus bogaraveo *B.) in VI, VII and VIII Subareas of ICES. ICES C.M. 1983/G:38.*

Sánchez-Garrido, J. C., Fiechter, J., Rose, K., Werner, F., & Curchitser, E. (2020). Dynamics of anchovy and sardine populations in the Canary Current off NW Africa: Responses to environmental and climate forcing in a climate-to-fish ecosystem model. *Fisheries Oceanography*, *30*. https://doi.org/10.1111/fog.12516

Sánchez-Garrido, J. C., García Lafuente, J., Álvarez Fanjul, E., Sotillo, M. G., & de los Santos, F. J. (2013). What does cause the collapse of the western alboran gyre? Results of an operational ocean model. *Progress in Oceanography*, *116*, 142–153. https://doi.org/10.1016/j.pocean.2013.07.002

Sánchez-Garrido, J. C., García Lafuente, J., Sammartino, S., Naranjo, C., de los Santos, F. J., & Álvarez Fanjul, E. (2014). Meteorologically-driven circulation and flushing times of the Bay of Algeciras, Strait of Gibraltar. *Marine Pollution Bulletin*, *80*(1), 97–106. https://doi.org/10.1016/j.marpolbul.2014.01.036

Sánchez-Garrido, J. C., & Nadal, I. (2022). The Alboran Sea circulation and its biological response: A review. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.933390

Sánchez-Garrido, J. C., Naranjo, C., Macías, D., García-Lafuente, J., & Oguz, T. (2015). Modeling the impact of tidal flows on the biological productivity of the Alboran Sea. *Journal of Geophysical Research: Oceans*, *120*(11), 7329–7345. https://doi.org/10.1002/2015JC010885

Sánchez-Garrido, J. C., Sannino, G., Liberti, L., García Lafuente, J., & Pratt, L. (2011). Numerical modeling of three-dimensional stratified tidal flow over Camarinal Sill, Strait of Gibraltar. *Journal of Geophysical Research: Oceans*, *116*(C12). https://doi.org/10.1029/2011JC007093

Sánchez-Garrido, J. C., & Vlasenko, V. (2009). Long-term evolution of strongly nonlinear internal solitary waves in a rotating channel. *Nonlinear Processes in Geophysics*, *16*(5), 587–598. https://doi.org/10.5194/npg-16-587-2009

Sanchez-Vidal, A., Calafat, A., Canals, M., & Fabres, J. (2004). Particle fluxes in the Almeria-Oran Front: Control by coastal upwelling and sea surface circulation. *Journal of Marine Systems*, *52*(1), 89–106. https://doi.org/10.1016/j.jmarsys.2004.01.010

Sannino, G., Carillo, A., Iacono, R., Ernesto, N., Palma, M., Pisacane, G., & Struglia, M. (2022). Modelling present and future climate in the Mediterranean Sea: A focus on sea-level change. *Climate Dynamics*, *59*. https://doi.org/10.1007/s00382-021-06132-w

Sannino, G., Herrmann, M., Carillo, A., Rupolo, V., Ruggiero, V., Artale, V., & Heimbach, P. (2009). An eddy-permitting model of the Mediterranean Sea with a two-way grid refinement at the Strait of Gibraltar. *Ocean Modelling*, *30*(1), 56–72. https://doi.org/10.1016/j.ocemod.2009.06.002

Santelices, B., Aedo, D., & Hoffmann, A. (2002). Banks of microscopic forms and survival to darkness of propagules and microscopic stages of macroalgae. *Revista Chilena de Historia Natural*, *75*(3), 547–555. https://doi.org/10.4067/S0716-078X2002000300006

Sarhan, T., García Lafuente, J., Vargas, M., Vargas, J. M., & Plaza, F. (2000). Upwelling mechanisms in the northwestern Alboran Sea. *Journal of Marine Systems*, *23*, 317–331.

Savina, M., Lacroix, G., & Ruddick, K. (2010). Modelling the transport of common sole larvae in the southern North Sea: Influence of hydrodynamics and larval vertical movements. *Journal of Marine Systems*, *81*(1), 86–98. https://doi.org/10.1016/j.jmarsys.2009.12.008

Schemmel, E., Bohaboy, E. C., Kinney, M. J., & O'Malley, J. M. (2022). An assessment of sampling approaches for estimating growth from fishery-dependent biological samples. *ICES Journal of Marine Science*, *79*(5), 1497–1514. https://doi.org/10.1093/icesjms/fsac075

Schilling, H. T., Kalogirou, S., Michail, C., & Kleitou, P. (2023). Testing passive dispersal as the key mechanism for lionfish invasion in the

Mediterranean Sea using Lagrangian particle tracking. *Biological Invasions*. https://doi.org/10.1007/s10530-023-03187-0

Schneider, D. (1991). The role of fluid dynamics in the ecology of marine birds. *Oceanography and Marine Biology Annual Review*, *29*, 487-521.

Schröder, A., & Schanz, D. (2023). 3D Lagrangian Particle Tracking in Fluid Mechanics. *Annual Review of Fluid Mechanics*, *55*(1), 511–540. https://doi.org/10.1146/annurev-fluid-031822-041721

Schunter, C., Carreras-Carbonell, J., Macpherson, E., Tintoré, J., Vidal-Vijande, E., Pascual, A., Guidetti, P., & Pascual, M. (2011). Matching genetics with oceanography: Directional gene flow in a Mediterranean fish species. *Molecular Ecology*, *20*(24), 5167–5181. https://doi.org/10.1111/j.1365-294X.2011.05355.x

Schunter, C., Pascual, M., Raventos, N., Garriga, J., Garza, J. C., Bartumeus, F., & Macpherson, E. (2019). A novel integrative approach elucidates fine-scale dispersal patchiness in marine populations. *Scientific Reports*, *9*(1), 10796. https://doi.org/10.1038/s41598-019-47200-w

Sciascia, R., Berta, M., Carlson, D. F., Griffa, A., Panfili, M., La Mesa, M., Corgnati, L., Mantovani, C., Domenella, E., Fredj, E., Magaldi, M. G., D'Adamo, R., Pazienza, G., Zambianchi, E., & Poulain, P.-M. (2018). Linking sardine recruitment in coastal areas to ocean currents using surface drifters and HF radar: A case study in the Gulf of Manfredonia, Adriatic Sea. *Ocean Science*, *14*(6), 1461–1482. https://doi.org/10.5194/os-14-1461-2018

Sempere-Valverde, J., Ostalé-Valriberas, E., Maestre, M., González Aranda, R., Bazairi, H., & Espinosa, F. (2021). Impacts of the non-indigenous seaweed *Rugulopteryx okamurae* on a Mediterranean coralligenous community (Strait of Gibraltar): The role of long-term monitoring. *Ecological Indicators*, *121*, 107135. https://doi.org/10.1016/j.ecolind.2020.107135

Sentchev, A., & Korotenko, K. (2003). *Effect of tides and frontal scale processes on larval transport in the eastern English Channel: Observations and numerical modelling*.

Ser-Giacomi, E., Martinez-Garcia, R., Dutkiewicz, S., & Follows, M. J. (2023). A Lagrangian model for drifting ecosystems reveals heterogeneity-driven enhancement of marine plankton blooms. *Nature Communications*, *14*(1), 6092. https://doi.org/10.1038/s41467-023-41469-2

Shanks, A. (2009). Pelagic Larval Duration and Dispersal Distance Revisited. *The Biological Bulletin*, *216*, 373–385. https://doi.org/10.2307/25548167

Shchepetkin, A. F., & McWilliams, J. C. (2005). The regional oceanic modeling system (ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling*, *9*(4), 347–404. https://doi.org/10.1016/j.ocemod.2004.08.002

Siegel, D. A., Kinlan, B. P., Gaylord, B., & Gaines, S. D. (2003). Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series*, *260*, 83–96. https://doi.org/10.3354/meps260083

Siegel, D. A., Mitarai, S., Costello, C. J., Gaines, S. D., Kendall, B. E., Warner, R. R., & Winters, K. B. (2008). The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences*, *105*(26), 8974–8979. https://doi.org/10.1073/pnas.0802544105

Simons, R. D., Siegel, D. A., & Brown, K. S. (2013). Model sensitivity and robustness in the estimation of larval transport: A study of particle tracking parameters. *Journal of Marine Systems*, *119–120*, 19–29. https://doi.org/10.1016/j.jmarsys.2013.03.004

Simpson, S., Piercy, J., King, J., & Codling, E. (2013). Modelling larval dispersal and behaviour of coral reef fishes. *Ecological Complexity*, *16*, 68–76. https://doi.org/10.1016/j.ecocom.2013.08.001

Sirviente, S., Bolado-Penagos, M., Gomiz-Pascual, J. J., Romero-Cózar, J., Vázquez, A., & Bruno, M. (2023). Dynamics of Atmospheric-Driven Surface Currents on The Gulf of Cadiz Continental Shelf and its link with The Strait of Gibraltar and The Western Alboran Sea. *Progress in Oceanography*, *219*, 103175. https://doi.org/10.1016/j.pocean.2023.103175

Solís-Díaz, M., Navarro-Barranco, C., Mateu-Vicens, G., & Espinosa, F. (2022). Distribution patterns of epibiotic macrobenthic foraminifera associated to coralligenous habitats of the strait of Gibraltar. *Regional Studies in Marine Science*, *49*, 102096. https://doi.org/10.1016/j.rsma.2021.102096

Somarakis, S., Palomera, I., García, A., Quintanilla, L., Koutsikopoulos, C., Uriarte, A., & Motos, L. (2004). Daily Egg Production of anchovy in European waters. *Ices Journal of Marine Science - ICES J MAR SCI*, *61*, 944–958. https://doi.org/10.1016/j.icesjms.2004.07.018

Sotillo, M. G., Amo-Baladrón, A., Padorno, E., Garcia-Ladona, E., Orfila, A., Rodríguez-Rubio, P., Conti, D., Madrid, J. A. J., de los Santos, F. J., & Fanjul, E. A. (2016). How is the surface Atlantic water inflow through the Gibraltar Strait forecasted? A lagrangian validation of operational oceanographic services in the Alboran Sea and the Western

Mediterranean. *Deep Sea Research Part II: Topical Studies in Oceanography*, *133*, 100–117. https://doi.org/10.1016/j.dsr2.2016.05.020

Sotillo, M. G., Cailleau, S., Lorente, P., Levier, B., Aznar, R., Reffray, G., Amo-Baladrón, A., Chanut, J., Benkiran, M., & Alvarez-Fanjul, E. (2015). The MyOcean IBI Ocean Forecast and Reanalysis Systems: Operational products and roadmap to the future Copernicus Service. *Journal of Operational Oceanography*, *8*(1), 63–79. https://doi.org/10.1080/1755876X.2015.1014663

Sotillo, M. G., Fanjul, E. A., Castanedo, S., Abascal, A. J., Menendez, J., Emelianov, M., Olivella, R., García-Ladona, E., Ruiz-Villarreal, M., Conde, J., Gómez, M., Conde, P., Gutierrez, A. D., & Medina, R. (2008). Towards an operational system for oil-spill forecast over Spanish waters: Initial developments and implementation test. *Marine Pollution Bulletin*, *56*(4), 686–703. https://doi.org/10.1016/j.marpolbul.2007.12.021

Soto Navarro, J. (2012). *Exchange through the Strait of Gibraltar in relation to the climatic forcing over the Mediterranean Sea* [PhD thesis]. Universidad de Málaga. Malaga, Spain.

Soto-Navarro, J., Jordá, G., Deudero, S., Alomar, C., Amores, Á., & Compa, M. (2020). 3D hotspots of marine litter in the Mediterranean: A modeling study. *Marine Pollution Bulletin*, *155*, 111159. https://doi.org/10.1016/j.marpolbul.2020.111159

Spall, M., & Robinson, A. (1989). A new open ocean, hybrid coordinate primitive equation model. *Mathematics and Computers in Simulation*, *31*, 241–269. https://doi.org/10.1016/0378-4754(89)90162-6

Specchiulli, A., Bignami, F., Marini, M., Fabbrocini, A., Scirocco, T., Campanelli, A., Penna, P., Santucci, A., & D'Adamo, R. (2016). The role of forcing agents on biogeochemical variability along the southwestern Adriatic coast: The Gulf of Manfredonia case study. *Estuarine, Coastal and Shelf Science*, *183*, 136–149. https://doi.org/10.1016/j.ecss.2016.10.033

Spiga, M. (2020). *A multidisciplinar approach to assess population structure of* Pagellus bogaraveo *for a correct delineation of stock units in the Alboran Sea.* [MSc Thesis]. Università di Bologna. Bologna, Italy.

Stewart, R. H. (2009). *Introduction to Physical Oceanography*. University Press of Florida.

Strong, J., & Dring, M. (2011). Macroalgal competition and invasive success: Testing competition in mixed canopies of *Sargassum muticum* and

Saccharina latissima. *Botanica Marina*, *54*, 223–229. https://doi.org/10.1515/bot.2011.034

Sun, R., Subramanian, A., Miller, A., Mazloff, M., Hoteit, I., & Cornuelle, B. (2019). SKRIPS v1.0: A regional coupled ocean–atmosphere modeling framework (MITgcm–WRF) using ESMF/NUOPC, description and preliminary results for the Red Sea. *Geoscientific Model Development*, *12*, 4221–4244. https://doi.org/10.5194/gmd-12-4221-2019

Sundby, S., & Kristiansen, T. (2015). The Principles of Buoyancy in Marine Fish Eggs and Their Vertical Distributions across the World Oceans. *PLOS ONE*, *10*(10), e0138821. https://doi.org/10.1371/journal.pone.0138821

Sundelöf, A., & Jonsson, P. R. (2012). Larval dispersal and vertical migration behaviour – a simulation study for short dispersal times. *Marine Ecology*, *33*(2), 183–193. https://doi.org/10.1111/j.1439-0485.2011.00485.x

Tamsitt, V., Abernathey, R. P., Mazloff, M. R., Wang, J., & Talley, L. D. (2018). Transformation of Deep Water Masses Along Lagrangian Upwelling Pathways in the Southern Ocean. *Journal of Geophysical Research: Oceans*, *123*(3), 1994–2017. https://doi.org/10.1002/2017JC013409

Taylor, G. I. (1922). Diffusion by Continuous Movements. *Proceedings of the London Mathematical Society*, *s2-20*(1), 196–212. https://doi.org/10.1112/plms/s2-20.1.196

Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity Is a Vital Element of Landscape Structure. *Oikos*, *68*(3), 571–573. https://doi.org/10.2307/3544927

Teles-Machado, A., Peliz, Á., Dubert, J., & Sánchez, R. F. (2007). On the onset of the Gulf of Cadiz Coastal Countercurrent. *GEOPHYSICAL RESEARCH LETTERS*, *34*. https://doi.org/10.1029/2007GL030091

Terradas-Fernández, M., Pena-Martín, C., Valverde-Urrea, M., Gran, A., Blanco-Murillo, F., Leyva, L., Abellán-Gallardo, E., Beresaluze, E., Izquierdo, A., del Pilar-Ruso, Y., Aguilar, J., & Fernández-Torquemada, Y. (2023). An outbreak of the invasive macroalgae *Rugulopteryx okamurae* in Alicante Bay and its colonization on dead *Posidonia oceanica* matte. *Aquatic Botany*, *189*, 103706. https://doi.org/10.1016/j.aquabot.2023.103706

Tintoré, J., La Violette, P., Bladé, I., & Cruzado, A. (1988). A Study of an Intense Density Front in the Eastern Alboran Sea: The Almeria-Oran Front. *Journal of Physical Oceanography*, *18*, 17. https://doi.org/10.1175/1520-0485(1988)018<1384:ASOAID>2.0.CO;2

Tonani, M., Nadia, P., S, D., Pujol, I., & Fratianni, C. (2008). A high-resolution free-surface model of the Mediterranean Sea. *Ocean Science (OS)*, *4*. https://doi.org/10.5194/osd-4-213-2007

Torrado, H., Mourre, B., Raventos, N., Carreras, C., Tintoré, J., Pascual, M., & Macpherson, E. (2021). Impact of individual early life traits in larval dispersal: A multispecies approach using backtracking models. *Progress in Oceanography*, *192*, 102518. https://doi.org/10.1016/j.pocean.2021.102518

Trautman, N., & Walter, R. K. (2021). Seasonal variability of upwelling and downwelling surface current patterns in a small coastal embayment. *Continental Shelf Research*, *226*, 104490. https://doi.org/10.1016/j.csr.2021.104490

Treml, E. A., Roberts, J. J., Chao, Y., Halpin, P. N., Possingham, H. P., & Riginos, C. (2012). Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. *Integrative and Comparative Biology*, *52*(4), 525–537. https://doi.org/10.1093/icb/ics101

Tsikliras, A., Antonopoulou, E., & Stergiou, K. (2010). Spawning period of Mediterranean marine fishes. *Reviews in Fish Biology and Fisheries*, *20*, 499–538. https://doi.org/10.1007/s11160-010-9158-6

Tsirintanis, K., Azzurro, E., Crocetta, F., Dimiza, M., Froglia, C., Gerovasileiou, V., Langeneck, J., Mancinelli, G., Rosso, A., Stern, N., Triantaphyllou, M., Tsiamis, K., Turon, X., Verlaque, M., Zenetos, A., & Katsanevakis, S. (2022). Bioinvasion impacts on biodiversity, ecosystem services, and human health in the Mediterranean Sea. *Aquatic Invasions*, *17*(3), 308–352. https://doi.org/10.3391/ai.2022.17.3.01

Umgiesser, G., Canu, D., Cucco, A., & Solidoro, C. (2004). A finite element model for the Venice Lagoon. Development, set up, calibration and validation. *Journal of Marine Systems*, *51*, 123–145. https://doi.org/10.1016/j.jmarsys.2004.05.009

Umgiesser, G., Ferrarin, C., Bajo, M., Bellafiore, D., Cucco, A., De Pascalis, F., Ghezzo, M., McKiver, W., & Arpaia, L. (2022). Hydrodynamic modelling in marginal and coastal seas—The case of the Adriatic Sea as a permanent laboratory for numerical approach. *Ocean Modelling*, *179*, 102123. https://doi.org/10.1016/j.ocemod.2022.102123

Umgiesser, G., Ferrarin, C., Cucco, A., De Pascalis, F., Bellafiore, D., Ghezzo, M., & Bajo, M. (2014). Comparative hydrodynamics of 10 Mediterranean lagoons by means of numerical modeling. *Journal of*

Geophysical Research: Oceans, *119*(4), 2212–2226. https://doi.org/10.1002/2013JC009512

UNEP/MAP-RAC/SPA. (2015). *Adriatic Sea: Description of the Ecology and Identification of the Areas that May Deserve to be Protected; Cerrano, C., Ed.; UNEP/MAP-RAC/SPA: Tunis, Tunisia, 2015; p. 92*. (Eds. Cerrano C., Cebrian D., Requena S. (Tunis: RAC/SPA), 92. doi: 10.13140/RG.2.2.14080.79368).

Ungaro, N., Rizzi, E., & Marano, G. (1993). Note sulla biologia e pesca di *Merluccius merluccius* (L.) nell'Adriatico pugliese. *Biol Mar Suppl al Notiziario SIBM*, *1*, 329–334.

Van Beveren, E. (2012). *Patterns of recruitment and early life history traits of* Trachurus trachurus *in a nearshore temperate reef* [MSc thesis]. Universidade do Algarve. Faro, Portugal.

van der Loos, L. M., Bafort, Q., Bosch, S., Ballesteros, E., Bárbara, I., Berecibar, E., Blanfuné, A., Bogaert, K., Bouckenooghe, S., Boudouresque, C.-F., Brodie, J., Cecere, E., Díaz-Tapia, P., Engelen, A. H., Gunnarson, K., Shabaka, S. H., Hoffman, R., Husa, V., Israel, Á., … De Clerck, O. (2023). Non-indigenous seaweeds in the Northeast Atlantic Ocean, the Mediterranean Sea and Macaronesia: A critical synthesis of diversity, spatial and temporal patterns. *European Journal of Phycology*, *0*(0), 1–30. https://doi.org/10.1080/09670262.2023.2256828

van Sebille, E., Aliani, S., Law, K. L., Maximenko, N., Alsina, J. M., Bagaev, A., Bergmann, M., Chapron, B., Chubarenko, I., Cózar, A., Delandmeter, P., Egger, M., Fox-Kemper, B., Garaba, S. P., Goddijn-Murphy, L., Hardesty, B. D., Hoffman, M. J., Isobe, A., Jongedijk, C. E., … Wichmann, D. (2020). The physical oceanography of the transport of floating marine debris. *Environmental Research Letters*, *15*(2), 023003. https://doi.org/10.1088/1748-9326/ab6d7d

van Sebille, E., Griffies, S. M., Abernathey, R., Adams, T. P., Berloff, P., Biastoch, A., Blanke, B., Chassignet, E. P., Cheng, Y., Cotter, C. J., Deleersnijder, E., Döös, K., Drake, H. F., Drijfhout, S., Gary, S. F., Heemink, A. W., Kjellsson, J., Koszalka, I. M., Lange, M., … Zika, J. D. (2018). Lagrangian ocean analysis: Fundamentals and practices. *Ocean Modelling*, *121*, 49–75. https://doi.org/10.1016/j.ocemod.2017.11.008

Vargas, J. M., García-Lafuente, J., Candela, J., & Sánchez, A. J. (2006). Fortnightly and monthly variability of the exchange through the Strait of Gibraltar. *Progress in Oceanography*, *70*(2), 466–485. https://doi.org/10.1016/j.pocean.2006.07.001

Vargas-Yáñez, M., Plaza, F., García-Lafuente, J., Sarhan, T., Vargas, J. M., & Vélez-Belchi, P. (2002). About the seasonal variability of the Alboran Sea circulation. *Journal of Marine Systems*, *35*(3–4), 229–248. https://doi.org/10.1016/S0924-7963(02)00128-8

Ventosa-Molina, J., Chiva, J., Lehmkuhl, O., Muela, J., Pérez-Segarra, C. D., & Oliva, A. (2017). Numerical analysis of conservative unstructured discretisations for low Mach flows. *International Journal for Numerical Methods in Fluids*, *84*(6), 309–334. https://doi.org/10.1002/fld.4350

Verlaque, M., Steen, F., & Clerck, O. (2009). *Rugulopteryx* Dictyotales, Phaeophyceae), a genus recently introduced to the Mediterranean. *Phycologia*, *48*, 536–542. https://doi.org/10.2216/08-103.1

Viette, M. (1997). Reproductive biology of scad, *Trachurus mediterraneus* (Teleostei, Carangidae), from the Gulf of Trieste. *ICES Journal of Marine Science*, *54*(2), 267–272. https://doi.org/10.1006/jmsc.1996.0185

Vilibić, I., Matijević, S., Šepić, J., & Kušpilić, G. (2012). Changes in the Adriatic oceanographic properties induced by the Eastern Mediterranean Transient. *Biogeosciences*, *9*(6), 2085–2097. https://doi.org/10.5194/bg-9-2085-2012

Virtanen, E. A., Moilanen, A., & Viitasalo, M. (2020). Marine connectivity in spatial conservation planning: Analogues from the terrestrial realm. *Landscape Ecology*, *35*(5), 1021–1034. https://doi.org/10.1007/s10980-020-00997-8

Viúdez, Á. (1997). An Explanation for the Curvature of the Atlantic Jet past the Strait of Gibraltar. *Journal of Physical Oceanography*, *27*(8), 1804–1810. https://doi.org/10.1175/1520-0485(1997)027<1804:AEFTCO>2.0.CO;2

Vrgoč, N., Arneri, E., Jukić-Peladić, S., Krstulović-Šifner, S., Mannini, P., Marčeta, B., Osmani, K., & Piccineti, C. U. (2004). *N.(2004): Review of current knowledge on shared demersal stocks of the Adriatic Sea. FAO-MiPAF Scientific Cooperation to Support Responsible Fisheries in the Adriatic Sea*. GCP/RER/010/ITA/TD-12. AdriaMed Technical Documents, 12.

Walsh, S. (2020). *Simulating Wintertime Lake Dynamics Using the MITgcm Ice Model* [MSc Thesis]. University of Waterloo. Waterloo, Canada.

Wang, Y., Raitsos, D. E., Krokos, G., Gittings, J. A., Zhan, P., & Hoteit, I. (2019). Physical connectivity simulations reveal dynamic linkages between coral reefs in the southern Red Sea and the Indian Ocean. *Scientific Reports*, *9*(1), 16598. https://doi.org/10.1038/s41598-019-53126-0

Wang, Z., Saebi, M., Grey, E. K., Corbett, J. J., Chen, D., Yang, D., & Wan, Z. (2022). Ballast water-mediated species spread risk dynamics and policy implications to reduce the invasion risk to the Mediterranean Sea. *Marine Pollution Bulletin*, *174*, 113285. https://doi.org/10.1016/j.marpolbul.2021.113285

Wejnerowski, Ł., Aykut, T., Pełechata, A., Rybak, M., Dulic, T., Meriluoto, J., & Dziuba, M. (2022). Plankton hitch-hikers on naturalists' instruments as silent intruders of aquatic ecosystems: Current risks and possible prevention. *NeoBiota*, *73*, 193–219. https://doi.org/10.3897/neobiota.73.82636

Werner, F., Cowen, R., & Paris, C. (2007). Coupled Biological and Physical Models: Present Capabilities and Necessary Developments for Future Studies of Population Connectivity. *Oceanography*, *20*(3), 54–69. https://doi.org/10.5670/oceanog.2007.29

Wesson, J. C., & Gregg, M. C. (1994). Mixing at Camarinal Sill in the Strait of Gibraltar. *Journal of Geophysical Research: Oceans*, *99*(C5), 9847–9878. https://doi.org/10.1029/94JC00256

Williams, J. J., & Esteves, L. S. (2017). *Guidance on Setup, Calibration, and Validation of Hydrodynamic, Wave, and Sediment Models for Shelf Seas and Estuaries.* https://doi.org/10.1155/2017/5251902

Williams, P. D., & Hastings, A. (2013). Stochastic dispersal and population persistence in marine organisms. *The American Naturalist*, *182*(2), 271–282. https://doi.org/10.1086/671059

Wor, C., McAllister, M. K., Martell, S. J. D., Taylor, N. G., & Walters, C. J. (2018). A lagrangian approach to model movement of migratory species. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(8), 1203–1214. https://doi.org/10.1139/cjfas-2017-0093

Wu, L., Chen, C., Guo, P., Shi, M., Qi, J., & Ge, J. (2011). A FVCOM-based unstructured grid wave, current, sediment transport model, I. Model description and validation. *Journal of Ocean University of China*, *10*(1), 1–8. https://doi.org/10.1007/s11802-011-1788-3

Xue, Q., Liang, S., Sun, Z., Xu, Y., & Tian, Z. (2023). Near-surface characteristics of velocity profile and momentum transport after wave-breaking in deep water. *Ocean Engineering*, *276*, 114223. https://doi.org/10.1016/j.oceaneng.2023.114223

Yuan, S., Zhu, S., Luo, X., & Mu, B. (2024). A deep learning-based bias correction model for Arctic sea ice concentration towards MITgcm. *Ocean Modelling*, *188*, 102326. https://doi.org/10.1016/j.ocemod.2024.102326

Zapata, C., Puente, A., García, A., García-Alba, J., & Espinoza, J. (2019). The Use of Hydrodynamic Models in the Determination of the Chart Datum Shape in a Tropical Estuary. *Water, 11*(5), 902. https://doi.org/10.3390/w11050902

Zardoya, R., Castilho, R., Grande, C., Favre-Krey, L., Caetano, S., Marcato, S., Krey, G., & Patarnello, T. (2004). Differential population structuring of two closely related fish species, the mackerel (*Scomber scombrus*) and the chub mackerel (*Scomber japonicus*), in the Mediterranean Sea. *Molecular Ecology, 13*(7), 1785–1798. https://doi.org/10.1111/j.1365-294X.2004.02198.x

Zhang, Y. J., Ye, F., Stanev, E. V., & Grashorn, S. (2016). Seamless cross-scale modeling with SCHISM. *Ocean Modelling, 102,* 64–81. https://doi.org/10.1016/j.ocemod.2016.05.002

Zhao, G., Gao, X., Zhang, C., & Sang, G. (2020). The effects of turbulence on phytoplankton and implications for energy transfer with an integrated water quality-ecosystem model in a shallow lake. *Journal of Environmental Management*, *256,* 109954. https://doi.org/10.1016/j.jenvman.2019.109954

Zore, M. (1956). On gradient currents in the Adriatic Sea. *Acta Adriatica*, *8*, 1–40.

Zorica, B., Anđelić, I., & Keč, V. Č. (2019). Sardine (*Sardina pilchardus*) spawning in the light of fat content analysis. *Scientia Marina*, *83*(3), Article 3. https://doi.org/10.3989/scimar.04898.07A

Zorica, B., Keč, V. Č., Vrgoč, N., Isajlović, I., Piccinetti, C., Mandić, M., Marčeta, B., & Pešić, A. (2020). A review of reproduction biology and spawning/ nursery grounds of the most important Adriatic commercial fish species in the last two decades. *Acta Adriatica*, *61*(1), Article 1. https://doi.org/10.32582/aa.61.1.7

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