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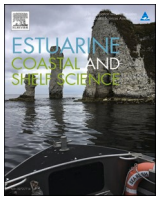

Larval dispersal and connectivity of *Ostrea edulis*: A biophysical modelling review for restoration planning

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A B S T R A C T

Increasing efforts to restore *Ostrea edulis* across Europe have intensified the need for robust understanding of larval dispersal and population connectivity. Although numerous local modelling studies have emerged, a consolidated synthesis of their methodological approaches, assumptions and management relevance has been lacking. This review critically evaluates hydrodynamic and biophysical models applied to *O. edulis*, examining model structure, behavioral representation, settlement treatment, validation practice and environmental context.

The synthesis reveals substantial heterogeneity in modelling frameworks and limited formal validation, constraining cross-system comparability and management interpretation. Nonetheless, consistent patterns emerge: larval behavior significantly modifies dispersal trajectories relative to passive transport, connectivity outcomes are highly sensitive to hydrodynamic setting and release timing, and semi-enclosed systems generally promote stronger local retention than open, advective environments.

By distinguishing potential dispersal from realized connectivity and highlighting persistent methodological gaps, particularly in empirical validation and uncertainty quantification, this review provides a structured framework for interpreting connectivity models in restoration planning. Strengthening transparency, integrating demographic processes and explicitly addressing environmental variability will be essential for translating modelling advances into effective, evidence-based restoration strategies for Europe's native oyster.

1. Introduction

The European flat oyster (*Ostrea edulis*) has experienced a severe decline in abundance and distribution across its native range, leading to its classification as “threatened and declining” under several conservation frameworks, including the OSPAR Convention (Pogoda, 2019). The decline of *Ostrea edulis* populations has been a growing concern due to several interrelated factors: coastal development, pollution and habitat loss. Without clean, undisturbed environments, oysters struggle to establish and thrive (Pogoda, 2019). Pollution, especially from agricultural runoff, industrial waste, and sewage, has caused the deterioration of water quality in many coastal regions; affecting oysters' health by impairing their feeding, growth, and reproduction, which contributes to population decline (Thurstan et al., 2013). The spread of diseases such as *Bonamia ostreae*, *B. exitiosa* and others, has caused significant mortality in *Ostrea edulis* populations (Narcisi et al., 2010; Oraić et al., 2021). The introduction of the Pacific oyster (*Crassostrea/Magallana gigas*) has intensified competition for space and resources (Rodriguez-Perez, 2019). Overfishing, disease outbreaks, and environmental stressors have led to a significant reduction in wild oyster stocks, impacting both the ecosystem services they provide as well as the availability of oysters for commercial harvest, and consequently local fisheries and the seafood industry (Beck et al., 2011; Ezgeta-Balić et al., 2021; Laing et al., 2006).

Oysters play a fundamental role in marine and coastal ecosystems by supporting their health and resilience, underscoring the importance of oyster conservation and restoration efforts (Beck et al., 2011; Coen and Luckenbach, 2000; Grabowski et al., 2012; zu Ermgassen et al., 2025). Given the ongoing decline of oyster populations worldwide, prioritizing the protection and re-establishment of oyster beds is essential for safeguarding these critical ecosystem services. Oyster reefs function as natural coastal barriers, reducing wave impact and limiting shoreline erosion. By absorbing wave energy and stabilizing sediments, oyster beds help protect vulnerable coastal habitats and human infrastructure from storms and flooding (Piazza et al., 2005; Scyphers et al., 2011). This protective function is particularly relevant in the context of climate change, where sea level rise and increased storm frequency pose a significant threat to coastal communities. Oyster reefs can also provide

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critical habitat for a diverse array of marine species, acting as natural structures that offer shelter, breeding grounds, and feeding areas (Grabowski and Peterson, 2007; Lenihan et al., 2001). The complex three-dimensional structure of oyster beds fosters biodiversity by supporting both mobile species, such as fish and crabs, and sessile organisms, like barnacles and sponges (Lenihan et al., 2001; Peterson et al., 2003). These reefs create a stable substrate for epibenthic fauna and promote species richness, thereby supporting ecosystem stability and functioning (Grabowski and Peterson, 2007). Oysters are also efficient filter feeders and ecosystem engineers that contribute to nutrient cycling and water quality improvement by removing plankton, bacteria, and suspended particles from the water column (Coen et al., 2007; Dame, 2016; Kent et al., 2017; Newell et al., 2007; Piehler and Smyth, 2011). This filtration process has several beneficial outcomes like nitrogen removal (Newell et al., 2007; Piehler and Smyth, 2011), turbidity reduction (Kent et al., 2017) and bacterial biomass removal. By significantly reshaping the physical structure of the seabed, oyster-bed formation creates complex microhabitats that enhance biodiversity, promote diverse species interactions, stabilize ecosystem processes, and lead to the development of distinct benthic communities, thereby strengthening overall ecosystem functioning and resilience (Grabowski et al., 2005).

Oyster reefs also contribute significantly to nutrient regeneration and biogeochemical cycling. Through biodeposition and benthic-pelagic coupling, oyster beds enhance the recycling of nitrogen and phosphorus, thereby supporting primary productivity and ecosystem functioning (Dame, 2016). In addition to removing particulate matter from the water column, oysters transfer organic material to the benthos, stimulating microbial processes and nutrient turnover. These mechanisms can influence local nutrient dynamics and improve ecosystem productivity, further reinforcing the ecological importance of oyster reefs as ecosystem engineers (Dame, 2016).

In addition to their ecological functions, oysters have long been harvested as a valuable seafood resource. The consumption of *Ostrea edulis* dates back to ancient civilizations, including the Romans, who valued oysters for their nutritional and culinary qualities (Lotze, 2007; Thurstan et al., 2013). Today, oysters remain an important component of local economies, particularly in Europe, where they are cultivated in aquaculture farms (Airoldi and Beck, 2007). Oyster farming provides a sustainable food source that supports coastal communities and contributes to cultural heritage (Grabowski and Peterson, 2007).

As outlined, *O. edulis* is a keystone species of ecological, economic, and cultural significance across coastal ecosystems. Once a dominant reef-forming species in many European estuaries, its populations and geographic distribution have markedly declined, reducing its contribution to habitat formation and ecosystem processes and prompting extensive conservation and restoration efforts across multiple countries (zu Ermgassen et al., 2025). Restoration strategies, particularly those involving active reef construction or seeding, rely fundamentally on a deep understanding of larval dispersion and population connectivity (Puckett et al., 2018). Collectively, these restoration efforts have become a priority for enhancing biodiversity, recovering ecosystem services, and promoting sustainable aquaculture practices (Beck et al., 2011; Pogoda, 2019; Pogoda et al., 2019; Rodriguez-Perez, 2019; Rodriguez-Perez et al., 2019).

As *O. edulis* is sessile during its adult stage, the dispersal of pelagic larvae represents the principal mechanism through which populations are maintained, expanded, or recolonized (Rodriguez-Perez et al., 2020). Consequently, an appropriate consideration of the ability of larvae to disperse over ecologically meaningful distances, coupled with their requirements for suitable settlement habitats, is crucial for addressing these knowledge gaps and supporting evidence-based conservation and management strategies. Among these are the design and placement of restoration projects, the optimization of aquaculture practices, and the design of marine protected areas (MPAs) or larval source reserves (Lowe and Allendorf, 2010). Accurate characterization of larval dispersal also underpins predictions of population dynamics, gene flow, and resilience to local extinctions (Cowen and Sponaugle, 2009), and the capacity of restored reefs to sustain themselves and support adjacent habitats (Rodriguez-Perez, 2019). Patterns of larval dispersal and connectivity are widely recognized as critical to the persistence of metapopulations in marine ecosystems (Hastings et al., 2006; Lipcius et al., 2008; Puckett et al., 2018). However, modelling larval dispersal and connectivity remains highly challenging due to the complex interplay between oceanographic processes and biological traits.

Dispersal is influenced by a combination of hydrodynamic forcings (e.g. currents, tides) and larval behaviors (e.g. swimming ability, vertical migration, and settlement timing) (Treml et al., 2008). These factors are non-linear and often site-specific, necessitating the use of biophysical models that couple ocean circulation with simulated larval trajectories (North et al., 2010). Furthermore, as climate change continues to alter region's hydrodynamic conditions, predictive models are essential for anticipating its effects on larval transport and ensuring the resilience of *O. edulis* populations (Bertolini and Pastres, 2023; Dekshenieks et al., 2000; North et al., 2010).

This review addresses two main questions: (1) to what extent hydrodynamic and biophysical models improve our understanding of larval dispersal and connectivity of *Ostrea edulis*, and (2) how reliable their outputs are for supporting restoration planning and the design of self-sustaining restoration networks.

To answer these questions, we conduct a critical synthesis of modelling studies that simulate larval transport, retention, export, and settlement of *O. edulis* across European coastal and shelf systems, with particular attention to behaviorally informed and biophysical approaches. Rather than providing a general overview of modelling tools, this review evaluates how different modelling choices (resolution, behavioral parameterization, competency windows, and validation strategies) influence connectivity outcomes and their interpretation in a restoration context. By systematically comparing approaches and assumptions, we identify consistent ecological patterns, methodological gaps, and key uncertainties that affect the use of connectivity models as decision-support tools for oyster restoration.

2. Species distribution and oyster beds in a connectivity perspective

The European flat oyster (*Ostrea edulis*) is native to the northeastern Atlantic, occurring from Norway to Morocco and including the British Isles and the western Mediterranean (Airoldi and Beck, 2007; Bertolini and Pastres, 2023; Bromley et al., 2016). The species has also been introduced to other regions, such as parts of the eastern Mediterranean, the Black Sea, North America and New Zealand, largely through aquaculture activities (Bromley et al., 2016). Historically, *O. edulis* formed extensive biogenic reef structures, or “oyster beds”, that represented dominant habitat-forming elements in many coastal ecosystems (Coen et al., 2007; Rodriguez-Perez, 2019). Widespread historical declines driven by overexploitation, habitat loss and disease have, however, resulted in fragmented and spatially discontinuous populations, with direct implications for larval dispersal, retention and connectivity among remaining beds.

2.1. Distribution in the Mediterranean and Adriatic: regional contexts for connectivity

In the Mediterranean Sea, *Ostrea edulis* currently persists in fragmented populations distributed across coastal lagoons, estuaries and semi-enclosed bays (Fig. 1) (Bertolini and Pastres, 2023; Bromley et al., 2016; Thurstan et al., 2024a,b). This spatial fragmentation, resulting from historical overexploitation, habitat degradation and disease outbreaks (Narcisi et al., 2010; Oraić et al., 2021), has direct implications for larval connectivity: remaining populations increasingly function as

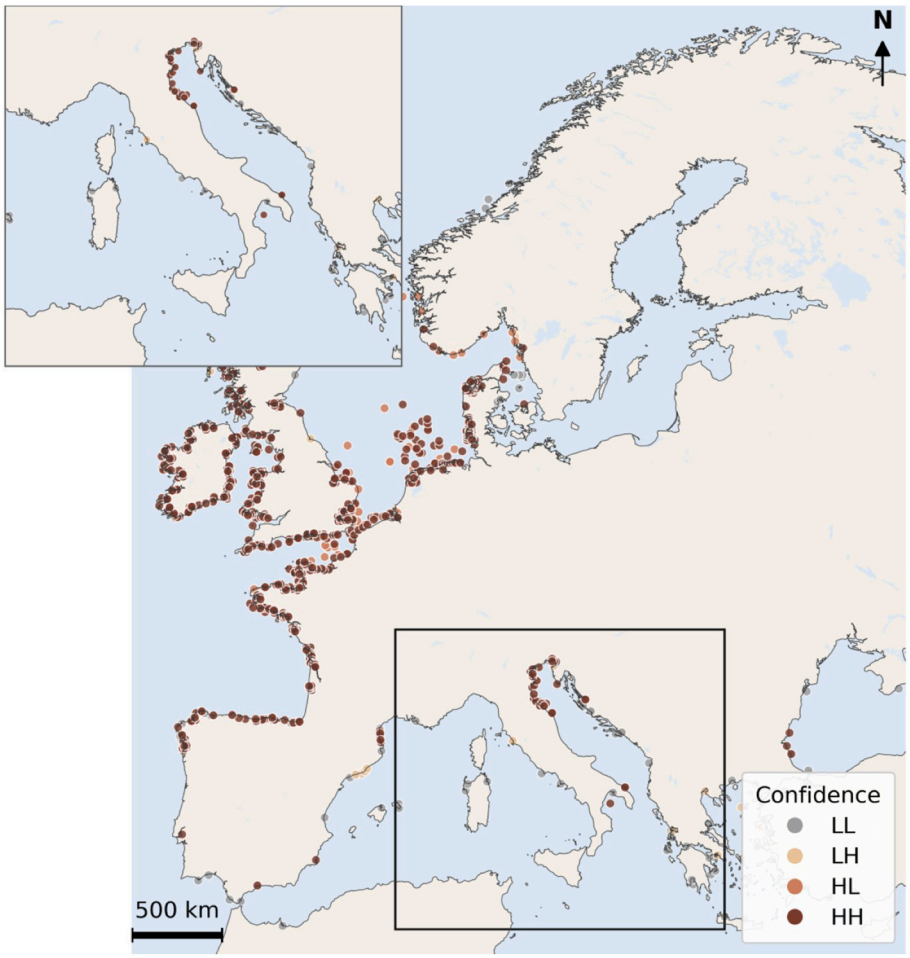

Fig. 1. Locations of historical *Ostrea edulis* reef records mapped from historical sources. Data from Thurstan et al., 2024a Figshare dataset (CC BY 4.0). Confidence classes indicate combined certainty of reef habitat existence (first letter) and spatial accuracy (second letter), where H = high and L = low.

isolated patches whose persistence may depend on limited local retention rather than sustained regional exchange. From a modelling perspective, this spatial configuration highlights the importance of fine-scale hydrodynamics, local retention, and stepping-stone connectivity when evaluating restoration potential (Rodriguez-Perez, 2019).

The Adriatic Sea represents a particularly relevant system for connectivity-oriented modelling due to the combination of historical habitat loss and strong spatial structuring of remaining populations (Bertolini and Pastres, 2023; Thurstan et al., 2024a,b). Oyster beds were historically widespread along both the Italian and eastern Adriatic coasts, forming extensive reef complexes that likely supported strong demographic connectivity. Their progressive contraction has resulted in a mosaic of remnant and restored sites embedded within a hydrodynamically structured basin, where circulation patterns and freshwater inputs (e.g. Po River plume) influence dispersal pathways and retention zones (Fig. 1) (Bertolini and Pastres, 2023). These characteristics make the Adriatic Sea an illustrative example of how hydrodynamic forcing and habitat fragmentation interact to shape connectivity networks, directly informing restoration planning.

From a modelling and restoration perspective, oyster beds should therefore be conceptualized not only as habitats but as functional nodes within spatial networks of larval exchange. Current restoration strategies increasingly aim to rebuild such networks through the strategic placement of cultch, protected areas and stepping-stone sites to enhance self-recruitment and metapopulation connectivity (Pogoda et al., 2019; Rodriguez-Perez, 2019). This network-based view provides a direct conceptual bridge between spatial ecology, biophysical modelling and the design of effective restoration interventions.

2.2. *Larval connectivity and the role of oyster beds within ecological restoration networks*

Oyster beds, whether natural or restored, consist of dense aggregations of oysters forming biogenic reef structures on hard substrate (Rodriguez-Perez, 2019). Within a connectivity framework, these beds function as discrete nodes in larval dispersal networks, linking spatially separated populations through the exchange of pelagic larvae (Cowen et al., 2007; Treml et al., 2008). Their spatial arrangement, size, and environmental setting determine their contribution to population persistence and recovery across fragmented coastal landscapes.

Depending on local hydrodynamic conditions and biological traits, individual beds may act as larval sources, exporting propagules to surrounding areas; sinks, receiving larvae but contributing little to onward dispersal; or self-recruiting units sustained primarily through local retention (Hastings et al., 2006; Lipcius et al., 2008; Cowen and Sponaugle, 2009). In highly fragmented systems, reduced connectivity can isolate remnant populations, increasing extinction risk and limiting natural recolonization, whereas even weak or intermittent larval exchange may enhance metapopulation resilience by maintaining demographic and genetic linkages among sites (Cowen et al., 2006; Lowe and Allendorf, 2010).

Connectivity among oyster beds emerges from the interaction between physical drivers - such as circulation patterns, tidal regimes, and hydrodynamic retention features - and biological processes including

larval swimming behavior, settlement timing, and substrate preference (Cragg and Gruffydd, 1975; Jonsson et al., 1991; Potet et al., 2021). These coupled processes underpin the spatial patterns predicted by dispersal and connectivity models and strongly influence whether restored beds contribute primarily to local persistence or to regional recovery.

From a restoration perspective, this implies that the ecological role of an oyster bed cannot be evaluated solely at the site scale. Instead, beds must be considered in relation to their position within broader dispersal networks, where their function as sources, sinks, or stepping-stone habitats shapes metapopulation connectivity and long-term restoration outcomes (Pogoda et al., 2019; Rodriguez-Perez, 2019; Theuerkauf et al., 2021). Connectivity-oriented modelling provides a quantitative framework to explore these dynamics and to support the design of restoration strategies that reinforce functional linkages among remnant and restored populations in the Mediterranean and Adriatic seas.

3. Methods

3.1. Review scope and analytical framework

The aim of this review is to evaluate how hydrodynamic and biophysical models have been used to investigate larval dispersal and connectivity of *Ostrea edulis*, and to assess the relevance and reliability of their outputs for restoration planning. Each retained modelling study was therefore examined according to five predefined categories: (i) model type and spatial–temporal resolution, (ii) representation of larval biology and behavior, (iii) treatment of settlement and habitat filtering, (iv) validation and uncertainty assessment, and (v) implications for restoration and management. These categories directly structure the synthesis presented in Sections 7 - 10.

3.2. Literature search strategy and study selection

A structured literature search was performed in Scopus, Web of Science, and Google Scholar, with the last search conducted in November 2025. To reduce publication bias and to capture underrepresented regions and non-indexed outputs, grey literature (technical reports, theses, and project deliverables) was screened during the exploratory phase to identify additional studies and citation networks; however, only peer-reviewed studies meeting the inclusion criteria were retained in the final comparative synthesis.Google Scholar was used to identify additional grey literature and citation networks but was not included in quantitative record counts due to limited reproducibility. Search strings combined three keyword groups related to (i) the species, (ii) dispersal/connectivity processes, and (iii) modelling approaches, using Boolean operators. The core query was adapted to each database syntax and included combinations of the following terms.

- species: “*Ostrea edulis*”, “European flat oyster”;
- process: “larval dispersal”, “larval transport”, “connectivity”, “self-recruitment”;
- method: “hydrodynamic model”, “particle tracking”, “Lagrangian”, “biophysical model”.

An example of the core string was: (“*Ostrea edulis*” OR “European flat oyster”) AND (“larval dispersal” OR “larval transport” OR “connectivity” OR “self-recruitment”) AND (“hydrodynamic model” OR “particle tracking” OR “Lagrangian” OR “biophysical”).

Records were screened first by title and abstract and then by full text. Studies were included when they: (i) modelled larval dispersal or connectivity of *O. edulis* (or explicitly used a closely related proxy to parameterize *O. edulis* behavior), (ii) coupled hydrodynamic circulation with Lagrangian particle tracking and/or behavioral routines, (iii) reported spatial or quantitative outputs relevant to retention, export, settlement or connectivity, (iv) focused on European coastal or shelf-sea systems, and (v) provided sufficient methodological detail to assess model configuration (e.g., grid resolution, Pelagic Larval Duration, behavioral rules, and validation). Studies were excluded if they were purely conceptual, laboratory-only without dispersal modelling, focused on non-*Ostrea* species without explicit behavioral transfer, or lacked sufficient methodological description.

Database searching identified 717 records across Scopus and Web of Science. After duplicate removal, 524 unique records were screened by title and abstract. A total of 34 studies were retained for full-text assessment. Following eligibility screening, 7 modelling studies were included as the core evidence base for the comparative synthesis (Table 1). Most exclusions at full-text stage were due to absence of dispersal modelling, focus on non-target species, or insufficient methodological detail. The final number reflects the limited availability of species-specific dispersal modelling studies.

3.3. Data extraction and comparative synthesis

For each retained study, information was extracted into a comparative matrix aligned with the five analytical categories. Extracted variables included model domain and spatial resolution, hydrodynamic forcing, spawning timing and Pelagic Larval Duration (PLD), representation of larval behavior (e.g., vertical migration or settlement delay), treatment of settlement and habitat suitability, and validation approach. When available, quantitative outputs such as self-recruitment estimates, connectivity between sites, dispersal distances, and temporal variability were also recorded. The extracted data were then compared to identify common dispersal and connectivity patterns, evaluate the influence of modelling choices on predicted outcomes, and highlight methodological gaps relevant to *O. edulis* restoration planning.

4. Larval traits of *Ostrea edulis* shaping dispersal and connectivity

The reproductive biology and larval ecology of *Ostrea edulis* are central to understanding the species’ dispersal capacity and the mechanisms underpinning population connectivity. The species is a protandric hermaphrodite, initially maturing as male and subsequently as female, with fertilization occurring internally and embryos being brooded within the mantle cavity for approximately 8-10 days (Korringa, 1940). Following this brooding phase, veliger larvae are released into the water column, where they enter a pelagic phase that typically lasts between 6 and 30 days, depending on temperature, food availability and other environmental drivers (Colsoul et al., 2020; Colsoul et al., 2021; Davis and Calabrese, 1969; Korringa, 1940; Robert et al., 2017; Rodriguez-Perez et al., 2021). During this planktonic period, larvae develop from the D-shaped veliger to the pediveliger stage, at which point they reach settlement competency (Rodriguez-Perez et al., 2021).

Historically, *O. edulis* larvae were treated as passive drifters, fully subjected to hydrodynamic transport. However, accumulating evidence demonstrates that they are capable of active vertical swimming, diel vertical migration and selective settlement in response to chemical and physical cues (Cragg and Gruffydd, 1975; Rodriguez-Perez et al., 2020). Such behavioral plasticity enables larvae to modulate their vertical position within the water column, thereby influencing horizontal displacement through interactions with vertically stratified currents (Metaxas and Saunders, 2009). These traits indicate that dispersal pathways emerge from the interplay between physical circulation and behavior, rather than from hydrodynamics alone.

Pelagic larval duration (PLD) is strongly temperature-dependent, with warmer conditions accelerating growth and reducing the time required to reach settlement capable pediveliger stage, resulting in PLDs as short as one week during peak summer periods (Robert et al., 1988). Conversely, cooler spring and autumn temperatures may extend the pelagic phase to nearly one month (Robert et al., 2017). Temperature

Table 1
Overview of modelling studies included in the literature analysis.
The table summarizes the main physical and biological components of the modelling frameworks, the spatial configuration of the study systems, and the key connectivity-related outputs analyzed. Reported horizontal resolutions refer to typical values stated in the original studies; unstructured models employ spatially variable mesh refinement. PTM means Particle Tracking Model.

Study	Region/system	Spatial scale	Hydrodynamic model (type; horizontal resolution)	Dispersal model type	Behavior represented	Settlement/ habitat filtering	Main variables analyzed
Holbrook (2021)	Solent (UK), semi-enclosed embayment	Multiple restoration sites	Hydrodynamic trajectory model of the Solent (model type not explicitly specified)	Lagrangian PTM driven by external hydrodynamic outputs	Diel vertical migration, vertical positioning	Not included	Retention, export, timing of dispersal
Rodriguez-Perez et al. (2019,2020)	Scottish sea lochs	Multiple lochs	ROMS (nested structured grid; ~100–500 m in inner lochs)	Behavior-informed PTM	Stage-dependent swimming, competency delay	Not included	Self-recruitment, local retention
Smyth et al. (2016)	Enclosed sea lough	Single system	Depth-integrated hydrodynamic model (MIKE 21–type; structured grid)	Transport-only PTM	None (larvae treated as passive)	Not included	Dispersal pathways, retention
Corrochano-Fraile et al. (2022)	Scottish coastal systems	Multiple systems	FVCOM (unstructured grid; ~100 m–1 km, spatially variable)	PTM with simplified biological assumptions	Variable among scenarios	Not included	Connectivity patterns among sites
Stechele et al. (2023)	North Sea (offshore reefs)	Multiple potential offshore sites	COHERENS (structured grid; ~5 km)	PTM coupled to DEB-based IBM (larvae passive)	Not explicitly included	Habitat suitability included	Self-recruitment potential and habitat suitability
Bertolini and Pastres (2023)	Northern Adriatic lagoon/coastal system	Lagoon to coastal scale	TELEMAC-3D (unstructured grid; ~10-100 m)	Behavior-informed PTM	Near-bed positioning at competency	Not included	Retention, seasonal variability
Clavel-Henry et al. (2023),[a]	Galway Bay	Bay-scale	ROMS (structured grid; bay-scale resolution)	PTM with simplified biological behavior	Simplified behavioral rules	Not included	Potential source-sink patterns

[a] Study focuses on *Magallana gigas* and is included for methodological comparison.

also constrains larval performance and behavior. Metabolic processes are highly temperature-sensitive, with optimal growth and swimming efficiency generally observed between 15 and 25 °C; outside this range, energetic costs increase and the ability to sustain vertical migration declines (Korringa, 1940; Rodriguez-Perez, 2019). Higher temperatures may enhance swimming speed (Rodriguez-Perez et al., 2020), although larvae must avoid overheating in shallow, warm surface layers (Rodriguez-Perez, 2019). Overall, temperatures between ~17.5 and 30 °C support growth and survival, whereas values below 10 °C or above 30 °C markedly reduce both (Davis and Calabrese, 1969). While some early studies suggested limited thermal influence on vertical migration except under strong gradients (Korringa, 1940), later work shows that features such as thermoclines can act as barriers to vertical movement (Daigle and Metaxas, 2011).

Salinity exerts an additional physiological constraint: values below ~20 ppt are associated with reduced survival and delayed metamorphosis (Colsoul et al., 2021; Davis and Calabrese, 1969), thereby limiting the range of environments that can contribute to effective connectivity. Larvae are also capable of delaying metamorphosis when suitable settlement substrates are absent, prolonging the planktonic phase for up to ~14 days and potentially increasing dispersal distance, although at the cost of higher exposure to predation and environmental stress (Cole and Jones, 1939; Rodriguez-Perez et al., 2021). Settlement probability, however, increases markedly in the presence of conspecifics, biofilms or appropriate substrate, emphasizing the functional role of existing oyster beds as facilitators of recruitment (Cole and Jones, 1939).

Selective settlement represents a critical mechanism influencing realized connectivity. Competent larvae actively respond to biological and physicochemical cues, including the presence of conspecifics, shell substrate, microbial biofilms and local hydrodynamic conditions, rather than settling randomly (Cole and Jones, 1939; Rodriguez-Perez et al., 2021). This behavior increases the probability of recruitment success and reinforces the role of existing oyster beds as facilitators of population persistence and reef recovery. Furthermore, larvae may delay metamorphosis when suitable settlement cues are absent, extending their pelagic duration and potentially altering dispersal trajectories and connectivity patterns (Cole and Jones, 1939; Rodriguez-Perez et al., 2021). As a consequence, realized recruitment depends not only on transport processes but also on habitat availability and settlement success, highlighting the importance of incorporating settlement behavior into dispersal and connectivity models.

Beyond physical and physiological controls, ecological processes such as food availability further influence larval behavior and survival. Larvae actively track productive water layers, remaining within food-rich strata to maximize energy intake, and may shift upwards in the water column under food-limited conditions, reflecting active foraging strategies (Rodriguez-Perez et al., 2020). Spawning and larval release commonly coincide with phytoplankton blooms in late spring and late summer, consistent with this trophic coupling (Rodriguez-Perez, 2019). Within this framework, larval survival constitutes a major demographic bottleneck: mortality rates frequently exceed 90% in marine invertebrate larvae, highlighting the combined influence of stochastic and deterministic processes on dispersal and realized connectivity (Rumrill, 1990).

These traits highlight the active role of larval physiology and behavior in shaping dispersal and connectivity.

5. Results of the literature analysis

Seven modelling studies addressing larval dispersal and connectivity of *Ostrea edulis* in European coastal systems were identified. These studies span six distinct geographic settings, including semi-enclosed embayments, fjord-like systems, shallow lagoons, and open shelf environments, encompassing a broad range of hydrodynamic regimes and spatial scales.

Across the reviewed studies, modelling objectives focused on quantifying larval retention and export, assessing the influence of larval behavior on dispersal pathways, identifying source-sink relationships among sites, and evaluating restoration potential under present or projected environmental conditions. Hydrodynamic frameworks ranged from high-resolution unstructured-grid coastal models to regional shelf-

sea configurations.

All studies employed Lagrangian particle-tracking approaches as the core method for simulating larval transport. However, the level of biological complexity varied markedly. One study represented larvae as passive tracers, whereas six explicitly incorporated biological processes such as vertical migration, delayed settlement, or time-dependent settlement readiness during larval development. The treatment of settlement also differed among studies, ranging from simple arrival-based metrics to explicit habitat filtering and, in one case, coupling with demographic and energetic post-settlement models.

Key characteristics of the modelling frameworks, spatial coverage, biological representation, and connectivity-related outputs are summarized in Table 1.

6. Emerging patterns in dispersal and connectivity modelling for *Ostrea edulis*

Larval dispersal and connectivity are key processes shaping the persistence and recovery of *Ostrea edulis* populations. In many modelling studies, connectivity is treated not only as physical transport but as an outcome mediated by retention, settlement success and spatial habitat configuration, particularly in a restoration context, while other contributions focus primarily on patterns of physical retention and export (Holbrook, 2021; Rodriguez-Perez et al., 2021; Smyth et al., 2016; Bertolini and Pastres, 2023; Stechele et al., 2023). Distinguishing between potential dispersal and realized connectivity consistently reveals the importance of self-recruitment and local exchange relative to long-distance export.

A recurrent pattern across case studies is the dominant role of local retention in semi-enclosed systems such as sea lochs, lagoons and embayments. Models applied in the Solent, Scottish sea lochs and Adriatic lagoon environments consistently predict high levels of self-recruitment and limited export under realistic circulation scenarios (Holbrook, 2021; Rodriguez-Perez et al., 2019; Bertolini and Pastres, 2023). In contrast, studies conducted in more open systems, including shelf environments and semi-open bays, report more variable source–sink dynamics and a stronger influence of hydrodynamic forcing on dispersal pathways (Clavel-Henry et al., 2023; Stechele et al., 2023). These differences suggest that restoration success in open systems is more likely to depend on coordinated, network-based strategies rather than isolated site interventions.

The reviewed studies further reveal substantial heterogeneity in the biological realism of connectivity models. While most frameworks employ Lagrangian particle tracking coupled to hydrodynamic circulation models, only a subset explicitly incorporates as well as key biological traits such as larval active swimming behavior, delayed competency (postponement of settlement after larvae become competent, allowing them to remain in the water column until suitable habitat is encountered) or habitat-dependent settlement processes (Rodriguez-Perez et al., 2020; Rodriguez-Perez et al., 2021; Stechele et al., 2023). Where behavioral components are included, simulations consistently predict reduced dispersal distances and enhanced self-recruitment compared with passive-particle scenarios, indicating that model structure strongly influences inferred connectivity patterns (Rodriguez-Perez et al., 2020; North et al., 2008).

Although this synthesis focuses specifically on modelling studies targeting *O. edulis*, several methodological approaches adopted in the reviewed literature are informed by broader advances in marine biophysical modelling. Recent applications demonstrate the increasing relevance of multi-scale hydrodynamic coupling, advanced particle-tracking schemes and integration with habitat suitability or individual-based frameworks, which offer promising directions for improving ecological realism and restoration relevance of future *O. edulis* connectivity models (Laurent et al., 2020; Melaku Canu et al., 2020; Stechele et al., 2023).

7. Hydrodynamic models in *Ostrea edulis* dispersal studies: emerging patterns

Across the reviewed literature, hydrodynamic modelling consistently represents the physical backbone of dispersal simulations for *Ostrea edulis*, providing the circulation fields on which connectivity estimates are built. All retained studies rely on hydrodynamic circulation outputs to drive Lagrangian particle tracking; however, the dimensionality (2D vs 3D) and the degree of online/offline coupling vary across studies. These studies confirm the central role of hydrodynamic circulation in shaping predicted transport, retention and export patterns (Smyth et al., 2016; Corrochano-Fraile et al., 2022; Bertolini and Pastres, 2023).

A clear pattern emerging from the analysis is that most applications focus on semi-enclosed or topographically complex systems. Studies conducted in these environments (e.g. Solent, Scottish sea lochs, Adriatic lagoons) report circulation regimes characterized by relatively long water residence times and structured retention zones, which favor high levels of self-recruitment in model outputs (Smyth et al., 2016; Holbrook, 2021; Bertolini and Pastres, 2023).

In contrast, studies that extend modelling to more open or advective environments report greater sensitivity of dispersal outcomes to boundary conditions, atmospheric forcing and interannual variability, leading to less stable connectivity patterns and higher uncertainty in predicted source–sink relationships (Corrochano-Fraile et al., 2022; Stechele et al., 2023). This highlights that hydrodynamic context itself constitutes a major driver of variability in connectivity outcomes across systems.

The review also reveals that explicit quantitative validation of hydrodynamic performance remains limited. Most studies rely on qualitative or indirect validation approaches, such as consistency with known circulation patterns, comparisons with available current measurements, or agreement with observed retention tendencies (North et al., 2008; Smyth et al., 2016). This methodological limitation represents a recurrent source of uncertainty that constrains confidence in dispersal predictions, particularly when models are used to support spatial planning decisions.

In addition, predicted connectivity patterns are highly sensitive to the timing of larval release within the circulation field. Differences in spawning windows, tidal phase, wind forcing, and seasonal stratification can substantially alter dispersal pathways and retention outcomes (North et al., 2008; Treml et al., 2008; Werner et al., 2007), and have been shown to influence connectivity estimates in European oyster systems (Rodriguez-Perez et al., 2020; Bertolini and Pastres, 2023; Clavel-Henry et al., 2023). Such variability is often explored through scenario-based simulations but rarely validated independently.

Finally, a consistent finding across studies is that hydrodynamic simulations alone tend to produce broader dispersal kernels than models incorporating biological processes. This reinforces the conclusion that hydrodynamics provide necessary but insufficient information for connectivity assessment, and that coupling with biological parameterization is essential to avoid systematic overestimation of dispersal and underestimation of local retention (Metaxas and Saunders, 2009; Rodriguez-Perez et al., 2020).

8. Biophysical and behavioral modelling of *Ostrea edulis* larval dispersal

8.1. Conceptual framework: biophysical coupling

Biophysical coupling integrates hydrodynamic circulation models with biological representations of larval behavior and development. These models explicitly account for the capacity of larvae to interact with their physical environment through swimming, vertical positioning, development and settlement processes (Cowen and Sponaugle, 2009; Metaxas and Saunders, 2009).

In the case of *Ostrea edulis*, biophysical frameworks combine

simulated flow fields with modules describing larval transport, development, vertical movement and settlement-related processes, allowing evaluation not only of potential dispersal pathways but also of how biological traits modulate realized connectivity (Smyth et al., 2016; Rodriguez-Perez et al., 2021). This shift from passive to biophysical modelling has been driven by growing evidence that models neglecting larval behavior tend to overestimate dispersal distance and connectivity while underestimating local retention and self-recruitment (Fiksen et al., 2007; North et al., 2008; Cowen and Sponaugle, 2009) (Fig. 2).

By incorporating time-varying biological traits such as settlement competence periods, mortality, stage-dependent vertical movement and behavioral responses to environmental conditions, biophysical models generate probabilistic dispersal patterns that more closely match field observations (Coolen et al., 2020; Stechele et al., 2023). These probabilistic representations of larval exchange are central to understanding metapopulation dynamics and to informing spatially explicit restoration design.

8.2. Behavioral representation in larval dispersal models

Experimental and modelling studies demonstrate that *O. edulis* larvae are not passive particles but exhibit behaviors such as diel vertical migration, buoyancy regulation and selective positioning within the water column, all of which influence dispersal trajectories and settlement outcomes (Cragg and Gruffydd, 1975; Rodriguez-Perez et al., 2020; Stechele et al., 2023). Accordingly, behavioral representation has become a key differentiating element among larval dispersal models applied to this species.

To enable systematic comparison across modelling approaches and environmental contexts, we synthesized the main characteristics of a management-oriented subset of the reviewed *O. edulis* dispersal and connectivity studies in a comparative framework (Table 2). The table contrasts system type, hydrodynamic configuration, level of behavioral representation, treatment of settlement and habitat filtering, and validation strategies. This synthesis allows evaluation of how methodological choices shape predicted connectivity patterns and highlights recurring sources of uncertainty with direct relevance for restoration planning.

Patterns emerging from Table 2 indicate that behavioral representation and hydrodynamic context jointly determine predicted connectivity outcomes. Behavior-explicit models implemented in retentive systems such as fjords, sea lochs and lagoons consistently predict higher levels of self-recruitment and local retention, whereas behavior-free or simplified approaches applied in advective shelf environments tend to emphasize export and episodic exchange. The extent to which settlement processes and habitat filtering are incorporated further distinguishes models that simulate potential dispersal from those approximating realized recruitment.

Behavioral particle-tracking experiments provide clear examples of these effects. In the Firth of Lorn, Scotland, behaviorally informed simulations showed that vertical migration substantially reduced net dispersal and enhanced self-recruitment compared with passive tracers, particularly in tidally energetic environments (Rodriguez-Perez et al., 2020). More recent implementations incorporate the ability of larvae to delay settlement until suitable substrate is encountered, extending dispersal duration and reshaping spatial settlement patterns, with direct implications for restoration site selection (Rodriguez-Perez et al., 2021).

8.3. Increasing complexity: stochasticity, physiology and habitat filtering

Beyond deterministic behavioral rules, several modelling frameworks have begun to incorporate stochasticity and inter-individual variability in larval responses to environmental conditions, producing more realistic and heterogeneous dispersal outcomes (Paris et al., 2013; Wood et al., 2021). However, parameterizing larval behavior remains a major source of uncertainty. Behavioral traits are difficult to measure *in situ* and are often inferred from laboratory experiments or derived from related species, limiting transferability across regions and environmental contexts (Geertsma et al., 2023).

Recent advances have extended biophysical models beyond dispersal alone by explicitly incorporating post-settlement processes and habitat suitability. For example Stechele et al., 2023, coupled a larval transport model with a Dynamic Energy Budget–based Individual-Based Model (DEB-IBM) and spatial habitat mapping to evaluate restoration potential for *O. edulis* in the North Sea. This approach integrates larval dispersal with post-settlement growth, survival and physiological performance,

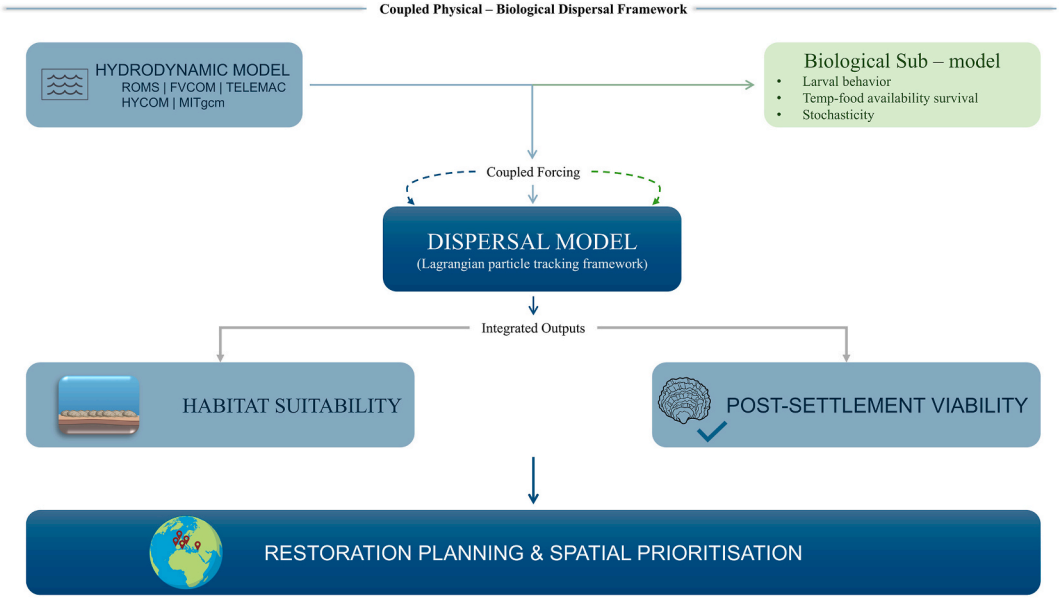

Fig. 2. Conceptual framework of a coupled biophysical modelling approach for *Ostrea edulis* larval connectivity. Hydrodynamic circulation models provide flow fields that drive a Lagrangian particle-tracking dispersal model, coupled with biological sub-models representing larval behavior, temperature- and salinity-dependent survival, and stochasticity. Model outputs are filtered by habitat suitability and extended to post-settlement viability, thereby supporting restoration planning, site prioritization, and adaptive spatial management.

Table 2
Comparative overview of modelling studies on larval dispersal and connectivity of *Ostrea edulis*. The comparison follows the five analytical categories defined in Section 2.1 and synthesizes how modelling framework structure, representation of larval biology, validation approach, and environmental context influence inferred connectivity patterns and their relevance for restoration planning. Only studies that explicitly frame larval dispersal in terms of connectivity outcomes or management-oriented implications are included. Studies primarily focused on physical transport or large-scale dispersal patterns without an explicit connectivity synthesis (e.g. purely transport-driven or regional dispersal studies) are therefore not considered in this comparative table.

Study/Region	System type	Modelling framework	Representation of larval behavior	PLD/ competency	Settlement/ habitat filtering	Validation approach	Main connectivity outcome	Implications for restoration
Holbrook (2021) – **Solent (UK)**	Semi-enclosed embayment	Lagrangian particle tracking driven by external hydrodynamic model outputs	Diel vertical migration and vertical positioning	Literature-based PLD with delayed competency	Not included	Qualitative, pattern-based comparison	Predominant local retention with episodic export	Potential for site-scale, self-sustaining restoration
Rodriguez-Perez et al. (2019, 2020) – **Scottish sea lochs**	Fjord-like basins	Nested ROMS with behavior-informed particle tracking	Stage-dependent swimming and competency delay	Variable; explicit competency window	Not included	Comparison with empirical biological constraints	Strong local retention	Retentive systems identified as priority candidates
Stechele et al. (2023) – **North Sea**	Open shelf	Particle tracking coupled to DEB-based IBM and habitat suitability layers	Not explicitly included	Fixed pelagic larval duration	Explicit habitat filtering	Hindcast comparison with historical oyster bed distribution	Potential stepping-stone connectivity	Support for network-based restoration planning
Bertolini and Pastres (2023) – **Adriatic lagoon**	Shallow lagoon–coastal system	TELEMAC-3D coupled with particle tracking	Near-bed positioning at competency	Seasonally variable, literature-based PLD	Not included	Not reported	Predominant intra-lagoon retention	Potential for localized restoration actions
Clavel-Henry et al. (2023) – **Galway Bay**	Semi-open bay	ROMS-based PTM with simplified biological behavior	Simplified behavioral representation	Species-specific, literature-based PLD	Not included	Partial validation against hydrodynamic and dispersal patterns	Potential source–sink patterns	Implications for adaptive restoration planning

representing an important step toward linking connectivity predictions with population viability and restoration success.

Climate variability operates across multiple temporal scales within biophysical modelling frameworks. Short-term meteorological variability (e.g. wind forcing, river discharge and seasonal stratification) can substantially modify dispersal pathways and retention patterns between spawning events, while longer-term climate projections alter baseline circulation regimes and thermal conditions (Stechele et al., 2023; Alves Monteiro et al., 2025). In addition, connectivity estimates are highly sensitive to initial condition inputs, including the timing of larval release relative to tidal phase and seasonal circulation state. Scenario-based simulations that explore combinations of meteorological variability, climate forcing and release timing therefore provide a more robust assessment of connectivity uncertainty and are particularly relevant for designing adaptive and climate-resilient restoration networks.

8.4. Model validation and remaining uncertainties

Despite considerable advances in biophysical and behavioral modelling, validation remains the most critical and unevenly addressed component of the modelling chain. Many *O. edulis* studies report qualitative agreement with observed circulation patterns or settlement trends but rarely provide quantitative accuracy metrics or formal uncertainty estimates (Cowen et al., 2006; North et al., 2008). Moreover, interactions between interannual variability in wind forcing, river discharge and spawning phenology and model performance are seldom evaluated explicitly (Werner et al., 2007).

Empirical validation is constrained by the difficulty of obtaining larval dispersal data across appropriate spatial and temporal scales. Among available approaches, genetic parentage analysis and population genetic structure assessments provide one of the few direct means of evaluating realized connectivity and gene flow, thereby offering a critical benchmark for model-based predictions (Coolen et al., 2020; Mackenzie et al., 2022). However, such studies are logistically demanding and often spatially limited, while plankton sampling and settlement monitoring typically capture only short-term or local processes. As a result, caution is required when interpreting connectivity predictions, particularly when models are used to inform restoration planning.

Overall, biophysical and behavioral modelling represents a transformative advance in understanding *O. edulis* larval connectivity. By explicitly linking physical circulation with larval behavior, development and settlement processes, these models provide a mechanistic basis for evaluating connectivity, identifying retentive systems and informing spatially coherent restoration strategies. At the same time, improving behavioral parameterization, validation practices and uncertainty quantification remains essential to strengthen the robustness and applicability of model-based connectivity assessments.

9. Case studies across Europe: key findings and patterns

Empirical and modelling-based case studies across Europe provide valuable insights into the spatial dynamics of *Ostrea edulis* larval dispersal and connectivity. Collectively, these studies highlight the ecological heterogeneity of oyster habitats and demonstrate how region-specific hydrodynamic and biological conditions critically influence restoration outcomes. Fig. 3 provides a graphical overview of the study areas.

A first group of studies relies primarily on hydrodynamic models to explore physical transport pathways. For example, hydrodynamic modelling in the Venice Lagoon has been used to evaluate the reintroduction potential of *O. edulis* and overall habitat suitability, highlighting strong local retention within lagoonal circulation patterns (Bertolini and Pastres, 2023).

A second group of studies incorporates larval behavior into biophysical particle-tracking frameworks. In the Solent (UK), particle-tracking simulations driven by external hydrodynamic outputs indicate high self-recruitment potential with episodic export toward the

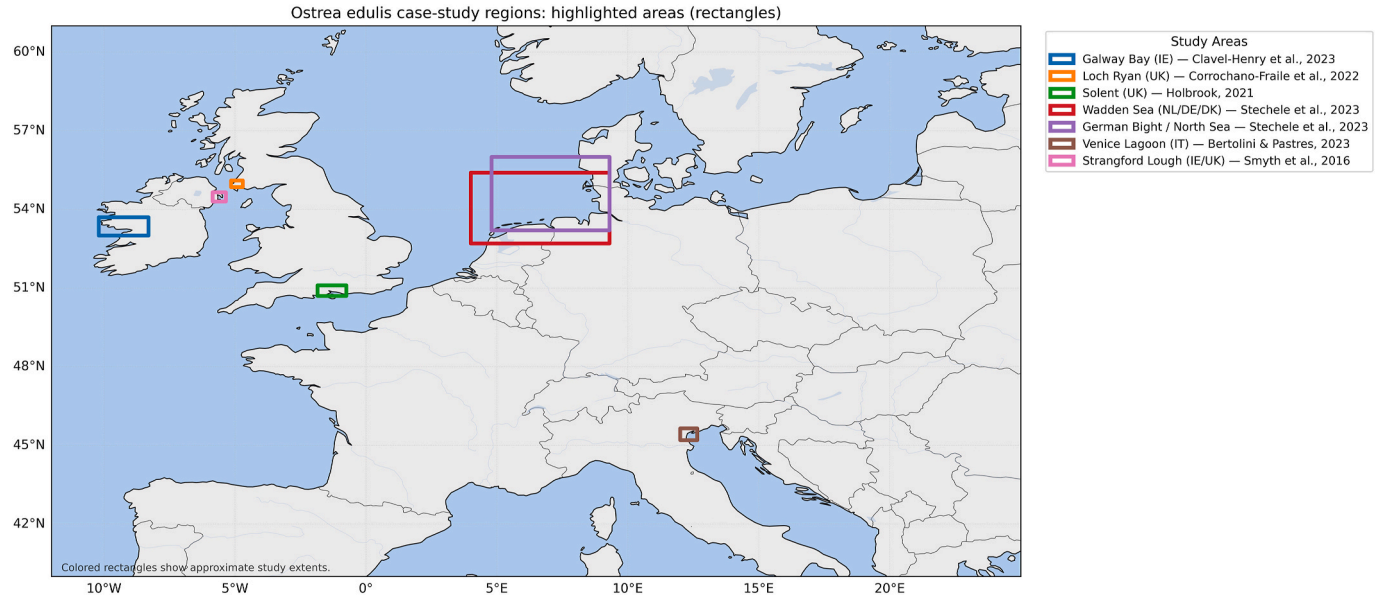

Fig. 3. Geographic distribution of European case-study regions included in the review of *Ostrea edulis* larval dispersal and connectivity modelling. Colored rectangles indicate the approximate spatial extent of the modelling domains for each study.

English Channel, supporting temporally targeted restoration strategies (Holbrook, 2021). Similarly, in Scottish sea lochs, behavior-informed models show that vertical migration and local circulation promote strong retention and limited dispersal beyond individual basins (Rodriguez-Perez et al., 2019). At broader regional scales along the Scottish west coast, FVCOM-based particle tracking highlights the sensitivity of dispersal to wind forcing and large-scale circulation variability (Corrochano-Fraile et al., 2022).

More recent approaches combine hydrodynamics, larval dispersal, and additional ecological components. In the Wadden Sea and German Bight (Stechele et al., 2023), employed coupled population–distribution modelling and habitat suitability analyses to assess larval connectivity among offshore restoration reefs. Their results indicate moderate connectivity, particularly when restoration sites function as stepping-stones, i.e., intermediate habitats that facilitate larval exchange between otherwise weakly connected areas.

Comparative modelling in semi-open systems further illustrates the context dependency of connectivity. In Galway Bay (Ireland), a ROMS-coupled biophysical model applied to the Pacific oyster (*Magallana gigas*) suggests that the system can alternate between acting as a larval source or sink depending on hydrodynamic conditions, emphasizing the strong role of temporal variability (Clavel-Henry et al., 2023).

Across European systems, several consistent patterns emerge. Strong local retention characterizes semi-enclosed environments such as the Solent, Adriatic lagoons, and Scottish sea lochs (Corrochano-Fraile et al., 2022; Holbrook, 2021; Rodriguez-Perez, 2019; Smyth et al., 2016). Export is generally constrained by local hydrodynamic features such as eddies, stratification, and wind-driven circulation, although moderate connectivity can occur in more open systems when suitable habitat patches facilitate multi-step dispersal (Stechele et al., 2023). Larval behavior, particularly diel vertical migration and delayed settlement, consistently modifies dispersal trajectories relative to passive transport (Broekhuizen et al., 2011; North et al., 2008; Rodriguez-Perez, 2019). Connectivity patterns also exhibit strong interannual variability driven by changes in stratification, freshwater inflow, and atmospheric forcing (Clavel-Henry et al., 2023). Finally, habitat suitability acts as a critical filter: successful recruitment depends not only on dispersal but also on substrate quality and local physicochemical conditions (Colsoul et al., 2021; Puckett et al., 2018; Theuerkauf et al., 2021).

Despite growing evidence, substantial geographic gaps remain. The Baltic Sea, large portions of the Mediterranean, and the Iberian-North African margin are still poorly represented in connectivity studies. These regions are characterized by contrasting oceanographic regimes. Low salinity in the Baltic, persistent stratification in the Mediterranean, and strong upwelling along Atlantic margins can directly influence larval survival, development, and vertical behavior. Expanding empirical observations and modelling efforts into these regions will be essential to determine whether patterns observed elsewhere can be generalized.

Collectively, these case studies illustrate how hydrodynamic setting, biological parameterization and habitat configuration interact to shape connectivity patterns across European systems. The comparative perspective underscores the importance of context-specific modelling when interpreting dispersal outcomes and translating them into restoration strategies.

10. Modelling limitations and uncertainties

Despite notable advancements in modelling the dispersal and connectivity of *Ostrea edulis* larvae, significant limitations and sources of uncertainty persist. These constraints affect the ecological realism, accuracy, and interpretability of model predictions-issues that must be acknowledged by both researchers and restoration practitioners (Cowen and Sponaugle, 2009; North et al., 2008).

A primary limitation lies in the incomplete understanding of larval behavior. Although recent studies have improved knowledge of swimming activity, vertical migration, and settlement cues, many biophysical models still rely on parameter values derived from other bivalves or assume uniform behavior across individuals (Bertolini and Pastres, 2023; Rodriguez-Perez, 2019). Key behavioral traits such as behavioral changes during development, movement in response to environmental conditions, and inter-individual variability are rarely incorporated, leading to oversimplified assumptions that can distort dispersal pathways (Corrochano-Fraile et al., 2022; Metaxas and Saunders, 2009; Willis et al., 2019).

Validation of model outputs remains challenging due to the scarcity of empirical data suitable for direct comparison with model predictions. Direct larval sampling is difficult because of the brief planktonic stage and small larval size, while genetic parentage analysis is resource-intensive and often spatially limited (Stechele et al., 2023). As a

result, many models depend on unvalidated behavioral assumptions and broad environmental parameterizations (Clavel-Henry et al., 2023).

Emerging validation tools are improving this landscape. Environmental DNA (eDNA) sampling offers high-resolution, non-invasive detection of larval presence without direct collection (Deiner et al., 2017). Traditional larval traps and plankton tows provide direct counts and developmental-stage data, while settlement tiles or artificial collectors measure successful recruitment in restoration zones-albeit with potential bias from habitat preferences. Genetic parentage and population assignment studies using molecular markers such as RAD-seq (Restriction-site Associated DNA sequencing, a genome-wide genotyping approach) or microsatellites (short, highly variable DNA repeat regions) remain invaluable for quantifying realized connectivity (the effective exchange of individuals or genes among populations); but are logistically demanding. Integrating these methods within complementary validation frameworks is increasingly considered best practice (Werner et al., 2007) (Table 3).

Hydrodynamic resolution represents another major constraint. Coarse spatial grids may fail to resolve retention-driving features such as estuarine fronts, eddies or tidal creeks, while low temporal resolution can miss tidal and diel signals critical for larval positioning (Shchepetkin and McWilliams, 2005). Uncertainty in boundary conditions and forcing (e.g. wind, freshwater inflow, sea level) further propagates into dispersal predictions (Corrochano-Fraile et al., 2022; Holbrook, 2021).

Biological simplifications add additional uncertainty. Many models assume fixed or neutral buoyancy despite evidence of environmentally mediated behavioral plasticity (Colsoul et al., 2021; Rodriguez-Perez, 2019). Moreover, arrival-based metrics often neglect post-settlement mortality, predation and habitat quality, potentially overestimating functional recruitment. Integration with habitat-suitability and demographic frameworks is therefore essential (Stechele et al., 2023; Wood et al., 2021).

Integration with habitat-suitability and demographic frameworks is thus essential (Wood et al., 2021). Recent modelling advances increasingly incorporate post-settlement dynamics through Dynamic Energy Budget (DEB) models, which describe how organisms acquire and allocate energy to maintenance, growth and reproduction, and Individual-Based Models (IBMs), which simulate the fate of individual organisms and their interactions with the environment. For example Stechele et al., 2023, coupled a Lagrangian larval dispersal model with a DEB-based IBM to represent not only larval transport but also the physiological performance of settled *Ostrea edulis* under North Sea conditions. When combined with Habitat Suitability Indices (HSIs), these approaches allow models to move beyond potential dispersal toward estimates of functional recruitment, thereby linking connectivity with post-settlement survival and performance, an essential step for ecologically realistic restoration planning.

Scenario-based simulations under future climate projections provide valuable insight into how connectivity patterns may change, but they also introduce additional uncertainty when extrapolating beyond validated conditions. Such uncertainty arises both from the physical domain, including altered circulation, stratification and forcing fields, and from the biological domain, particularly limited knowledge of how larval behavior, physiological tolerance and adaptive capacity of *O. edulis* may respond to changing environmental regimes (Corrochano-Fraile et al., 2022).

Finally, transparency and reproducibility remain uneven across studies. Standardized reporting of model parameters, biological assumptions, codes, and validation metrics would enhance comparability and enable meta-analyses of connectivity (Bertolini and Pastres, 2023; Paris et al., 2013).

In summary, larval dispersal modelling for *O. edulis* has advanced substantially but remains limited by behavioral uncertainty, sparse empirical validation, model resolution constraints, and inconsistent reporting.

Table 3
Overview of empirical methods used to validate larval dispersal and connectivity models, summarizing their main advantages, limitations, and typical applications in marine connectivity studies.

Validation Method	Advantages	Limitations	Best Use Case
eDNA sampling	Non-invasive; high resolution; species-specific	May not distinguish larval stages; degradation affects accuracy	Broad spatial mapping of larval presence
Larval traps/ plankton tows	Direct larval counts; stage identification	Labor-intensive; spatially constrained	Quantifying larval abundance in specific locations
Settlement tiles	Measures actual recruitment	May miss mobile or selective settlers; influenced by habitat context	Verifying settlement success in restoration sites
Genetic parentage/ assignment	High-resolution connectivity inference	Expensive; requires high-quality reference samples	Testing realized connectivity over known spatial scales

11. Applications to restoration ecology

The modelling of larval dispersal and connectivity in *Ostrea edulis* has evolved from theoretical frameworks into operational tools that inform restoration planning and spatial management across Europe. As restoration initiatives scale up, insights from coupled hydrodynamic–biological models increasingly support site prioritization, network design and adaptive management (Stechele et al., 2023).

Connectivity simulations help identify broodstock reserves and sites that maximize larval retention while maintaining strategic export. In the Solent (UK), particle-tracking analyses indicate strong self-recruitment with episodic export toward the English Channel, supporting temporally targeted restoration strategies (Holbrook, 2021).

Beyond single-site optimization, connectivity matrices can be used to delineate management subareas and evaluate functional linkages among spawning, nursery and harvesting grounds. This approach has been successfully applied in the Adriatic Sea for *Nephrops norvegicus*, where multiannual biophysical modelling integrated hydrodynamics, larval behavior and habitat suitability to define spatially coherent management units and essential fish habitats (Melaku Canu et al., 2020). The study demonstrated how ensemble simulations capturing interannual variability can reveal subpopulation structure and inform area-based fisheries management. Similar ecosystem-based spatial planning frameworks have been proposed for the northern Adriatic to integrate hydrodynamic connectivity with habitat and conservation priorities (Bandelj et al., 2020).

For oyster restoration, such approaches are directly transferable. Connectivity modelling enables the identification of larval corridors, retention hotspots and stepping-stone sites, supporting network-based restoration strategies rather than isolated reef construction (Treml et al., 2008). Scenario simulations incorporating interannual shifts in circulation, temperature and spawning timing further allow practitioners to test resilience under climate variability (Andrello et al., 2015; Smyth et al., 2016).

Importantly, model outputs allow population-level assessment of whether restored reefs are demographically linked to broader metapopulations rather than functioning as isolated patches (Lowe and Allendorf, 2010; Rodriguez-Perez et al., 2021). By identifying larval sources and sinks, biophysical models provide a quantitative basis for aligning oyster restoration with marine protected area (MPA) design and regional ecosystem management objectives.

Connectivity-informed planning also improves resource allocation by targeting areas with strong natural larval supply and reduced reseeding requirements (Bertolini and Pastres, 2023; Colsoul et al., 2021).

Together, these developments indicate that larval connectivity modelling now provides a robust decision-support framework for scaling oyster restoration in ecologically coherent and cost-effective ways.

12. Future directions

As *Ostrea edulis* restoration efforts expand across Europe, enhancing the accuracy and applicability of larval dispersal and connectivity models is essential for evidence-based and adaptive management. Future developments should focus on increasing biological realism, improving empirical validation, integrating biophysical models into ecosystem and socio-economic frameworks, and adopting open-science practices that facilitate reproducibility and collaboration.

Most existing models still simplify larval behavior due to limited empirical data. Yet *O. edulis* larvae display complex dynamics, including vertical migration, environmentally cued swimming, and variable competency windows (Rodriguez-Perez, 2019). Controlled laboratory experiments, flume-tank assays, and *in situ* observations are required to parameterize these behaviors accurately. Enhanced behavioral parameterization will reduce reliance on surrogate species and strengthen model transferability across environmental contexts.

Quantitative validation remains a critical bottleneck in larval dispersal modelling. Combining genetic parentage analysis, otolith microchemistry, and intensive larval sampling can generate independent datasets for model testing. Longitudinal studies encompassing multiple spawning seasons are necessary to capture interannual variability in larval transport and settlement. Genetic validation studies in coral reef fishes have demonstrated the feasibility of this approach (Bode et al., 2019), underscoring its potential for *O. edulis*. Emerging methods such as environmental DNA (eDNA) sampling offer non-invasive, high-resolution detection of larval presence and can be integrated into citizen-science programs, for example by enabling trained volunteers to collect water samples across multiple locations and time periods, thereby extending spatio-temporal monitoring coverage (Deiner et al., 2017).

Coupling hydrodynamic particle-tracking and associated biological models with post-settlement demographic and ecosystem models represents a major step toward ecological realism. Such integrated frameworks can incorporate post-settlement processes including growth, mortality, and competition, thus forecasting not only settlement locations but also local population viability and metapopulation persistence (Stechele et al., 2023). These models are critical for designing spatially coherent restoration networks and for aligning oyster reef restoration with marine protected area (MPA) connectivity goals.

Projected changes in sea level, stratification, and circulation will alter larval transport pathways, while warming and acidification may affect larval behavior and survival. Ensemble-based, scenario simulations can be used to identify potential climate refugia and dispersal corridors under future oceanographic conditions (Espinel-Velasco et al., 2018). Such foresight is vital for climate-resilient restoration and adaptive policy design.

Advances in cloud computing, automated workflows, and open-source Lagrangian tools (e.g., Parcels, Ichthyop) now enable near-real-time forecasting of larval transport (Delandmeter and Van Sebille, 2019; Lett et al., 2008). Integrating these pipelines with GIS-based planning layers can support dynamic decision-making by visualizing predicted recruitment hotspots and connectivity corridors.

Oyster restoration operates within coupled human–natural systems that involve fisheries, tourism, regulation, and conservation priorities. Consequently, future modelling efforts should incorporate stakeholder participation, socio-economic valuation, and governance scenarios to ensure feasible and equitable outcomes.

Harmonizing model protocols-behavioral modules, input parameters, and validation methods, will enable cross-system comparability. The Native Oyster Restoration Alliance (NORA) plays a central role in coordinating transnational initiatives and establishing shared guidelines for monitoring and modelling (Pogoda et al., 2019). The adoption of the FAIR data principles and the use of open-source modelling platforms can substantially improve transparency, reproducibility, and cross-system comparability of connectivity studies (Wilkinson et al., 2016; Delandmeter and Van Sebille, 2019; Lett et al., 2008). At the same time, strengthening interdisciplinary collaboration across oceanography, ecology, genetics, socio-economics, and management, and expanding access to training and user-friendly modelling tools, will be essential to ensure broad participation and to translate modelling outputs into effective, evidence-based restoration strategies.

13. Conclusion

This review provides a critical synthesis of how hydrodynamic and biophysical modelling has been applied to investigate larval dispersal and connectivity of *Ostrea edulis* across European coastal systems. The comparative analysis reveals substantial heterogeneity in model structure, biological parameterization and validation practice, limiting direct comparability among regions and constraining management-oriented interpretation. Quantitative performance metrics and formal uncertainty assessment remain scarce, highlighting a persistent methodological gap (Cowen and Sponaugle, 2009; Werner et al., 2007).

Despite these limitations, several robust patterns emerge. Behavioral representation consistently alters predicted dispersal trajectories relative to passive transport, generally increasing local retention and spatial structuring of connectivity. However, model outcomes are not governed by behavior alone. Hydrodynamic setting, spawning timing, and interannual variability in forcing conditions strongly influence predicted connectivity, underscoring the sensitivity of model results to environmental context and initial conditions.

Semi-enclosed systems such as lagoons and fjord-like basins tend to promote retention and self-recruitment, whereas open and advective environments exhibit more episodic and spatially variable connectivity. These differences indicate that restoration strategies cannot rely on generalized assumptions but must be grounded in system-specific modelling and explicit evaluation of connectivity networks.

Key limitations remain. Behavioral parameters are often poorly constrained, empirical validation, particularly through genetic inference of realized connectivity, is limited, and post-settlement processes are frequently excluded. As a result, many existing models estimate potential dispersal rather than functional recruitment. Integrating demographic processes, habitat filtering and multi-scenario forcing into connectivity frameworks represents a necessary step toward more ecologically realistic and decision-relevant modelling.

Ultimately, larval connectivity modelling has matured into a practical decision-support tool for oyster restoration. Its future development will depend less on increasing structural complexity and more on improving transparency, uncertainty quantification and empirical grounding. By aligning modelling outputs with ecological processes and management objectives, connectivity-based approaches can support coherent, adaptive and spatially informed strategies for the long-term recovery of *Ostrea edulis* ecosystems across Europe.

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CRediT authorship contribution statement

Davide Carratù: Conceptualization, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Célia Laurent:** Conceptualization, Writing – review & editing. **Cosimo Solidoro:** Conceptualization, Writing – review & editing. **Donata Melaku**

Canu: Conceptualization, Funding acquisition, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

References

Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanogr. Mar. Biol. 45, 345–405. https://doi.org/10.1201/9781420050943.ch7.

Alves Monteiro, H.J., Bekkevold, D., Pacheco, G., Mortensen, S., Lou, R.N., Therkildsen, N.O., et al., 2025. Genome-Wide population structure in a marine keystone species, the European flat oyster (*Ostrea edulis*). Mol. Ecol. 34 (23), e17573. https://doi.org/10.1111/mec.17573.

Andrello, M., Mouillot, D., Somot, S., Thuiller, W., Manel, S., 2015. Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. Divers. Distrib. 21 (2), 139–150. https://doi.org/10.1111/ddi.12250.

Bandelj, V., Solidoro, C., Laurent, C., Querin, S., Kaleb, S., Gianni, F., Falace, A., 2020. Cross-scale connectivity of macrobenthic communities in a patchy network of habitats: the mesophotic biogenic habitats of the northern Adriatic Sea. Estuar. Coast Shelf Sci. 245, 106978. https://doi.org/10.1016/j.ecss.2020.106978.

Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G., Guo, X., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61 (2), 107–116. https://doi.org/10.1525/bio.2011.61.2.5.

Bertolini, C., Pastres, R., 2023. Understanding the influence of swarming timing on the dispersal of *Ostrea edulis* larvae in the Northern Adriatic Sea. Open Research Europe 3 (212), 212. https://doi.org/10.12688/openreseurope.16776.1.

Bode, M., Leis, J.M., Mason, L.B., Williamson, D.H., Harrison, H.B., Choukroun, S., Jones, G.P., 2019. Successful validation of a larval dispersal model using genetic parentage data. PLoS Biol. 17 (7). https://doi.org/10.1371/journal.pbio.3000380.

Broekhuizen, N., Lundquist, C.J., Hadfield, M.G., Brown, S.N., 2011. Dispersal of Oyster (Ostrea Chilensis) larvae in tasman bay inferred using a verified particle tracking model that incorporates larval behavior. J. Shellfish Res. 30 (3), 643–658. https://doi.org/10.2983/035.030.0307.

Bromley, C., McGonigle, C., Ashton, E.C., Roberts, D., 2016. Bad moves: pros and cons of moving oysters - a case study of global translocations of *Ostrea edulis* Linnaeus, 1758 (Mollusca: bivalvia). In: Ocean and Coastal Management, 122. Elsevier Ltd, pp. 103–115. https://doi.org/10.1016/j.ocecoaman.2015.12.012.

Clavel-Henry, M., Dabrowski, T., Giesler, R.J., Crowe, T.P., Yearsley, J.M., 2023. Predicting the export of retention-oriented larvae from their natal population using coastal features: a modelling study on the Pacific oyster. Mar. Ecol. Prog. Ser. 724, 81–95. https://doi.org/10.3354/meps14456.

Coen, L.D., Brumbaugh, R.D., Bushek, D., Grizzle, R., Luckenbach, M.W., Posey, M.H., et al., 2007. Ecosystem services related to oyster restoration. Mar. Ecol. Prog. Ser. 341, 303–307. https://doi.org/10.3354/meps.

Coen, L.D., Luckenbach, M.W., 2000. Developing success criteria and goals for evaluating oyster reef restoration: ecological function or resource exploitation? Ecol. Eng. 15 (3–4), 323–343. https://doi.org/10.1016/S0925-8574(00)00084-7.

Cole, H.A., Jones, E.K., 1939. Some observations and experiments on the setting behaviour of larvae of *Ostrea edulis*. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 14 (1), 86–105. https://doi.org/10.1093/icesjms/14.1.86.

Colsoul, B., Boudry, P., Pérez-Parallé, M.L., Bratoš Cetinić, A., Hugh-Jones, T., Arzul, I., Mérou, N., Wegner, K.M., Peter, C., Merk, V., Pogoda, B., 2021. Sustainable large-scale production of European flat oyster (*Ostrea edulis*) seed for ecological restoration and aquaculture: a review. Rev. Aquacult. 13 (3), 1423–1468. https://doi.org/10.1111/raq.12529. John Wiley and Sons Inc.

Colsoul, B., Pouvreau, S., Di Poi, C., Pouil, S., Merk, V., Peter, C., Boersma, M., Pogoda, B., 2020. Addressing critical limitations of oyster (*Ostrea edulis*) restoration: identification of nature-based substrates for hatchery production and recruitment in the field. Aquat. Conserv. Mar. Freshw. Ecosyst. 30 (11), 2101–2115. https://doi.org/10.1002/aqc.3454.

Coolen, J.W.P., Boon, A.R., Crooijmans, R., van Pelt, H., Kleissen, F., Gerla, D., Beermann, J., Birchenough, S.N.R., Becking, L.E., Luttikhuizen, P.C., 2020. Marine stepping-stones: connectivity of Mytilus edulis populations between offshore energy installations. Mol. Ecol. 29 (4), 686–703. https://doi.org/10.1111/mec.1364.

Corrochano-Fraile, A., Adams, T.P., Aleynik, D., Bekaert, M., Carboni, S., 2022. Predictive biophysical models of bivalve larvae dispersal in Scotland. Front. Mar. Sci. 9. https://doi.org/10.3389/fmars.2022.985748.

Cowen, R.K., Gawarkiewicz, G., Pineda, J., Thorrold, S.R., Werner, F.E., 2007. Population connectivity in marine systems An overview. Oceanography (Wash. D. C.) 20 (3), 14–21. https://doi.org/10.2307/24860093.

Cowen, R.K., Paris, B., Srinivasan, A., 2006. Scaling of connectivity in marine populations. Science 311 (5760), 518–522. https://doi.org/10.1126/science.1120847.

Cowen, R.K., Sponaugle, S., 2009. Larval dispersal and marine population connectivity. Ann. Rev. Mar. Sci 1, 443–466. https://doi.org/10.1146/annurev.marine.010908.163757.

Cragg, S., Gruffydd, L., 1975. The swimming behaviour and the pressure responses of the veliconcha larvae of *Ostrea edulis* (L.). In: Proceedings of the 9th European Marine Biology Symposium. Aberdeen University Press, pp. 43–57. http://scholar.google.com/scholar_lookup?author=S.+Cragg&author=L.+Gruffydd+&publication_year=1975&title=The+swimming+behaviour+and+the+pressure+responses+of+the+veliconcha+larvae+of+Ostrea+edulis.

Daigle, R.M., Metaxas, A., 2011. Vertical distribution of marine invertebrate larvae in response to thermal stratification in the laboratory. J. Exp. Mar. Biol. Ecol. 409 (1–2), 89–98. https://doi.org/10.1016/j.jembe.2011.08.008.

Dame, R.F., 2016. Ecology of Marine Bivalves: an Ecosystem Approach. CRC press. https://doi.org/10.1201/b11220.

Davis, H.C., Calabrese, A., 1969. Survival and growth of larvae of the European oyster (*Ostrea edulis* L.) at different temperatures. Biol. Bull. 136 (2), 193–199. http://www.jstor.org/stable/1539813.

Deiner, K., Bik, H.M., Mächler, E., et al., 2017. Environmental DNA metabarcoding: transforming how we survey animal and plant communities. Mol. Ecol. 26, 5872–5895. https://doi.org/10.1111/mec.14350.

Dekshenieks, M.M., Hofmann, E.E., Klinck, J.M., Powell, E.N., 2000. Quantifying the effects of environmental change on an oyster population: a modeling study. Estuaries 23 (5), 593–610. https://doi.org/10.2307/1352887.

Delandmeter, P., Van Sebille, E., 2019. The Parcels v2.0 Lagrangian framework: new field interpolation schemes. Geosci. Model Dev. 12 (8), 3571–3584. https://doi.org/10.5194/gmd-12-3571-2019.

Espinel-Velasco, N., Hoffmann, L., Agüera, A., Byrne, M., Dupont, S., Uthicke, S., Webster, N.S., Lamare, M., 2018. Effects of ocean acidification on the settlement and metamorphosis of marine invertebrate and fish larvae: a review. Mar. Ecol. Prog. Ser. 606, 237–257. https://doi.org/10.3354/meps12754. Inter-Research.

Ezgeta-Balić, D., Vrgoč, N., Isajlović, I., Medvešek, D., Vujević, A., Despalatović, M., Cvitković, I., 2021. Comparison of beam trawl catch, by-catch and discard in fishing and non fishing areas – a case study from the northern Adriatic Sea. Mediterr. Mar. Sci. 22 (1), 108–120. https://doi.org/10.12681/mms.24973.

Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F., Huse, G., 2007. Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. Mar. Ecol. Prog. Ser. 347, 195–205. https://doi.org/10.3354/meps06978.

Geertsma, R.C., Kamermans, P., Murk, A.J., Wijgerde, T., 2023. Real-time high resolution tracking of coral and oyster larvae. J. Exp. Mar. Biol. Ecol. 565. https://doi.org/10.1016/j.jembe.2023.151910.

Grabowski, J.H., Brumbaugh, R.D., Conrad, R.F., Keeler, A.G., Opaluch, J.J., Peterson, C. H., Piehler, M.F., Powers, S.P., Smyth, A.R., 2012. Economic valuation of ecosystem services provided by oyster reefs. Bioscience 62 (10), 900–909. https://doi.org/10.1525/bio.2012.62.10.10.

Grabowski, J.H., Hughes, A.R., Kimbro, D.L., Dolan, M.A., 2005. How habitat setting influences restored oyster reef communities. Ecology 86 (7), 1926–1935. https://doi.org/10.1890/04-0690.

Grabowski, J.H., Peterson, C.H., 2007. Restoring oyster reefs to recover ecosystem services. Theoretical ecology series 4 (7), 281–298. https://doi.org/10.1016/S1875-306X(07)80017-7.

Hastings, A., Botsford, L.W., Levin, S.A., 2006. Persistence of spatial populations depends on returning home. Proc. Natl. Acad. Sci. USA 103. www.pnas.orgcgidoi10.1073pnas.0506651103.

Holbrook, Z., 2021. Restocking the European Flat Oyster *Ostrea edulis* in the Solent–a Model for Ecosystem Service Restoration Across Europe. Doctoral thesis. University of Southampton. http://eprints.soton.ac.uk/id/eprint/450587.

Jonsson, P.R., André, C., Lindegarth, M., 1991. Swimming behaviour of marine bivalve larvae in a flume boundary-layer flow: evidence for near-bottom confinement. Mar. Ecol. Prog. Ser. 79, 67–76. https://doi.org/10.3354/meps079067.

Kent, F.E.A., Mair, J.M., Newton, J., Lindenbaum, C., Porter, J.S., Sanderson, W.G., 2017. Commercially important species associated with horse mussel (Modiolus modiolus) biogenic reefs: a priority habitat for nature conservation and fisheries benefits. Mar. Pollut. Bull. 118 (1–2), 71–78. https://doi.org/10.1016/j.marpolbul.2017.02.051.

Korringa, P., 1940. Experiments and observations on swarming, pelagic life and setting in the European flat oyster. Ostrea edulis L (Doctoral thesis, Joh. Enschede). http://scholar.google.com/scholar_lookup?author=P.+Korringa+&publication_year=1940&title=Experiments+and+observations+on+swarming+pelagic+life+and+setting+in+the+European+flat+oyster+Ostrea+edulis+L.

Laing, I., Walker, P., Areal, F., 2006. Return of the native - is European oyster (*Ostrea edulis*) stock restoration in the UK feasible? Aquat. Living Resour. 19 (3), 283–287. https://doi.org/10.1051/alr:2006029.

Laurent, C., Querin, S., Solidoro, C., Canu, D.M., 2020. Modelling marine particle dynamics with LTRANS-Zlev: implementation and validation. Environ. Modell. Software 125. https://doi.org/10.1016/j.envsoft.2020.104621.

Lenihan, H.S., Peterson, C.H., Byers, J.E., Grabowski, J.H., Thayer, G.W., Colby, D.R., 2001. Cascading of habitat degradation: oyster reefs invaded by refugee fishes escaping stress. Ecol. Appl. 11 (3), 764–782. https://doi.org/10.1890/1051-0761(2001)011[0764:COHDOR]2.0.CO;2.

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

Lipcius, R.N., Eggleston, D.B., Schreiber, S.J., Seitz, R.D., Shen, J., Sisson, M., Stockhausen, W.T., Wang, H.V., 2008. Importance of metapopulation connectivity to

restocking and restoration of marine species. Rev. Fish. Sci. 16 (1–3), 101–110. https://doi.org/10.1080/10641260701812574.
Lotze, H.K., 2007. Rise and fall of fishing and marine resource use in the Wadden Sea, southern North Sea. Fish. Res. 87 (2–3), 208–218. https://doi.org/10.1016/j.fishres.2006.12.009.
Lowe, W.H., Allendorf, F.W., 2010. What can genetics tell us about population connectivity? Mol. Ecol. 19 (15), 3038–3051. https://doi.org/10.1111/j.1365-294X.2010.04688.x.
Mackenzie, C.L., Kent, F.E.A., Baxter, J.M., Gormley, K.S.G., Cassidy, A.J., Sanderson, W. G., Porter, J.S., 2022. Genetic connectivity and diversity of a protected, habitat-forming species: evidence demonstrating the need for wider environmental protection and integration of the marine protected area network. Front. Mar. Sci. 9. https://doi.org/10.3389/fmars.2022.772259.
Melaku Canu, D., Laurent, C., Morello, E.B., Querin, S., Scarcella, G., Vrgoc, N., Froglia, C., Angelini, S., Solidoro, C., 2020. Nephrops norvegicus in the Adriatic Sea: connectivity modeling, essential fish habitats, and management area network. Fish. Oceanogr. 30 (4), 349–365. https://doi.org/10.1111/fog.12522.
Metaxas, A., Saunders, M., 2009. Quantifying the "bio-" components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. Biol. Bull. 216 (3), 257–272. https://doi.org/10.1086/BBLv216n3p257.
Narcisi, V., Arzul, I., Cargini, D., Mosca, F., Calzetta, A., Traversa, D., Robert, M., Joly, J. P., Chollet, B., Renault, T., Tiscar, P.G., 2010. Detection of Bonamia ostreae and B. exitiosa (haplosporidia) in *Ostrea edulis* from the Adriatic Sea (italy). Dis. Aquat. Org. 89 (1), 79–85. https://doi.org/10.3354/dao02167.
Newell, R.I.E., Kennedy, V.S., Shaw, K.S., 2007. Comparative vulnerability to predators, and induced defense responses, of eastern oysters Crassostrea virginica and non-native Crassostrea ariakensis oysters in Chesapeake Bay. Marine Biology 152 (2), 449–460. https://doi.org/10.1007/s00227-007-0706-0.
North, E.W., King, D.M., Xu, J., Hood, R., Newell, R.I.E., Paynter, K., Kellogg, M.L., Liddel, M.K., Boesch, D.F., 2010. Linking optimization and ecological models in a decision support tool for oyster restoration and management. Ecol. Appl. 20 (3), 851–866. https://doi.org/10.1890/08-1733.1.
North, E.W., Schlag, Z., Hood, R.R., Li, M., Zhong, L., Gross, T., Kennedy, V.S., 2008. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Mar. Ecol. Prog. Ser. 359, 99–115. https://doi.org/10.3354/meps07317.
Oraić, D., Beck, R., Pavlinec, Ž., Zupičić, I.G., Maltar, L., Miškić, T., Acinger-rogić, Ž., Zrnčić, S., 2021. Bonamia exitiosa in european flat oyster (*Ostrea edulis*) on the croatian adriatic coast from 2016 to 2020. J. Mar. Sci. Eng. 9 (9). https://doi.org/10.3390/jmse9090929.
Paris, C.B., Helgers, J., van Sebille, E., Srinivasan, A., 2013. Connectivity modeling System: a probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. Environ. Modell. Software 42, 47–54. https://doi.org/10.1016/j.envsoft.2012.12.006.
Peterson, C.H., Grabowski, J.H., Powers, S.P., 2003. Estimated enhancement of fish production resulting from restoring oyster reef habitat: quantitative valuation. Mar. Ecol. Prog. Ser. 264, 249–264. https://doi.org/10.3354/meps.
Piazza, B.P., Banks, P.D., La Peyre, M.K., 2005. The potential for created oyster shell reefs as a sustainable shoreline protection strategy in Louisiana. Restor. Ecol. 13 (3), 499–506. https://doi.org/10.1111/j.1526-100X.2005.00062.x.
Piehler, M.F., Smyth, A.R., 2011. Habitat-specific distinctions in estuarine denitrification affect both ecosystem function and services. Ecosphere 2 (1). https://doi.org/10.1890/ES10-00082.1.
Pogoda, B., 2019. Current status of European oyster decline and restoration in Germany. Humanities 8 (1). https://doi.org/10.3390/h8010009.
Pogoda, B., Brown, J., Hancock, B., Preston, J., Pouvreau, S., Kamermans, P., Sanderson, W., Nordheim, H. Von, 2019. The Native Oyster Restoration Alliance (NORA) and the Berlin Oyster Recommendation: bringing back a key ecosystem engineer by developing and supporting best practice in Europe. Aquat. Living Resour. 32. https://doi.org/10.1051/alr/2019012. EDP Sciences.
Potet, M., Fabien, A., Chaudemanche, S., Sebaibi, N., Guillet, T., Gachelin, S., Cochet, H., Boutouil, M., Pouvreau, S., 2021. Which concrete substrate suits you? *Ostrea edulis* larval preferences and implications for shellfish restoration in Europe. Ecol. Eng. 162. https://doi.org/10.1016/j.ecoleng.2021.106159.
Puckett, B.J., Theuerkauf, S.J., Eggleston, D.B., Guajardo, R., Hardy, C., Gao, J., Luettich, R.A., 2018. Integrating larval dispersal, permitting, and logistical factors within a validated habitat suitability index for oyster restoration. Front. Mar. Sci. 5 (APR), 76. https://doi.org/10.3389/fmars.2018.00076, 76.
Robert, R., His, E., Dinet, A., 1988. Combined effects of temperature and salinity on fed and starved larvae of the European flat oyster *Ostrea edulis*. Marine Biology 97. https://doi.org/10.1007/BF00391249.
Robert, R., Vignier, J., Petton, B., 2017. Influence of feeding regime and temperature on development and settlement of oyster *Ostrea edulis* (Linnaeus, 1758) larvae. Aquac. Res. 48 (9), 4756–4773. https://doi.org/10.1111/are.13297.
Rodriguez-Perez, A., 2019. Informing the Conservation and Restoration of a Keystone Species: the Larval Behaviour of the European Oyster *Ostrea edulis* (Doctoral Thesis). Heriot-Watt University and University of St Andrews. https://doi.org/10.17630/sta/7.
Rodriguez-Perez, A., James, M., Donnan, D.W., Henry, T.B., Møller, L.F., Sanderson, W. G., 2019. Conservation and restoration of a keystone species: understanding the settlement preferences of the European oyster (*Ostrea edulis*). Mar. Pollut. Bull. 138, 312–321. https://doi.org/10.1016/j.marpolbul.2018.11.032.
Rodriguez-Perez, A., James, M.A., Sanderson, W.G., 2021. A small step or a giant leap: accounting for settlement delay and dispersal in restoration planning. PLoS One 16 (8 August). https://doi.org/10.1371/journal.pone.0256369.
Rodriguez-Perez, A., Sanderson, W.G., Møller, L.F., Henry, T.B., James, M., 2020. Return to sender: the influence of larval behaviour on the distribution and settlement of the European oyster *Ostrea edulis*. Aquat. Conserv. Mar. Freshw. Ecosyst. 30 (11), 2116–2132. https://doi.org/10.1002/aqc.3429.
Rumrill, S.S., 1990. Natural mortality of marine invertebrate larvae. Ophelia 32 (1–2), 163–198. https://doi.org/10.1080/00785236.1990.10422030.
Scyphers, S.B., Powers, S.P., Heck, K.L., Byron, D., 2011. Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. PLoS One 6 (8). https://doi.org/10.1371/journal.pone.0022396.
Shchepetkin, A.F., McWilliams, J.C., 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Model. 9 (4), 347–404. https://doi.org/10.1016/j.ocemod.2004.08.002.
Smyth, D., Kregting, L., Elsäßer, B., Kennedy, R., Roberts, D., 2016. Using particle dispersal models to assist in the conservation and recovery of the overexploited native oyster (*Ostrea edulis*) in an enclosed sea lough. J. Sea Res. 108, 50–59. https://doi.org/10.1016/j.seares.2015.12.009.
Stechele, B., Hughes, A., Degraer, S., Bossier, P., Nevejan, N., 2023. Northern Europe's suitability for offshore European flat oyster (*Ostrea edulis*) habitat restoration: a mechanistic niche modelling approach. Aquat. Conserv. Mar. Freshw. Ecosyst. 33 (7), 696–707. https://doi.org/10.1002/aqc.3947.
Theuerkauf, S.J., Puckett, B.J., Eggleston, D.B., 2021. Metapopulation dynamics of oysters: sources, sinks, and implications for conservation and restoration. Ecosphere 12 (7). https://doi.org/10.1002/ecs2.3573.
Thurstan, R.H., Hawkins, J.P., Raby, L., Roberts, C.M., 2013. Oyster (*Ostrea edulis*) extirpation and ecosystem transformation in the Firth of Forth, Scotland. J. Nat. Conserv. 21 (5), 253–261. https://doi.org/10.1016/j.jnc.2013.01.004.
Thurstan, R.H., McCormick, H., Preston, J., Ashton, E.C., Bennema, F.P., et al., 2024b. Records reveal the vast historical extent of European oyster reef ecosystems. Nat. Sustain. 7 (12), 1719–1729. https://doi.org/10.1038/s41893-024-01441-4. https://www.nature.com/articles/s41893-024-01441-4. (Accessed 3 October 2024).
Thurstan, R.H., McCormick, H., Preston, J., Ashton, E.C., Bennema, F.P., Bratoš Cetinić, A., et al., 2024a. Historical dataset details the distribution, extent and form of lost *Ostrea edulis* reef ecosystems. Sci. Data 11 (1), 1198. https://doi.org/10.1038/s41597-024-04048-8.
Treml, E.A., Halpin, P.N., Urban, D.L., Pratson, L.F., 2008. Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. Landsc. Ecol. 23 (Suppl. 1), 19–36. https://doi.org/10.1007/s10980-007-9138-y.
Werner, F.E., Cowen, R.K., Paris, C.B., 2007. Coupled biological and physical models: present capabilities and necessary developments for future studies of population connectivity. Oceanography (Wash. D. C.) 20 (3), 54–69. https://doi.org/10.2307/24860096.
Wilkinson, M.D., Dumontier, M., Aalbersberg, Ij J., Appleton, G., Axton, M., Baak, A., Blomberg, N., Boiten, J.W., da Silva Santos, L.B., Bourne, P.E., Bouwman, J., Brookes, A.J., Clark, T., Crosas, M., Dillo, I., Dumon, O., Edmunds, S., Evelo, C.T., Finkers, R., et al., 2016. Comment: the FAIR Guiding Principles for scientific data management and stewardship. Sci. Data 3. https://doi.org/10.1038/sdata.2016.18.
Willis, J., Kamphausen, L., Jensen, A., Herbert, R.J., Jones, E., 2019. Restoration, dispersal and settlement of native European oyster (*Ostrea edulis*) in energetic tidal areas. bioRxiv, 853911. https://doi.org/10.1101/853911.
Wood, L.E., Silva, T.A.M., Heal, R., Kennerley, A., Stebbing, P., Fernand, L., Tidbury, H. J., 2021. Unaided dispersal risk of Magallana gigas into and around the UK: combining particle tracking modelling and environmental suitability scoring. Biol. Invasions 23 (6), 1719–1738. https://doi.org/10.1007/s10530-021-02467-x.
zu Ermgassen, P.S.E., McCormick, H., Debney, A., Fariñas-Franco, J.M., Gamble, C., Gillies, C., Hancock, B., Laugen, A.T., Pouvreau, S., Preston, J., Sanderson, W.G., Strand, Å., Thurstan, R.H., 2025. European native oyster Reef ecosystems are universally collapsed. Conserv. Lett. 18, e13068. https://doi.org/10.1111/conl.13068.