



Contribution to the Theme Section 'Marine functional connectivity'



## INTRODUCTION

# Advancing research in marine functional connectivity for improved policy and management

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**ABSTRACT:** Marine functional connectivity (MFC) refers to the dynamic spatial exchange of biomass, individuals, genes, and energy via the collective movements of all marine organisms during their lifetimes. In addition to controlling the distribution and resilience of marine biodiversity and exploited stocks, MFC plays a key role in the structure and functioning of ecosystems, at sea and at the land-sea interface. As marine ecosystems and their species face climate change and unprecedented multiple anthropogenic pressures, rapid action is needed to comprehend MFC patterns and their changes in order to anticipate the fates of ocean services to humanity. Despite many advances in techniques to measure or infer marine species' distributions and spatial dynamics, significant progress is still necessary. A full understanding of MFC requires better knowledge of the relationships between marine communities and their habitats, quantification of fluxes of matter and energy, and the capacity to forecast how the many services provided by the ocean may change. The 17 papers in this Theme Section showcase the range of approaches and scales applied in contemporary MFC studies and encompass the diversity of ecosystems and taxa investigated worldwide. The innovative approaches presented here to advance MFC science pave the way to enrich current understanding of MFC's role in ecosystem functioning, and flag how MFC knowledge can be better applied to protect marine resources and manage marine and littoral habitats.

**KEY WORDS:** Marine biodiversity · Movement ecology · Dispersal · Ecosystem modeling · Marine management · Fisheries management · Biodiversity conservation

## 1. INTRODUCTION

The world's oceans and seas are home to a rich marine biodiversity, provide billions of dollars' worth of ecosystem services to the global economy (Bennett et al. 2016, Sumaila et al. 2021), and play an essential role in regulating the earth's climate and the overall functioning of the biosphere (Macreadie et al. 2019, Filbee-Dexter & Wernberg 2020). However, the marine environment faces unprecedented climatic

changes and accelerated human exploitation and alteration of the seascape (Halpern et al. 2019, Jouffray et al. 2020). Sea temperatures are rising rapidly, ocean currents are deflecting, and the qualities of water masses are increasingly altered (IPCC 2021). Furthermore, while many marine species or ecosystems are disappearing (IPBES 2019) and global marine animal biomass is predicted to decline (Lotze et al. 2019), fishing and human demand for marine goods have never been higher and are set to further increase

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(FAO 2020). Sustainable management of marine ecosystems and their resources is therefore urgently needed to halt the ongoing global biodiversity loss (IPBES 2019) and mitigate climate change impacts (IPCC 2023), and also to meet UN Sustainable Development Goals for 2030 (OECD 2016, 2022).

Because changes in biodiversity can seriously affect ecosystem function and vice versa (Dahlin et al. 2021), a comprehensive insight into marine functional connectivity (MFC) is required. MFC refers to the dynamic spatial exchange of biomass, individuals, genes, and energy that results from the collective lifetime movements of all marine organisms, from bacteria to top-predators (Darnaude et al. 2022). As well as determining the fate of marine biodiversity and associated bioresources, MFC plays a fundamental role in the structure and functioning of many ecosystems, both at sea and at the land-sea interface. Understanding the drivers and dynamics of MFC is an essential requirement to identify the conditions necessary to maintain ecological processes that occur at multiple scales across biological realms and is ultimately key to securing the future of human societies (Cumming et al. 2022).

For more than a century, species' distributions and lifetime movements have been the main focus of marine connectivity research. Data have been gathered throughout the world's oceans, using various approaches from distinct research fields, including genetics, natural tags, biologging, and biophysical or environmental niche modeling. These complementary research fields have allowed significant advances in MFC knowledge and have driven an appreciation of the links between wild populations and habitats across a broad range of organisms and across all marine ecoregions (Bryan-Brown et al. 2017). The growing cross-discipline focus on connectivity has nurtured an increasingly multidisciplinary community of scientists, who have convened at the International Marine Connectivity (I-MarCo) Conferences regularly organized over the past decade to share advances in the field. The papers in this Theme Section include a selection of the research presented at the 6<sup>th</sup> I-MarCo hosted in December 2021 in Paris (France) and contributions generated in the framework of the COST Action CA19107 SEA-UNICORN (Darnaude et al. 2022). This international initiative, funded in 2020 by the European Union, aims to advance research in the rapidly evolving field of MFC science.

The Theme Section presents state-of-the-art MFC research, with contributions from across disciplines that demonstrate advances in MFC science to

(1) improve multiscale connectivity assessments by inter-calibrating methods and integrating data between disciplines, (2) address major knowledge gaps on the functioning and productivity of the ocean, and (3) propose solutions to better integrate MFC research and ocean management. The collection of articles spans all levels of biological organization (from individual to ecosystem) and diverse taxa (from primary producers to top-predators). Contributions tackle different types of connectivity (passive, active, vector-driven) and cover coastal and open ocean realms around the globe (temperate and tropical Atlantic, Pacific, and Indian Oceans). Finally, they highlight the close interplay between models and observations, propose methodological advances to improve understanding of connectivity, and demonstrate how connectivity knowledge can better support marine management to mitigate or reverse human impacts (e.g. fishing, climate change, habitat loss). Thus, this Theme Section lays the foundations for predicting how marine systems will react to change, advancing our capacity to protect and restore marine life into the future.

## 2. IMPROVING MFC ASSESSMENTS

Over the course of the past century, a rich repository of data describing the past and present distributions and movements of marine species has been amassed across all marine ecoregions (Bryan-Brown et al. 2017). Rapidly progressing scientific concepts and technological advances are yielding fresh insights into MFC patterns and their drivers. However, because of differences in underlying assumptions, geographical or temporal scales and the types of connectivity metrics produced between methods (Bryan-Brown et al. 2017, Balbar & Metaxas 2019), a true oversight of MFC requires the aggregation and integration of data across disciplines (Darnaude et al. 2022). This Theme Section provides examples of recent advances in several methods, improved calibration in connectivity models through application of empirical data from other disciplines, and examples of effective and rigorous integration of multidisciplinary data.

With regard to method improvement, Jeannot et al. (2024 in this Theme Section) illustrate how population-based and kinship-based genetic inference methods can now be combined for more accurate assessments of population connectivity, especially in species with high gene flow. Applying this innovative dual approach to a small sedentary fish commonly

found along the coast of the Western Iberian Peninsula, they highlight its potential to reveal previously undetected fine-scale genetic differentiation within well-connected populations. By deriving informed estimates of isolation-by-distance at large scales, the maximum spacing required to facilitate adequate gene flow between MPAs can be defined. Several of the articles in this Theme Section probe the sensitivity and reliability of the state-of-the-art biophysical models currently used to predict the dispersal of small marine organisms transported by marine currents. Matching field observations of Fuegian sprat (*Sprattus fuegensis*) early life-stages distribution with passive particle-tracking simulations in the SW Atlantic, García Alonso et al. (2024 in this Theme Section) demonstrate the effectiveness of hydrodynamic models for describing the early-life connectivity of this important fish resource and for future wider large-scale assessment of planktonic dispersal in the SW Atlantic. Yet, there is still considerable scope for optimizing the application of biophysical models to predict realistic connectivity patterns at all relevant scales. By comparing different approaches of varying complexity for the biophysical modeling of the dispersal of kelp propagules and the larvae of 2 invertebrate species along the Atlantic coast of Nova Scotia (Canada) in the NW Atlantic, Balbar et al. (2024 in this Theme Section) show that 3D models of ocean currents are not always necessary to generate the ecological connectivity outputs required by spatial managers. Based on a 12 yr case study of spatio-temporal variability in the recruitment of sole (*Solea solea*) in the North Sea and English Channel, Barbut et al. (2024 in this Theme Section) provide insights into how the accuracy of Lagrangian transport models predicting larval dispersal of coastal fish can be improved. Accurate parameterization of the biological factors in the model, such as pelagic larval duration, spawning period, and larval behavior, is crucial for obtaining precise estimates of *in situ* recruitment. This primary importance of biological parameters is also supported by the model-data comparison of Muller et al. (2024 in this Theme Section). Their results on the dispersal of blacktail seabream (*Diplodus capensis*) along the coasts of South Africa show that variability in spawning behavior, larval physiology, and post-settlement behavior should all be taken into account in future biophysical models of larval fish connectivity. These collected works point towards a future for biophysical modeling in which complexity in modeling ocean currents can potentially be reduced, but with a greater emphasis on integrating organism behavior.

Concerning the multidisciplinary integration of data, Lett et al. (2024 in this Theme Section) illustrate how drawing on distribution and connectivity data from ecological, molecular, and biophysical modeling approaches in multiple species around southern Africa can allow identifying the main corridors and barriers to global MFC at a broad geographical scale. By matching genetic and biophysical modeling data for an endemic New Zealand bivalve along ~15000 km of coastline, Quigley et al. (2024 in this Theme Section) show how multi-generational modeling of larval dispersal using a biophysical model that encompasses the entire species distribution can provide novel insights by identifying potentially important source populations or stepping-stone sites from which molecular samples may not be available. This study lays the groundwork for future widespread use of multigenerational connectivity models integrating both biophysical dispersal and local demography to better understand large-scale connectivity and infer future range shifts in marine species. Finally, the study from Daban et al. (2024 in this Theme Section) on the 'near threatened' undulate skate in the Eastern Atlantic is an example of the value of combining acoustic telemetry with stable isotope analysis to provide insights into the spatial and resource ecology of large migrating fish. All these studies pave the way for multidisciplinary approaches to become the norm for understanding marine connectivity patterns at varied temporal and spatial scales, and provide sounder science-based evidence for the protection of marine biodiversity. Connectivity modeling is also evolving fast, with the emergence of new methods and tools allowing quantitative connectivity estimates. In this regard, Allgayer et al. (2024 in this Theme Section) present MerMADE, a novel model tool coupling biophysical modeling of dispersal with spatial population demography and allowing to predict within-stock patterns of connectivity of fish, as illustrated for the lesser sandeel *Ammodytes marinus* in the North Sea. Finally, Stuart et al. (2024 in this Theme Section) exemplify the efficiency of the emerging use of spatial graph models to identify potential functional connectivity for multi-habitat-utilizing fish within the coastal seascape, here applied to the Florida Keys to quantify the resulting nutrient transport from nearshore to offshore habitats. In the years to come, the application of these spatial models promises to become increasingly integrative and data-driven, with a gradual increase in the accuracy of their quantitative estimates of MFC and associated biomass or nutrient fluxes.

### 3. MFC AND THE FUNCTIONING AND PRODUCTIVITY OF THE OCEAN

MFC strongly impacts local ecosystem dynamics, productivity, functioning, and resilience (Massol et al. 2017, Cannizzo et al. 2021) through changes in food web structure (Melián et al. 2015) and in population or community sizes and compositions (De Guzman et al. 2019, Gladstone-Gallagher et al. 2019, Fontoura et al. 2022). This calls for directly linking MFC to ecosystem processes, to allow upscaling connectivity research from species to functions and elucidating the mechanisms responsible for the productivity and resilience of the ocean. One of the most pressing current challenges for MFC science is to gather data on transboundary matter fluxes along inshore-coastal-offshore gradients, to quantify interdependencies in the functioning of open ocean, coastal, and inshore aquatic ecosystems (Darnaude et al. 2022). Estuarine habitats in particular are key nursery areas for a variety of fish and invertebrate species, many with high commercial value (Beck et al. 2001). Yet, the importance of estuarine nurseries and their significance to the productivity of marine fisheries remains under-explored (Stamp et al. 2022). In this regard, this Theme Section presents valuable new insights, all based on state-of-the-art analyses of otolith chemical composition to infer the lifetime migratory histories of bony fishes. Gonzalez et al. (2024 in this Theme Section) demonstrate that an important part of the productivity of exploited stocks of the horse-eye jack (*Caranx latus*) in Brazil is sustained by inshore estuarine habitats. The primary importance of land-sea connectivity highlighted by this work is likely to apply to many other exploited tropical fish with an estuarine juvenile stage and should therefore be taken into account in the sustainable management of tropical fisheries. Working in the temperate zone, Bassi et al. (2024 in this Theme Section) also confirm the primary contribution of estuarine nursery grounds to the exploited stocks of the Greenland halibut *Reinhardtius hippoglossoides* in the St. Lawrence system (NW Atlantic). Their work demonstrates an important asymmetry in the source-sink dynamics between local estuarine and offshore marine areas, with the juvenile fish remaining in estuarine areas until ages 2 to 3 yr. Ryan et al. (2024 in this Theme Section) reach similar conclusions for the commercially sought-after European sea bass *Dicentrarchus labrax*, showing a strong site fidelity to estuarine nursery areas in southern Ireland (NE Atlantic) over the first 2 yr of life. These findings confirm the close relationship between

inshore and offshore habitat productivity in the littoral zone (Broadley et al. 2022, Whitfield et al. 2023) and call for the conservation and/or restoration of environmental quality of inshore littoral areas for the sustainable management of high-quality marine coastal fisheries.

Several of the Theme Section papers consider the impact of multiple habitat use by fish on the functioning and biodiversity of distant ecosystems in the seascape, advancing our still limited understanding of the key role that fish play in the health and resilience of the ocean. Hendrick et al. (2024 in this Theme Section) provide insights into the rarely studied ecological role of parasite transfers by diel-migrating fish. From field experiments in the Caribbean (NW Atlantic) and on the Great Barrier Reef (Pacific), they show that the hematophagous ectoparasites (gnathiids) attached to fish at the time they depart reef habitats are transported by their hosts and relocated to distant seagrass habitat. Because the parasites remain there until their next feeding (and potentially transport), they have a direct impact on the trophic connectivity between coral reefs and associated habitats. These results provide long-missing information on population connectivity in marine parasites and further complement existing research on the direct and indirect roles of fish in trophic connectivity. Focussing on trophic transfers between food webs through predation, Daban et al. (2024 in this Theme Section) provide insights into the implications of fish interindividual variability in life strategies for seascape connectivity. By matching data on detailed habitat use and trophic niche width in ~100 adult undulate skates (*Raja undulata*) in NW Spain, they show the existence of significant interindividual variability of migratory and trophic strategies in large migratory fish, with important implications for connectivity between distant food webs and specific habitats. Finally, Stuart et al. (2024 in this Theme Section) examine potential nutrient flows from nearshore mangrove and seagrass habitats to offshore reefs caused by the ontogenetic habitat shifts of the subadults of 2 species of *Lutjanidae* fish in Florida, USA (NW Atlantic). Collectively, these studies lay the foundations for future work to infer fish-derived MFC fluxes across marine seascapes. Applying them in different parts of the world promises significant advances in our estimation of the functional significance of marine fish movements, at varied spatio-temporal scales.

Valuable new data on species resilience at diverse taxonomic scales is also provided within this Theme Section. Defining shared ecoscapes that facilitate the

movement of species shifting their geographic ranges to mitigate the adverse impacts of global change is one of the most pressing requirements of marine conservation (Keeley et al. 2021). For this, Lett et al. (2024 in this Theme Section), list 7 main migration corridors and 8 barriers to cross-taxon connectivity around southern Africa. A further requirement of advancing MFC research is an understanding of the drivers and obstacles to MFC, particularly in species or areas understudied thus far. In this context, Fleming et al. (2024 in this Theme Section) scrutinize the still largely unknown processes driving MFC in the deep ocean. By comparing the similarity in species composition of the benthic community and associated larval supply across 3 deep-sea vent regions in the Pacific, they show that realized connectivity is only partially consistent with expectations derived from geographic or oceanographic isolation. In describing the respective roles of larval transport and subsequent recruitment success on community composition, several sites are identified where species sorting by local abiotic and biotic conditions appears to be the principal process ultimately driving observed MFC. This finding calls for closer consideration of post-recruitment environmental filtering in studies modeling MFC for species with a predominant larval dispersal phase, which potentially applies to marine communities in all oceanic domains. Focusing on the dispersal of an abundant coastal fish along the southern coast of South Africa, Muller et al. (2024 in this Theme Section) reach similar conclusions. Their work confirms that thermally mediated spawning behavior, the physical transport of larvae by oceanic currents, and post-settlement processes can all play equivalent and important roles in determining local abundances and defining the corridors and barriers to the final connectivity between fish subpopulations at a broad regional scale. Finally, working on the green-lipped mussel *Perna canaliculus* endemic to New Zealand (Pacific), Quigley et al. (2024 in this Theme Section) shed new light on the complexity of long-term connectivity and source-sink population dynamics throughout a species' range. The importance of modeling connectivity for all known habitats and over multiple generations is shown to be essential to capture the directionality of connections between locations, through identification of important unknown source and stepping-stone populations. These studies signpost a future in which widespread use of connectivity models merging biophysical dispersal and local demography data will enrich our understanding and inference of species range shifts and large-scale, multigenerational connectivity patterns.

#### 4. SOLUTIONS TO BETTER INTEGRATE MFC RESEARCH AND OCEAN MANAGEMENT

Sustainable development requires informed decisions on where, when, and how to conserve or restore marine species and ecosystems (Darnaude et al. 2022). Applying a more robust and comprehensive knowledge of MFC can significantly improve the resilience of species and ecosystems in the face of global change, leading to social and economic benefits. By facilitating range shifts of native species and supporting the adaptation of species and ecosystems to environmental change (Beger et al. 2022), the establishment of well-connected, ecologically coherent networks of protected areas can provide scalable solutions to many environmental, social, and economic challenges (Hilty et al. 2020). However, achieving scalable solutions demands a better understanding of fundamental MFC patterns and processes essential for sustainable marine management, such as the importance of self-recruitment and life-cycle diversity in marine populations (Riginos et al. 2014, Jones 2015), or how MFC will respond to ongoing climate change and impact community composition and ecosystem functioning (Darnaude et al. 2022). This Theme Section provides many useful examples of how MFC data from modeling and empirical approaches can be applied to better conserve, manage, or restore marine ecosystems and resources. Drawing on data from various disciplines and multiple taxa, Lett et al. (2024 in this Theme Section) identify the main corridors and barriers to the dispersal and movement of marine communities around southern Africa to serve as baselines against which existing local MPAs can be critically assessed and future spatial management efforts prioritized. Daban et al. (2024 in this Theme Section) illustrate how combining individual telemetry data and sex-specific isotopic niche widths in a large, migratory fish species can provide valuable new insights on interindividual variation in spatial resource use, to assess whether and how existing MPAs are effective in preserving vital feeding and breeding habitats for local metapopulations. Schwanck et al. (2024 in this Theme Section) show how assessment of mitochondrial genomic diversity from non-invasive sampling can be used to evaluate gene flow from MPAs and assess MPA efficiency in protecting the genetic diversity of vulnerable species. Using the example of the critically endangered flapper skate *Dipturus intermedius* around the British Isles, they demonstrate that the relevant regional MPA hosts only a small subset of the species' local haplotypic diversity, which is insufficient to guaran-

tee the maintenance of local populations or to supply surplus individuals to other locations. They therefore advocate systematic monitoring of genetic diversity, at least for some key species, to improve assessment of the value of MPAs compared to other areas for species and ecosystem resilience. Allgayer et al. (2024 in this Theme Section) propose a new way to couple biophysical modeling of larval drift and spatial population demography to predict within-stock patterns of connectivity to inform fishery management. Through a case study focussed on North Sea sandeels, they challenge the commonly held assumption that stocks are well mixed within fisheries assessment regions and further highlight the importance of juvenile and adult fish migration, notably where larval dispersal capacity is limited. Finally, Muller et al. (2024 in this Theme Section) illustrate how ocean circulation dispersal models with temperature-based constraints on fish spawning and larval survival can inform fishery management and the design of effective MPA networks. For the blacktail seabream, their approach allowed producing realistic estimates of local recruitment rates and spatial gradients in catches but also revealed that the distance between South African MPAs exceeds the larval dispersal distance modeled for local breeding zones, calling into question the value of the current MPA network to conserve the species in particular and coastal fisheries in general.

Finally, a selection of the Theme Section contributions examines how MFC data could be produced to better match the management requirements of stakeholders. Building on recent recommendations and rules of thumb for incorporating connectivity into the design of MPAs (Balbar & Metaxas 2019, Cannizzo et al. 2021), Balbar et al. (2024 in this Theme Section) use biophysical models of larval dispersal for 3 keystone and foundation species along the Canadian NW Atlantic coast to evaluate the role of proposed local MPAs in supporting connectivity. Their research helps bridge the gap between connectivity research and ocean management by demonstrating that simple 2D oceanographic models for estimating dispersal area can suffice to realistically identify connectivity patterns from multiple key species when applied to coastal MPAs with unidirectional current regimes. Several articles in this Theme Section highlight the utility of cutting-edge approaches using spatial graphs as a data- and resource-efficient technique for quantifying and communicating complex ecological connectivity information in support of conservation and restoration efforts. Using graph models relating seascape structural patterns to subadult dispersal ability in multi-habitat-utilizing reef fish species of the

Florida Keys (USA), Stuart et al. (2024 in this Theme Section) were able to pinpoint seascape locations that are most likely to facilitate the survival, growth, and resiliency of restored corals through enhanced nutrient provisioning and other consumer-driven processes in the coastal seascape. Their study also paves the way to identifying multi-species connectivity hotspots for fish in the area, with important implications for local fishery management. Simulating long-term dispersal across a full species distribution range, Quigley et al. (2024 in this Theme Section) illustrate how graph models incorporating biophysical dispersal and local demographic data can reveal complex multi-generational connectivity patterns of sessile species. This approach further supports spatially explicit management of the exploited green-lipped mussel endemic to New Zealand (Pacific) by informing better adapted conservation strategies, notably by protecting all relevant source and stepping-stone populations for the species. Lastly, Hansen et al. (2024 in this Theme Section) used graph-theory based connectivity metrics derived from the outputs of biophysical models of larval dispersal to quantify the links between wild and exploited populations of the common cockle *Cerastoderma edule* in a shallow enclosed strait connecting the North Sea and the Kattegat. This enabled them to show that the most productive and commercially important local cockle beds are almost exclusively dependent on distant larval imports from unexploited spawning biomass, allowing exploitation levels that would be otherwise unsustainable. Thus, graph models allow unraveling and quantifying diverse complex demographic connectivity patterns, between exploited and wild populations or across the mosaic of habitats in the seascape, with important implications both for the sustainable exploitation of marine resources and the protection or restoration of marine life and habitats.

## 5. CONCLUSIONS

The papers compiled in this Theme Section are representative of the state-of-the-art methodology and baseline knowledge required to advance our understanding of MFC patterns, at sea and at the land-sea interface. They illustrate the multifaceted role of MFC in (meta)ecosystem functioning and species resilience, and suggest new approaches that will improve and enrich strategies for managing the oceans and their bio-resources. Thus, through profiling the methodological foundations for future integrative research

in the emerging field of MFC science, this Theme Section illustrates the advances in population and ecosystem-level knowledge that are both possible and desired. Advances in the understanding of MFC at national and international scales will yield novel and holistic datasets to better inform managers and policy-makers on how to best conserve the ocean's biodiversity, productivity, and functioning, all of which are essential to human existence in the future.

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