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REVIEW

A systematic review of the current state of marine functional connectivity research

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ABSTRACT: Marine functional connectivity underpins biodiversity and ecosystem functions, ensuring resilience in marine and land–sea interface ecosystems. Research on this topic has advanced rapidly in recent decades, as reflected in the growing body of primary literature and the increasing number of reviews covering a variety of topics and methodologies. Here, we systematically extracted and analysed information from 215 reviews across the entire field to synthesize the current state of marine functional connectivity research, highlighting the main topics, methods, taxa, geographic areas, and future research priorities. Word co-occurrence and network analyses revealed imbalances in review topics, with certain habitats (e.g. coral reefs), taxa (e.g. fish), and geographic areas (e.g. North Atlantic) receiving disproportionate attention. These disparities likely arise from variations in funding, field site accessibility, public interest, and/or delays in adopting new concepts and methodologies. Research priorities were broadly grouped into 2 themes: (1) 'Methods', highlighting the need to integrate and advance sampling, modelling, and analysis techniques, and (2) 'Ecology and Application', stressing the need to understand connectivity drivers, particularly the impacts of climate change, and to integrate connectivity knowledge into marine conservation and management. There was also a third overarching theme emphasizing the importance of expanding spatial and temporal coverage of connectivity knowledge and data by embracing new technologies, growing collaborative networks and targeting understudied habitats, areas, and taxa. Tackling the identified research priorities will further improve our ability to quantify connectivity patterns and drivers, and facilitate efforts to actively apply this knowledge and data in marine management and conservation.

KEY WORDS: Marine biodiversity · Dispersal · Movement · Umbrella review · Climate change · Conservation · Resource and ecosystem management

1. INTRODUCTION

Over recent decades, the study of connectivity in marine ecosystems has progressed from a relatively niche topic, primarily focused on genetics and dispersal ecology, to a vast research field at the heart of national and international agendas for biodiversity conservation (e.g. Aichi target, UN Sustainable Development Goals, EU Nature Restoration law, Kunming Montreal Global Biodiversity Framework). Mar-

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ine functional connectivity refers to all spatial transfers of individuals, genes, nutrients, matter, and energy resulting from the movements of organisms at sea or across the land–sea interface (Cowen et al. 2000, 2006, Sale et al. 2005, Auffret et al. 2015, Beger et al. 2022, Darnaude et al. 2022). These fluxes often occur across jurisdictional units, requiring transboundary coordination and collaboration, in terms of both research and governance (Brondizio et al. 2009, Popova et al. 2019, Keeley et al. 2022). Marine functional connectivity is a critical component of healthy, resilient ecosystems by supporting biodiversity and ecosystem functions, such as habitat formation, biogeochemical processes, and nutrient and energy transfer (Hillman et al. 2018).

Understanding the movements, interactions, and adaptability of organisms is also fundamental for predicting how species and communities will respond to rapid environmental change, forecasting species' range shifts, and enhancing the effectiveness of different management and restoration actions (Gilby et al. 2018, Beger et al. 2022). In terrestrial and freshwater ecosystems, connectivity is regularly considered in management and conservation efforts, in part due to the conspicuous influence humans have had on migratory corridors (e.g. dams, roads) (Martensen et al. 2017, De Montis et al. 2018, Hilty et al. 2020). Conversely, in the marine realm, outdated assumptions of openness and physical homogeneity, combined with the challenges and costs associated with field access, have historically hampered progress in and uptake of marine connectivity research (e.g. Cowen et al. 2000, 2006, Pineda et al. 2007). Today, however, there is a growing understanding of how environmental factors (e.g. temperature, currents), species' biology (e.g. pelagic larval duration), ecology (e.g. competition, predation), behaviour (e.g. migration), and demography (e.g. density-dependence) shape marine connectivity and organism survival (Treml et al. 2015). This growing awareness is resulting in connectivity metrics being increasingly incorporated into marine management and conservation, particularly for designing marine protected areas (MPAs) (Fernandes et al. 2005, Magris et al. 2014, Endo et al. 2019, Chamberlain et al. 2022) and improving fisheries stock assessments (Cadrin et al. 2019, Goethel & Cadrin 2021).

Since the early 2000s, connectivity studies in the marine realm and at the land–sea interface have grown rapidly, in part due to increased research interest and technological advancements (Hixon 2011, Bryan-Brown et al. 2017). The term connectivity is now used across a range of disciplines, topics, and methodological approaches, making it increasingly difficult to perform a systematic review of the entire field. This is illustrated by a simple search of the primary literature yielding >12 000 articles (Web of Science search performed on 9 December 2024 using the search string provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m764p237_supp.pdf, without paper type specified). Parallel to this growth, increasing numbers of review articles have been published over the last 20 yr, many focusing on particular methods (e.g. Swearer et al. 2019, Gagnaire 2020), life stages (e.g. Gillanders et al. 2003, Pineda et al. 2010), geographic areas (e.g. García-Machado et al. 2018, Lett et al. 2024), taxa (e.g. Curley et al. 2013, Sequeira et al. 2013), or ecozones (e.g. deep sea, Hilário et al. 2015). We chose to build on these synthesis efforts to provide a broad overview of the current state of marine functional connectivity research, by systematically reviewing and mapping existing reviews across the entire field. Systematic mapping provides an efficient mechanism to synthesize information from a wide range of species and systems, and to identify key knowledge gaps and areas showing promise for future innovation (Torraco 2005). Furthermore, for identifying research priorities, taking a review-of-reviews approach (otherwise termed an 'umbrella review') is particularly powerful, given that syntheses of knowledge gaps and future directions tend to be far better represented in review articles than in the primary literature. Such information is critical for improving data collection and quality, for effective decision-making and resource allocation, and for driving new research directions (Elsbach & van Knippenberg 2020).

Here, we performed a broad search and systematically extracted information from selected review articles to identify the main topics, taxa, geographic areas, and ecozones focused on, building on previous efforts (e.g. Bryan-Brown et al. 2017). In addition, we used bibliometric maps to describe the networks of authors involved in these review efforts, and synthesized identified research priorities. Ultimately, we aimed to collate data across a broad range of species and systems to guide future marine functional connectivity research and support its broader application into resource and ecosystem management.

2. MATERIALS AND METHODS

2.1. Literature search and selection criteria

We conducted a literature search of peer-reviewed review publications in the Web of Science (WoS; Clarivate Analytics, London; https://www.webofscience.

com/) and Scopus (Elsevier, Amsterdam; https://www.scopus.com/) databases on 4 September 2024. The search strategy was designed to locate published reviews focused on marine functional connectivity research from the 2 databases without incorporating systematic bias in the search results. Narrative reviews, systematic reviews, systematic reviews with meta-analysis, opinion papers, and perspective papers were all considered. Preliminary searches were performed to finetune the search string that contained the following terms relating to (1) the environment (marine OR sea OR ocean* OR estuar* OR brackish OR coast*), (2) the paper type (review* OR meta-analysis OR meta* analy* OR metaanaly*), and (3) the subject area (connectivity). Exact strings and wildcards (*) used in WoS and Scopus are provided in Table S1. Throughout the process, we adhered to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocol (Moher et al. 2015). We used the open-access online tool CADIMA (https://www.cadima.info/) to streamline and document our systematic review, and to eliminate duplicate publications from the search results (Kohl et al. 2018).

A first round of expert filtering was performed to include only publications meeting all the following criteria: (1) is a peer-reviewed review or meta-analysis written in English; (2) is in or connected to marine/coastal/brackish ecosystems; and (3) addresses topics related to functional, demographic, ecological, genetic, trophic, or seascape connectivity. We explicitly specified that reviews should focus on the movements of organisms (living or dead, genes, biomass, or energy), so, for example, this would include connectivity of organism excrement, but not of physical processes or non-organism-derived chemicals (e.g. wave attenuation across the seascape or fluxes of dissolved pollutants). Books, book chapters, and conference proceedings were not included. To evaluate the consistency of the inclusion/exclusion process among coauthors, we carried out a kappa test in which 19 coauthors were individually assigned the same 50 randomly selected publications from the search output. Each coauthor independently reviewed the publications at the title, abstract, and/or full-text level to designate them as included or excluded. We then calculated Fleiss' kappa statistics (McHugh 2012) using the 'irr' package (Gamer et al. 2012) in R v.4.4.1 (R Core Team 2023) to assess the level of agreement among coauthors. After this assessment, which showed a good level of agreement among coauthors ($\kappa = 0.712$, $p < 0.001$), the remaining publications were randomly allocated to each coauthor to perform inclusion/exclusion expert filtering.

2.2. Data extraction

Metadata of the included publications (title, author key words, year of publication, author names and affiliations, and journal names) were retrieved from WoS and Scopus. The second round of expert processing consisted of manual extraction of a specific set of descriptors from each publication by the coauthor to which the publication was assigned. To ensure consistency in the data extraction approach, as a group, we discussed the process at length and developed specific instructions and predefined levels (outlined in Table S2). The data extraction fields included review type and focus, method focus, geographic region(s), direction of connectivity (e.g. horizontal, vertical), ecozones, depths, and organism groups. For ecozones and organism groups, coauthors selected up to 3 predefined levels, and if the review focused on more than 3, they specified '>3'. We also included fields allowing free-text entries where coauthors described the primary objective(s) of each review, the terms used to describe connectivity, the data/knowledge gaps and future research priorities identified, and the specific geographic area(s) and taxa considered in the review (when fewer than 4). For free-text fields, text passages were copied directly to avoid misinterpretation. Finally, we used checkboxes to highlight reviews that had a particular focus on 5 'hot topics' in connectivity research that were identified by the expert group of coauthors: MPAs, bioinvasions, climate change, food webs, and fisheries management.

2.3. Data analysis

The R package 'bibliometrix' v.4.1.3 (Aria & Cuccurullo 2017) was used to perform bibliometric and scientometric analyses of the included publications and knowledge mapping (Nakagawa et al. 2019). The metadata on the country affiliation of the coauthors for each publication was extracted and used for the country collaboration analysis (Batagelj & Cerinšek 2013). We generated a country network plot using the Kamada–Kawai algorithm that positions nodes so that the geometric (Euclidean) distance is as close as possible to the graph-theoretic (path) distance between them. In other words, countries that are more closely connected in the network are positioned closer together in the resulting plot, while those with fewer connections appear farther apart. We also performed a co-occurrence analysis to map and cluster terms extracted from key words in the included reviews. We visualized the results with a network plot using the Fruchterman–Reingold algorithm and the Louvain clustering method in which the thickness of links corresponds to the level of co-occurrence (Aria & Cuccurullo 2017). Data for word clouds were prepared and visualized using the R packages 'tm' v.0.7-11 (Feinerer & Hornik 2023) and 'wordcloud' (Fellows 2018), respectively. For the co-occurrence network and the word cloud, a synonym list was included and terms used in the search string were excluded (i.e. 'marine', 'connectivity', 'review').

To identify recurring common topics within the data/knowledge gaps and future priorities text extracted from the reviewed publications, we classified each review into broad themes manually, and then used ChatGPT-3.5 (OpenAI) to identify common themes. Four queries using slightly different prompts were performed to allow for variability in reading and wording (see Table S3 for all prompts used). We inspected the outcomes of the 4 queries for overlap and replication among categories, compared them to the manually identified themes, and then, in discussion, regrouped them into 3 overarching themes containing 6 subcategories of research priorities and future needs. Finally, we manually assigned each review to 1 or more themes and subcategories, based on the extracted quotes on data/knowledge gaps and research priorities. Resulting research priorities and needs (themes and subcategories) were then linked to the previously extracted fields (review type and method) and visualized using Sankey diagrams and stacked bar plots. We calculated statistics and visualized the data using the R packages 'dplyr' v.1.0.10 (Wickham et al. 2023), 'ggplot2' v.3.4.3 (Wickham 2016), 'tidyverse' v.1.3.2 (Wickham et al. 2019), and 'ggsankey' (Sjoberg 2023).

3. RESULTS AND DISCUSSION

From the initial 842 publications identified through the literature searches, our expert group retained 215 reviews fitting our selection criteria for data extraction and further analysis (Fig. 1). Of the excluded publications (n = 627), 56 were conference proceedings, books, book chapters, additional duplicates, or not written in English, and 571 did not meet one or more of the established selection criteria. Of the 215 selected reviews (Table S4), the majority (62.3%) were classified as narrative reviews (including narrative, perspective, opinion, conceptual, and other), followed by systematic reviews (25.1%) and systematic reviews with meta-analysis (12.6%). As quantified in more detail in Section 3.3, reviews covered a variety of topics in marine connectivity research, including new and existing methods (e.g. McMahon et al. 2013, Riginos et al. 2016, Marandel et al. 2019, Jahnke & Jonsson 2022), specific habitats, taxa, or life stages (e.g. Pineda et al. 2010, Kendrick et al. 2017, Turner et al. 2017, Sambrook et al. 2019), important conservation and management issues (e.g. von der Heyden et al. 2014, Di Lorenzo et al. 2016, Munguia-Vega et al. 2018, Podda & Porporato 2023), as well as more theoretical and conceptual reviews (e.g. Pante et al. 2015, Fang et al. 2018, Alzate & Onstein 2022, Swanborn et al. 2022).

3.1. Publication year and venue

Selected reviews spanned from 2002 to August 2024, presenting an increasing trend in the number of publications per year until 2018, followed by an apparent plateau (Fig. 2). The majority of reviews published within the first 4 yr of the time series (2002–2005) were dominated by a small group of authors, mostly tackling topics related to larval dispersal and spatial management (Sale & Kritzer 2003, Sale et al. 2005) and fish population structure using otolith chemistry (Elsdon & Gillanders 2003, Gillanders et al. 2003, Gillanders 2005). Overall, the 215 reviews were written by over 1000 coauthors from 35 countries and published in 104 different journals, illustrating the diverse, global, and multidisciplinary nature of marine functional connectivity research. Reviews were frequently published (5 or more) in marine science-related journals (e.g. Marine Ecology Progress Series, Frontiers in Marine Science, Oceanography and Marine Biology: an Annual Review), multidisciplinary ecological journals (e.g. Biological Reviews, Global Change Biology), taxa-specific journals (e.g. Reviews in Fish Biology and Fisheries, Fish and Fisheries), and a journal focused on the use of molecular markers (Molecular Ecology) (Fig. S1). This is also reflected in the journals' 'research areas' identified in the WoS, which were dominated by 'Environmental Sciences & Ecology', 'Marine & Freshwater Biology' and 'Oceanography' (assigned to 63% of the 104 journals) followed by 'Fisheries', 'Biodiversity & Conservation' and 'Evolutionary Biology'.

3.2. Author networks and geographic coverage

International collaboration is crucial in marine connectivity research, given how vast the ocean is and the multitude of connections that cross ecological and

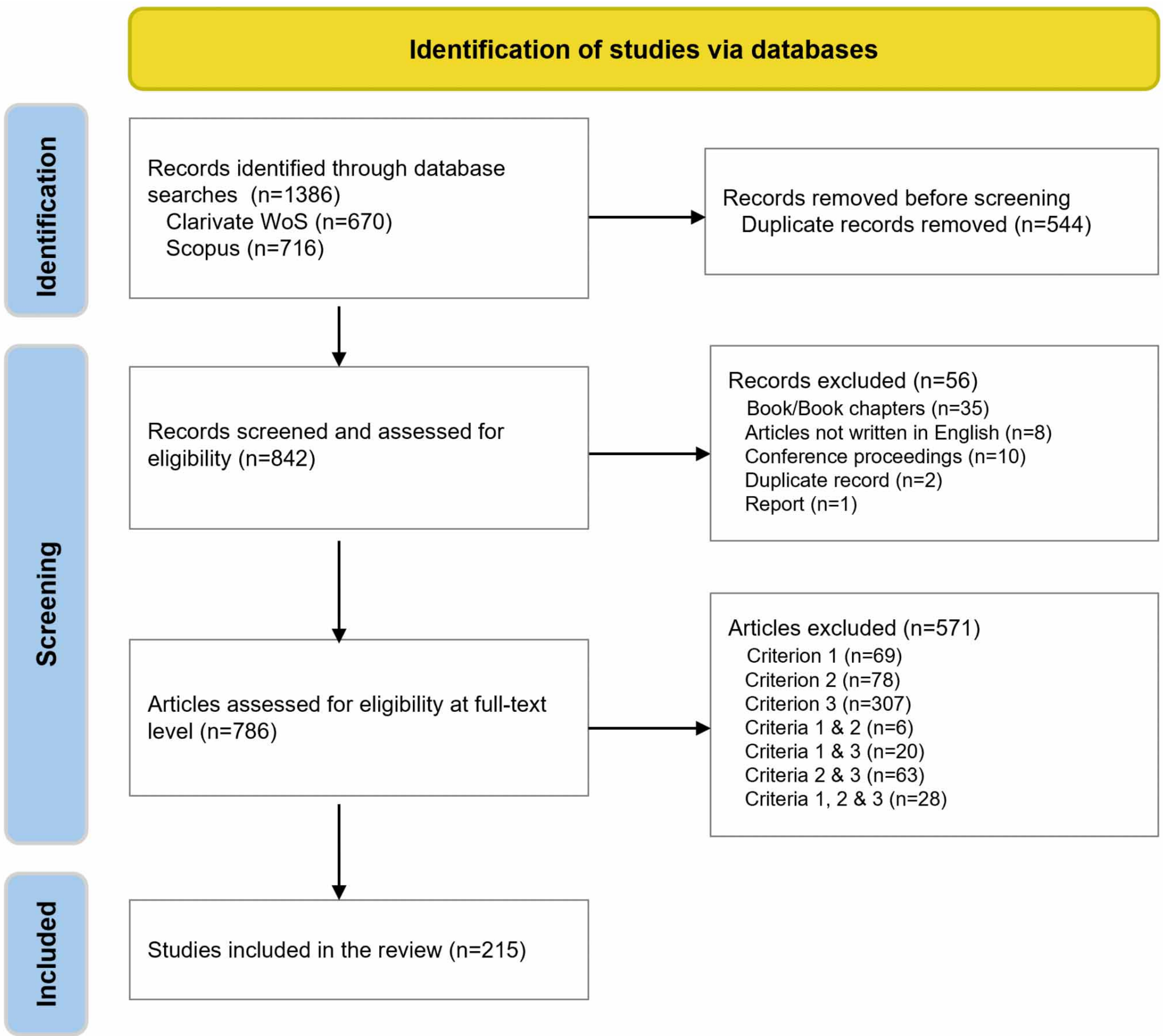

Fig. 1. PRISMA flow diagram detailing the inclusion/exclusion of review articles. At the screening stage (see blue boxes), inclusion of review articles was based on the following 3 criteria: (1) a review or meta-analysis; (2) in or connected to a marine/coastal/brackish ecosystem; (3) topic focused on functional, demographic, ecological, genetic, trophic, or seascape connectivity. WoS: Web of Science

jurisdictional boundaries. Researchers based in the USA, Australia, and the UK have authored most marine functional connectivity reviews based on the co-author affiliation(s). Along with Canada and France, these countries also showed the highest number of author links, suggesting that they act as international 'research hubs' (Fig. 3), characterised by extensive networks, international collaborators, research capacity, and funding. While this concentration of resources and collaboration promotes scientific exchange and innovation, it also risks overshadowing less represented countries, potentially widening the global research divide highlighted in other ecological literature (Nuñez et al. 2021). As seen in other studies, marine functional connectivity research networks are often led by countries with well-established scientific and educational systems, while barriers such as differences in language, funding availability, research infrastructure, and academic traditions can limit the extent and depth of collaboration with other countries (Nuñez et al. 2021). Some regions may be underrepresented because relevant research is published in languages

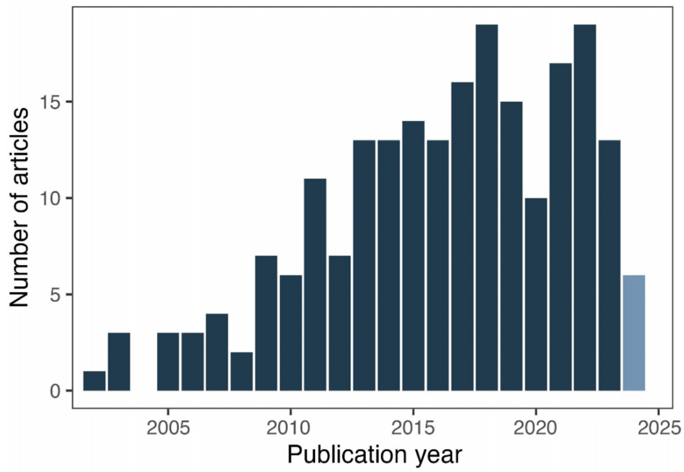

Fig. 2. Number of review articles included in the study per year over the studied period (2002–2024). In 2024 (light blue), only reviews published before 4 September were considered

other than English. To foster a more inclusive global research environment, policies should support international collaborations involving underrepresented countries, foster capacity-building, and broaden funding mechanisms to promote a more equitable distribution of research opportunities and benefits, ensuring balanced global scientific progress.

Regional collaborations among countries bordering the same waterbody, driven by the need to address common marine issues around habitat or species conservation, fisheries management, and pollution control, are particularly important (Blaber et al. 2005, Rochette et al. 2015, Mahon & Fanning 2019). For example, European countries such as France, Spain, and Italy maintain strong collaborative networks due to their common interests in the Mediterranean Sea and their membership in the European Union, providing a structured framework for regional research partnerships and shared funding opportunities (Pascual et al. 2017, Pazzaglia et al. 2021, Di Stefano et al. 2023). Similarly, authors from eastern African countries (e.g. South Africa, Mozambique, Tanzania, Kenya) are strongly linked through their common interest in tackling connectivity-related issues in the Western Indian Ocean (van de Geer et al. 2022, Lett et al. 2024). The same can also be seen in the dense network of collaborations among North American countries (e.g. USA, Cuba, Mexico), linked by connectivity research focused on the North Atlantic Ocean and the Caribbean Sea (Claro et al. 2019, Díaz-Ferguson & Hunter 2019) as well as the Eastern Pacific (Munguia-Vega et al. 2018, Ferrera-Rodríguez et al. 2024).

While 24% of the reviews did not focus on a specific geographic area, the remaining reviews either included case studies from particular regions (36% focused on 1–3 regions, as shown in Fig. 4, and 21% included >3 regions) or adopted a global perspective (19%) (Fig. 4). Reviews with a global focus addressed connectivity patterns of widely distributed taxa, con-

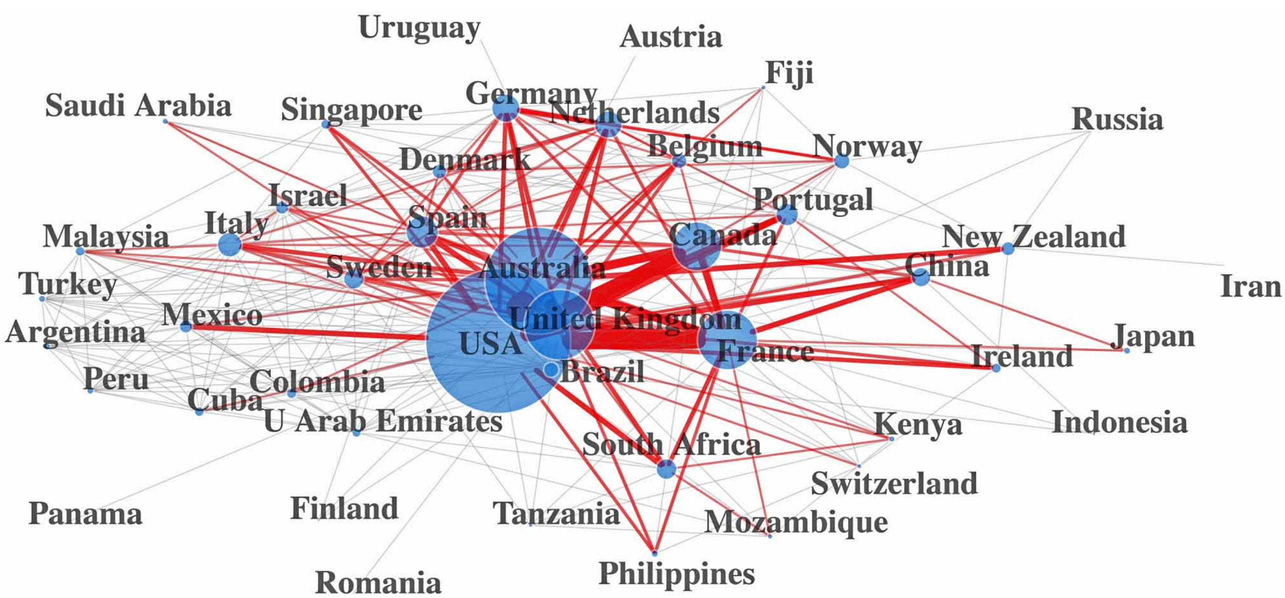

Fig. 3. Collaborative network of countries based on coauthors' affiliations (n = 215 publications) showing the extent of international cooperation in marine connectivity research. In this network, the size of each circle corresponds to the number of coauthored publications of a country, while the thickness of the lines connecting the circles illustrates the intensity of collaboration between countries. Links corresponding to a single publication are shown in grey, while those corresponding to multiple publications are shown in red

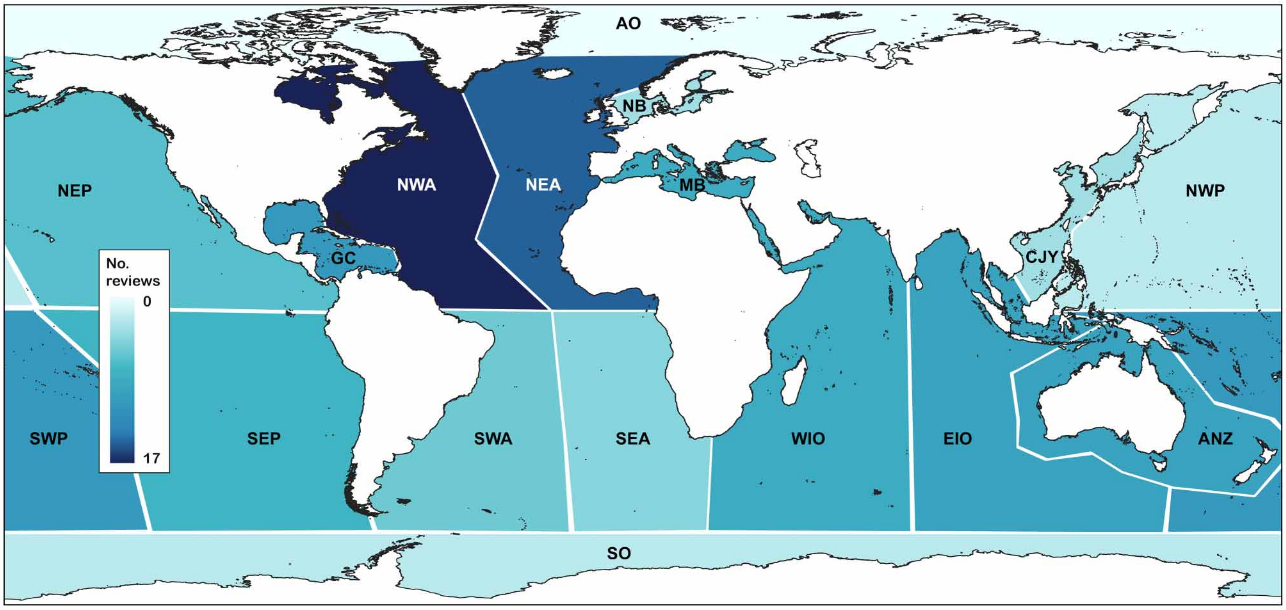

Fig. 4. Frequency of reviews that focused on particular geographic regions (n = 78, which excluded reviews that did not highlight a specific region [e.g. conceptual reviews; n = 52], those including >3 regions [n = 45], and those with a global focus [n = 40]). Note: the numbers on the scale bar denote occurrences, so a single review could be included 3 times if it included case studies focused on 3 regions. Region boundaries are approximated and purely for visualisation purposes. Region codes are AO: Arctic Ocean; NEP: Northeast Pacific; GC: Gulf of Mexico and Carribean Sea; NWA: Northwest Atlantic; NEA: Northeast Atlantic; NB: North and Baltic Seas; MB: Mediterranean and Black Seas; CJY: China, Japan, and Yellow Seas; NWP: Northwest Pacific; SWP: Southwest Pacific; SEP: Southeast Pacific; SWA: Southwest Atlantic; SEA: Southeast Atlantic; WIO: West Indian Ocean; EIO: East Indian Ocean; ANZ: Australia and New Zealand coastal waters; SO: Southern Ocean

sidering processes such as long-distance migration (Sequeira et al. 2013, Kot et al. 2022, Zhang 2022) and larval dispersal (Cerca et al. 2018). Reviews focusing on several specific regions tended to be compilations of case studies (e.g. Wolanski 2017, Signa et al. 2021, van Woesik et al. 2022). The geographic areas most frequently studied were regions around the USA and Europe (i.e. the North Atlantic Ocean, Gulf of Mexico, and Caribbean Seas), and Australia (local coastal areas, and the east Indian and southwest Pacific Oceans) (Fig. 4). Conversely, the areas with the lowest coverage in terms of review papers (which we assume correlates with lower numbers of empirical studies) were the Arctic and Southern Oceans, the South Atlantic, and the Northwest Pacific (Fig. 4).

3.3. Review focus

3.3.1. Title analysis

Not considering the terms included in the original search string ('marine', 'connectivity', and 'review', appearing 82, 61, and 34 times, respectively), the title terms most frequently featured suggested a disproportionate focus on 'fish' as the reviewed taxa, 'population' as the main ecological organisational level, and 'dispersal' as the main connectivity process (Fig. 5A). The most popular habitat-related terms ('coastal' and 'coral') highlighted the prevalence of connectivity studies in shallow, nearshore environments. Other common title words demonstrated the growing importance of connectivity in marine 'spatial' 'management', 'conservation', and MPA design (Fig. 5A). Finally, title words also often focused on the methods used to estimate connectivity, such as genetic(s), modelling, and genomics (Fig. 5B).

3.3.2. Key word analysis

Cluster analysis of the key word co-occurrence network provided insights into both the general focal topics in connectivity reviews, but also the broader research landscape, with key words grouping into 5 distinct clusters (Fig. 5C). Cluster 1 (red) focused on connectivity processes ('dispersal', 'movement', 'migration', 'distribution') and how they related to climate change ('climate change', 'global', 'warming') (e.g. Munday et al. 2009, Gerber et al. 2014, Crook et al. 2015). Clusters 2 (green) and 3 (blue) focused on 'conservation', with the former focused more on 'bio-

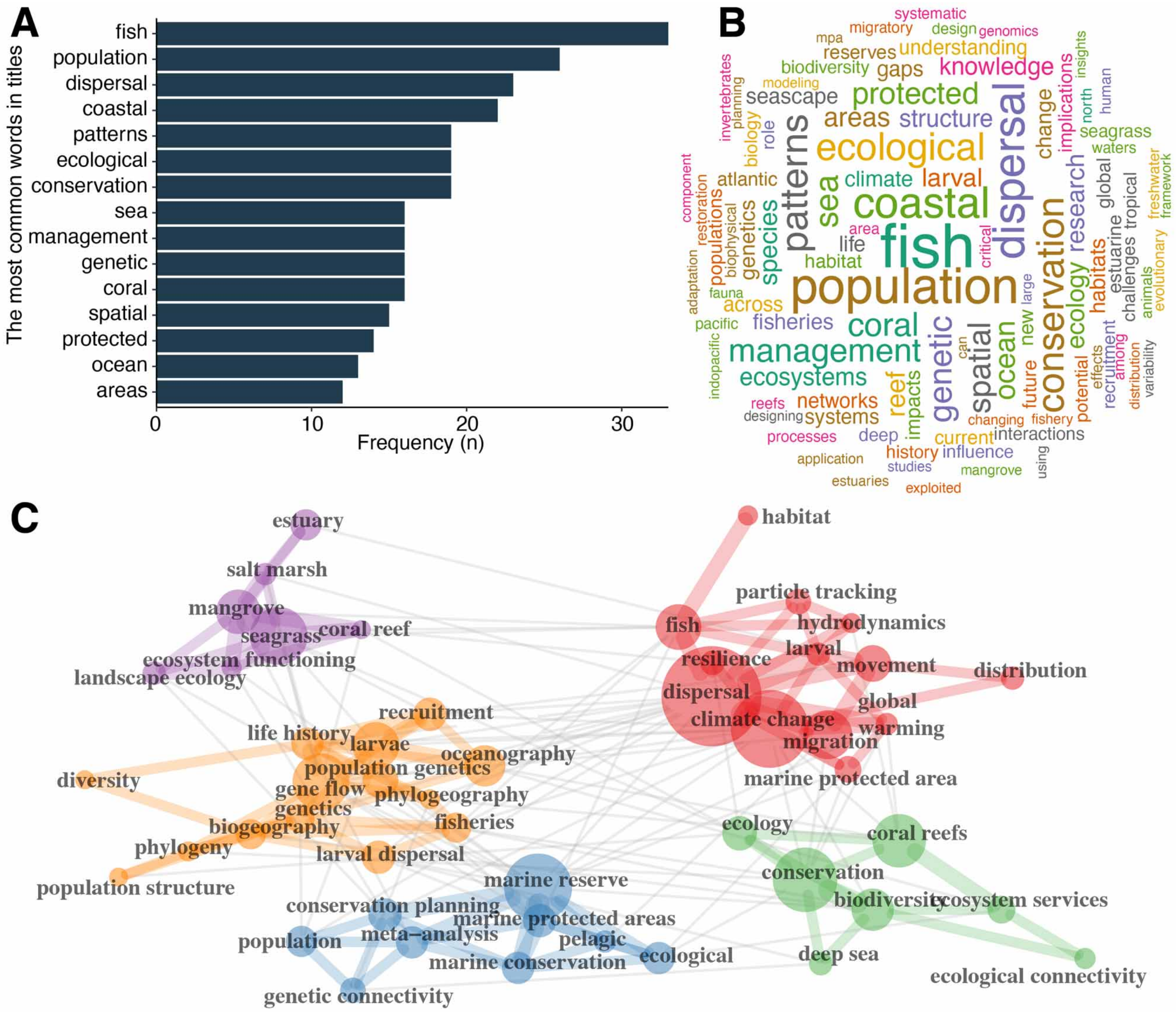

Fig. 5. (A,B) Most commonly used words in marine connectivity review titles. (C) Co-occurrence network of the 50 most frequently used key words, where colours indicate cluster membership. In all examples, the words 'marine', 'connectivity', and 'review' were excluded given their direct inclusion in the search string. More details on the clusters are provided in Section 3.3.2

diversity' and threatened or vulnerable habitats, such as 'coral reefs' and 'deep sea' (e.g. McCook et al. 2010, Levin et al. 2018, Perez et al. 2021), and the latter more directed towards spatial planning and MPAs (e.g. Eger & Baum 2020, Ceccarelli et al. 2021, Goetze et al. 2021). Cluster 4 (orange), positioned closely to Cluster 3 (blue) and strongly linked to Cluster 1 (red), focused on biological aspects of connectivity, such as 'gene flow' (e.g. Rocha et al. 2007, Derycke et al. 2013, Dawson et al. 2014), 'life history' traits (e.g. Friess et al. 2012, Bashevkin et al. 2020, Moser et al. 2021), and 'recruitment' (e.g. Wolanski 2017, Cadrin et al. 2019, Morgan 2022). Finally, Cluster 5 (purple) showed links between habitat types, with a particular focus on those in nearshore ecosystems, estuarine habitats (e.g. 'seagrass', 'mangroves', 'saltmarsh') (e.g. Gillis et al. 2014, Nagelkerken et al. 2015, Sambrook et al. 2019). A clear link between the Cluster 5 key words describing different nearshore habitats (i.e. 'estuary', 'seagrass', 'mangrove', 'coral reef') and the key word 'fish' in Cluster 1 (red) evidenced the importance of these habitats as fish nursery areas (e.g. Martinho et al. 2012, Nagelkerken et al. 2015, Whitfield 2020). This key word co-occurrence network also highlighted areas within connectivity research that have received less attention, such as shelf and polar habitats, methods other than genetics and dispersal modelling for estimating connectivity, and physical and biological barriers to connectivity in the marine realm.

3.3.3. 'Hot topics' in marine connectivity research

Among the review focus categories included in this analysis, the majority of reviews focused on 'biology and ecology' (58%), 'conservation and management' (23%), 'methods' (11%), and 'conceptual' or theoretical aspects of connectivity (8%). Besides the broad review focus, we also collated information on how frequently reviews focused on what we considered to be 5 current 'hot topics' in marine functional connectivity research, with 25% of reviews focusing on MPA design, 23% on fisheries management, 17% on climate change, 7% on food webs, and 7% on bioinvasions.

The focus on MPA design in marine functional connectivity reviews reflects a growing global interest in developing the science and policies necessary to achieve interconnected MPA networks, and to move towards transnational ecosystem-based management (Hull et al. 2019). Indeed, several global and regional initiatives (e.g. Kunming-Montreal Global Biodiversity Framework, EU Biodiversity Strategy for 2030, EU Marine Strategy Framework Directive) have prioritized the establishment and management of MPA networks. In this context, several reviews highlighted the largely positive influence of connectivity on reserve performance and conservation outcomes (Olds et al. 2016, Goetze et al. 2021, Ferreira et al. 2022). Other reviews pointed out key knowledge gaps in this sphere, emphasizing the need for more targeted research to support integration of connectivity data to area-based management (Balbar & Metaxas 2019, Kot et al. 2023) and to understand how long-distance connectivity can be incorporated into MPA planning to maximise conservation benefits (Manel et al. 2019).

The reviews focusing on fisheries management were primarily aimed at understanding the importance of stock spatial structure and connectivity on population dynamics (Stephenson et al. 2009, Ulrich et al. 2013). Accurately accounting for population structure and movement dynamics in stock assessment models can greatly improve the reliability of predictions of recruitment and year class strength, which are essential components of sustainable fisheries management (Cadrin et al. 2019, Goethel & Cadrin 2021). However, operational application of spatial stock assessment models often remains limited due to lack of ecological knowledge and challenges in incorporating knowledge into stock assessment, which in part may be improved in the future by technological advancements in areas such as genomics and telemetry (Nordeide et al. 2011, Özgül et al. 2024).

Reviews exploring the impacts (measured and potential) of climate change on marine functional connectivity were also common. Incorporation of connectivity data and climate change into conservation planning (e.g. MPA design, placement, and spacing in networks) was at the core of several reviews (Gerber et al. 2014, Green et al. 2014, Magris et al. 2014, Goetze et al. 2021). Many of these reviews focused on the impacts of climate change on the development, survival, and dispersal patterns of early life stages (Munday et al. 2009, Wilson et al. 2016), while others focused on changes in ecosystem resilience and individual adaptation capacity in the face of rapidly changing environmental conditions (Bernhardt & Leslie 2013, Xuereb et al. 2021).

Relatively few reviews focused on the role of marine functional connectivity in marine food webs and bioinvasions. Studies linking connectivity with food webs primarily focused on specific marine systems that contain complex habitat mosaics (e.g. tropical seascape, Berkström et al. 2012; deep sea, Woodstock & Zhang 2022). In contrast, studies on bioinvasions showed how methodological and conceptual advances like evolutionary genomics can provide insights into invasion patterns and processes (Sherman et al. 2016), and how artificial structures (e.g. oil and gas platforms; wind farms) can facilitate or alter the spread of invasive species (McLean et al. 2022).

3.3.4. Methods investigated in marine connectivity reviews

A wide variety of methodological approaches were used to estimate marine connectivity, and many were explicitly discussed in the selected reviews, with 69% of papers discussing or addressing one or more methodological approaches to estimate connectivity. Of these, most reviewed a single method (52%), of which genetics was the most frequently represented (21% of reviews), followed by abundance/presence–absence data (13%) and modelling (12%), the latter covering dispersal modelling, network analysis, and species distribution modelling. Other methods such as chemical markers (3%) and artificial tags (3%), were represented to a lesser extent, and only 1 study (Tully & Nolan 2002) used parasites to assess connectivity patterns. These results clearly underscore the importance and widespread use of genetic approaches to estimate marine connectivity patterns (e.g. Hellberg 2007, Dawson et al. 2014, Cooke et al. 2016, Gagnaire 2020, Perez et al. 2021). Furthermore, genetics was also included in most of the reviews that included more than one methodology (e.g. Miyake et al. 2017, Puerta et al. 2020, Lett et al. 2024).

3.3.5. Focus organism groups, depth, and ecozones

In 36 of the reviews, focus taxa were not identified, as these papers were mostly related to specific methods and theory (e.g. McMahon et al. 2013, van Sebille et al. 2018, Gagnaire 2020) and/or conceptual approaches (e.g. Heino et al. 2015, Buckner et al. 2018). A considerable number of the selected publications (58) reviewed connectivity-related information for multiple taxa (here 'multiple' being defined as >3) (e.g. Hori 2008, Allen et al. 2018, Levin et al. 2018). Among the reviews focusing on specific taxonomic groups, teleost fishes were the most commonly examined (e.g. Able 2005, Flitcroft et al. 2019, Pickens et al. 2021), followed by hard corals (e.g. van Oppen & Gates 2006, Turner et al. 2017, Alvarado-Cerón et al. 2023) and large crustaceans (excluding zooplankton) (e.g. Giménez 2003, Cruz et al. 2021, Farhadi et al. 2024) (Fig. 6A). Commercially important species dominated the literature, with many reviews focusing on resource management and spatial planning (e.g. Curley et al. 2013, Smialek et al. 2021, Farhadi et al. 2024). Teleost fishes, which are largely studied in marine biological sciences given their high economic, cultural, and conservation values, and their pivotal position in marine food webs, display diverse life histories and habitat preferences, and high dispersal potential at different life history stages, which makes them highly relevant for investigating connectivity within and among ecosystems (e.g. Berkström et al. 2012, Vasconcelos et al. 2015, Whitfield 2017, 2020). Hard corals form the foundation of tropical and cold-water reef habitats, whose complex, 3-dimensional structures support a diversity of marine life by providing shelter and food (Harvey et al. 2018). Tropical coral reef degradation due to ongoing climate change and anthropogenic impacts motivated a variety of research to evaluate the role of connectivity in the resilience of marine benthic ecosystems, and our ability to quantify and forecast it (e.g. van Oppen & Gates 2006, Schleyer et al. 2018, van Woesik et al. 2022). Other taxonomic groups were less frequently reviewed (Fig. 6A). Yet, expanding our knowledge on these groups, particularly endangered, threatened, and/or protected taxa, such as mammals and reptiles, will improve our ability to put effective conservation measures in place.

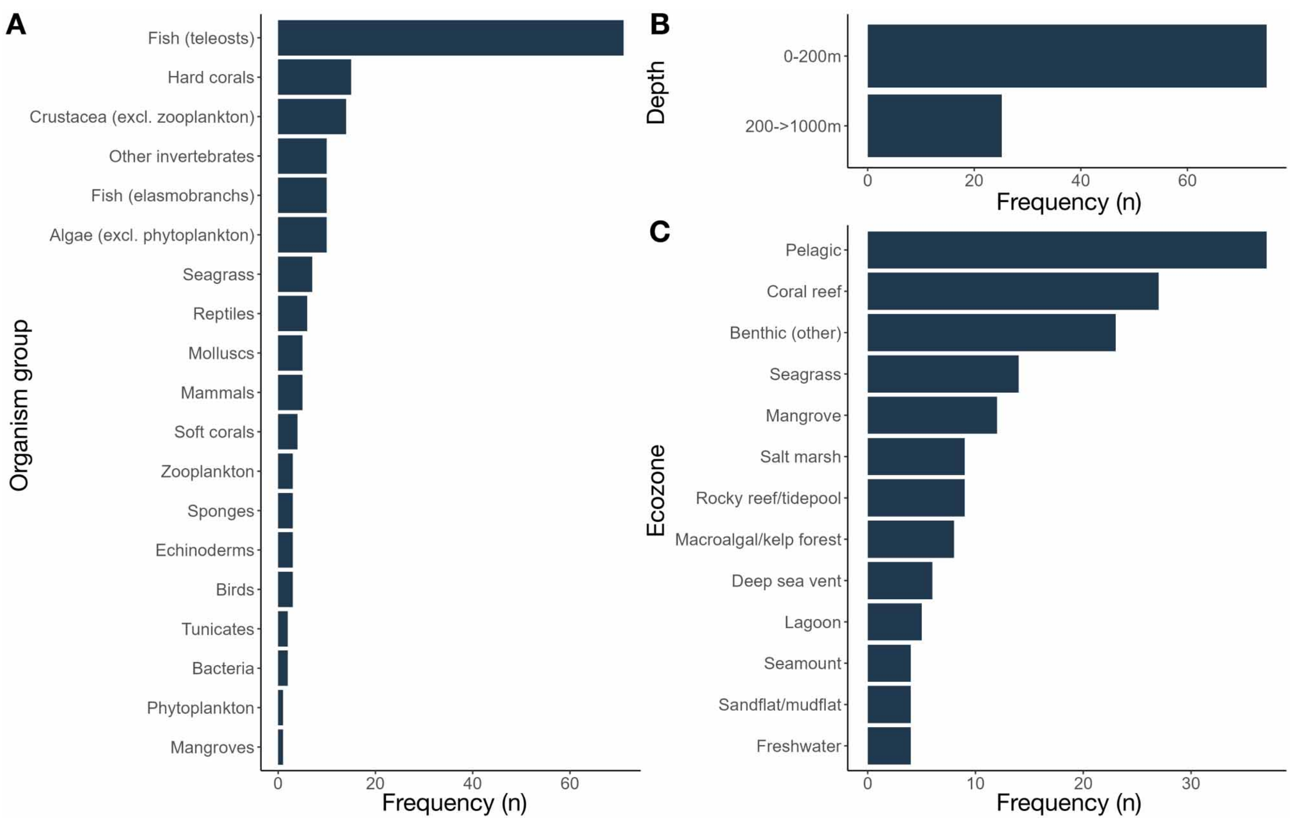

Fig. 6. Frequency of reviews that focused on particular (A) taxa (n = 94 excluded as either 'not specified' [n = 36] or '>3' [n = 58]), (B) depth strata (n = 87 excluded as 'not specified'), and (C) ecozones (n = 107 excluded as either 'not specified' [n = 54] or '>3' [n = 53]). Note that these numbers represent occurrences, and thus a single review could include multiple categories

Out of the 128 reviews that focused on a particular depth stratum, the shallowest habitats between 0 and 200 m strongly dominated (Fig. 6B). The disproportionate focus on the epipelagic zone (0–200 m) likely relates to the higher abundance of shallow-water species and the technological constraints associated with sampling in deep environments. However, as global demersal fisheries have progressively shifted from shallow- to deep-water species in recent decades (Morato et al. 2006), understanding population and life-cycle connectivity is crucial for the sustainable management of deep-water fisheries (e.g. Clark et al. 2010, Woodstock & Zhang 2022). Target species in these ecosystems are generally less resilient to exploitation due to slower population growth rates, delayed maturation, and lower productivity compared to shallow-water species (reviewed by Norse et al. 2012).

In the reviews where fewer than 4 ecozones were identified (162 studies), pelagic, coral reef, and benthic environments were the most frequently discussed (Fig. 6C). Conversely, seagrasses, mangroves, saltmarshes, rocky reefs/tidepools, macroalgae/kelp forests, deep sea vents, and lagoons were each represented in fewer than 15 reviews (Fig. 6C). The rarest ecozones featured in the selected reviews were seamounts, sand/mudflats, and freshwater environments (diadromous fishes only). The frequent focus on pelagic environments was mainly linked to (1) studies reviewing migratory connectivity in teleosts (e.g. Pope et al. 2010, Graves & McDowell 2015, Ashford et al. 2017), elasmobranchs (e.g. Sequeira et al. 2013, Jourdain et al. 2019, Zhang 2022), marine mammals (Liu et al. 2023, Palacios & Cantor 2023), and mixed-taxa migratory megafauna (e.g. Allan et al. 2021, McIvor et al. 2022); and (2) studies on larval dispersal (e.g. Pineda et al. 2010, Kaplan et al. 2017, Costantini et al. 2018, Bashevkin et al. 2020). While the extensive literature amassed in coral reef environments has been pivotal for incorporating connectivity data into MPA design (Green et al. 2015, Olds et al. 2016, Goetze et al. 2021), the extent to which these data can be generalised or extrapolated to other ecosystems is unclear, given that these iconic habitats are restricted to a narrow range of depths, temperatures, and geographic regions (Indian, Western Atlantic and Pacific Oceans, Oceania, Caribbean). Among the ecozones most frequently overlooked, seamounts deserve particular attention given the growing interest in deep-sea mining and fisheries, but information on the species and processes that these habitats support remains scarce (Clark et al. 2010). Also, while mudflats are one of the most common marine habitats globally and at the centre of current Blue Carbon discussions (Chen & Lee 2022), they are poorly represented in the connectivity literature (Fig. 6C). Understanding the connectivity patterns of mudflat-associated species and their role in carbon sequestration should be a high priority in the future.

3.3.6. Connectivity terminology

The top terms used to describe marine connectivity in the selected reviews were 'dispersal', 'population connectivity', 'migration', and 'connectivity', all exhibiting more than 40 occurrences (Fig. 7). A second group comprised terms with at least 20 occurrences, and included 'genetic connectivity', 'movement', 'gene flow', 'habitat connectivity', and 'larval dispersal'. The less common connectivity terms (<20 occurrences) tended to be represented by terminology featuring spatial ('seascape -', 'landscape -', and 'geographic connectivity') and organismal ('ecological -', 'demographic -', 'functional -', and 'biological

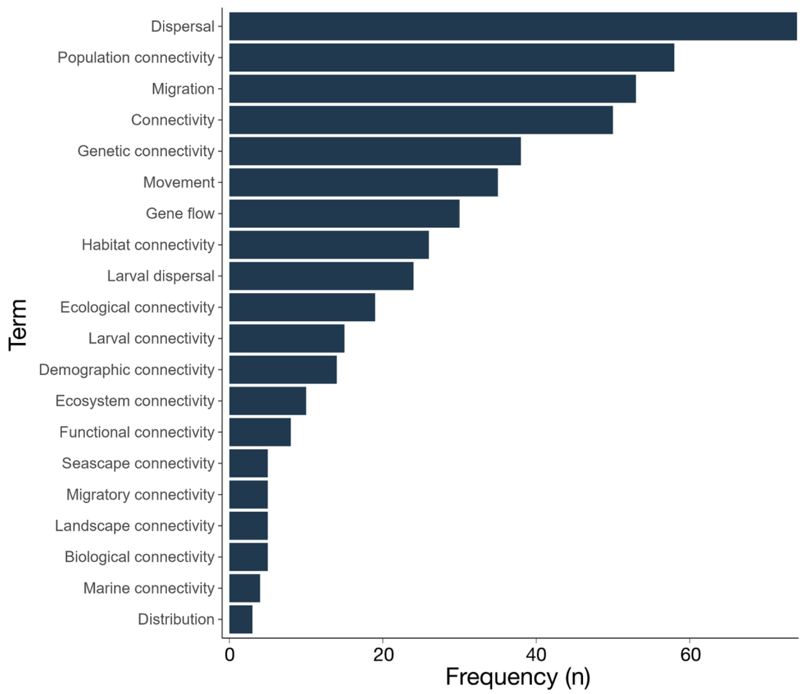

Fig. 7. Top 20 terms used to describe connectivity in the reviewed literature. The numbers represent term occurrences across all included reviews, and a single review may contain multiple terms. Note that the terms are presented as they appeared in the original sources

connectivity') concepts (Fig. 7). This wide variety of terms highlights the diverse nature of the field and its users and can potentially introduce confusion and misinterpretation. To improve clarity and foster cohesive research efforts, we recommend that all publications include clear definitions for the terms used, but more broadly for the community to work collaboratively to unify terminology and establish clear definitions for connectivity-related concepts across studies.

3.4. Future research directions and priorities

The future directions and research priorities for the field of marine functional connectivity identified in the reviews were grouped into 2 major themes: (1) 'Methods' and (2) 'Ecology and Application', interconnected by a third overarching theme 'Spatial and Temporal Scales and Coverage' (Fig. 8). The future avenues for the 'Methods' theme were primarily related to (1) 'Multiple/Integrated approaches' (advancing multidisciplinary approaches and data integration), (2) 'Modelling and data analysis' (progressing connectivity modelling and analysis methods), and (3) 'Sampling and analytical techniques' (advancing research methodologies, technology and data collection). In contrast, the future research priorities within the 'Ecology and Application' theme were focused on (1) 'Connectivity drivers' (understanding the biotic and abiotic drivers of connectivity), (2) 'Conservation and management' (using connectivity data to inform conservation, restoration and management), (3) 'Climate Change' (linking connectivity, adaptation, resilience and climate change) (Fig. 8). Notably, while the importance of incorporating connectivity data into marine spatial management (e.g. MPA design and fisheries stock assessment) is widely recognized, a significant operational gap still remains, with these data rarely being integrated (Balbar & Metaxas 2019).

About half of the reviews highlighted future research avenues belonging to 2 or 3 major themes (Fig. 8), while the other half typically only focused on 'Methods' or 'Ecology and Application'. The themes identified were not linked to review type; however, narrative and systematic reviews were roughly split between single and multi-themed reviews, and systematic reviews with meta-analysis were mainly focused on a single theme (Fig. 9).

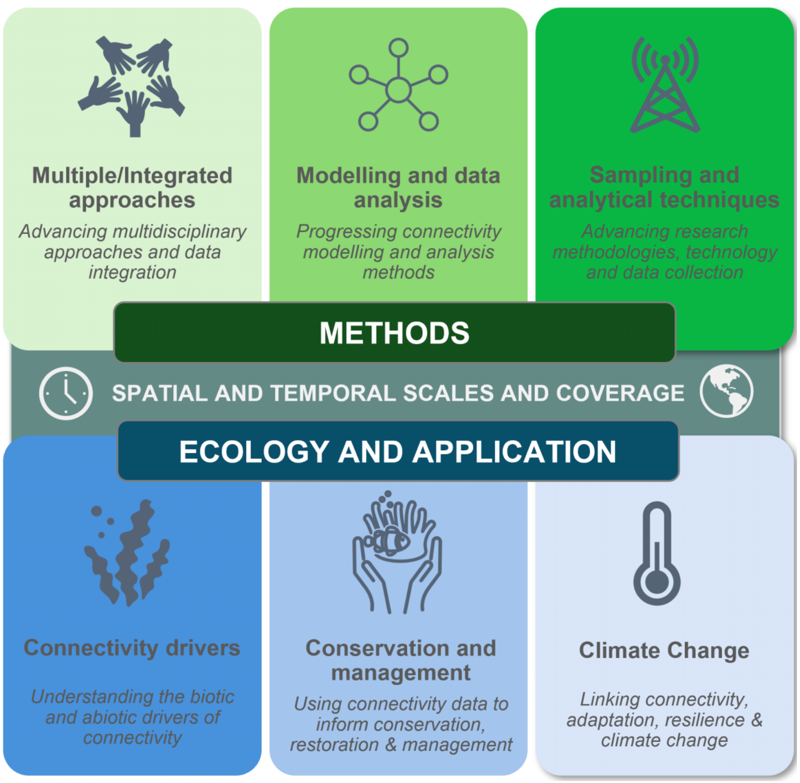

Fig. 8. The main research priorities identified by the 215 reviews were broadly categorized into 2 main themes: 'Methods' (green) and 'Ecology and Application' (blue), with 'Scales and Coverage' sitting at the intersection between the 2 main themes. The 2 main themes were each represented by 3 subcategories

Among the reviews highlighting research priorities in 'Methods' and 'Ecology and Application', most focused on one subcategory only, with 'Sampling and analytical techniques', 'Conservation and management', and 'Connectivity drivers' dominating (Fig. 9). Reviews addressing data collection and conservation and management were generally focused on specific taxa (e.g. Nordeide et al. 2011, Parsons et al. 2014, Docker et al. 2021, Farhadi et al. 2024), geographic areas (e.g. McCook et al. 2010, Calò et al. 2013, Torres-Pulliza et al. 2013, García-Machado et al. 2018) or ecozones (e.g. coral reefs, mangroves, van Oppen & Gates 2006, Berkström et al. 2012, Buelow & Sheaves 2015, Van der Stocken et al. 2019). Reviews highlighting 'Connectivity drivers' as a future research priority tended to be more focused on passive fluxes, such as larval dispersal (Kaplan et al. 2017, Alzate & Onstein 2022), nutrient subsidies (Zuercher & Galloway 2019), and carbon transfer (Hyndes et al. 2014).

A large number of reviews highlighted the importance of increasing

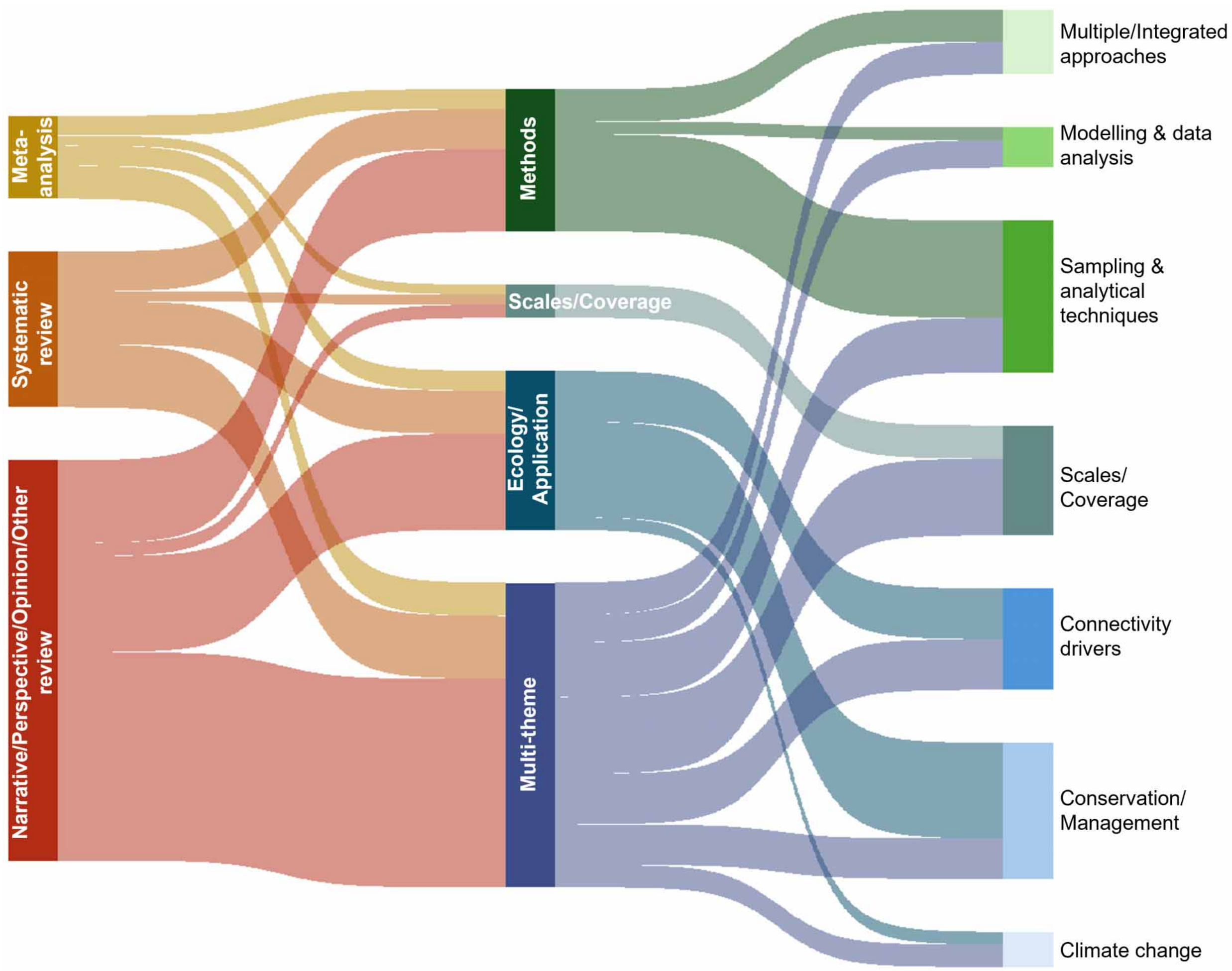

Fig. 9. Sankey diagram linking review types (column 1) with the research priority themes (column 2) and their various subcategories (column 3), as outlined in Fig. 8. Note that 'Scales/Coverage' was an overarching concept referred to by many reviews and was thus included at both theme and subcategory level

'Scales and Coverage' for improved data collection and multi-method approaches, and/or improving our understanding of connectivity drivers and the use of connectivity data in marine conservation and management. Reviews focused on 'Sampling and analytical techniques' that highlighted Scale and Coverage were often method-specific (Elsdon et al. 2008, Vrijenhoek 2010) while those focused on 'Connectivity drivers' were often investigating land−sea connectivity (Able 2005, Meynecke et al. 2007, Fang et al. 2018, Flitcroft et al. 2019) or genetic structure (Dawson et al. 2014, Riginos et al. 2016, Costantini et al. 2018).

Future directions and research priorities in modelling reviews were mainly linked to the themes of 'Ecology and Application' and 'Scales and Coverage' (Fig. 10). The 'Methods' theme and, in particular, 'Sampling and analytical techniques' were an important focus of future directions in reviews using multi-method approaches and chemical tracers, as well as for genetics (Fig. 10). Aspects related to spatiotemporal 'Scales and Coverage' were mentioned in reviews using all the different methodological approaches, albeit with varying degrees of importance (Fig. 10).

Overall, the identified research priorities spanned a range of themes, emphasizing the need to leverage methodological and technological advancements to improve data collection and integration, and advance multidisciplinary approaches and modelling capabilities. At the intersection between 'Methods' and 'Scales and Coverage', several reviews discussed how technological innovations and diverse collaborations are enabling increased sample sizes and geographic coverage, and diversifying the taxa and life stages being studied (Starrs et al. 2016, Jourdain et al. 2019, Pickens et al. 2021, Alvarado-Cerón et al. 2023, Lett et al. 2024). Expanding sampling coverage across both time and space enhances our understanding of connectivity patterns at various management-relevant

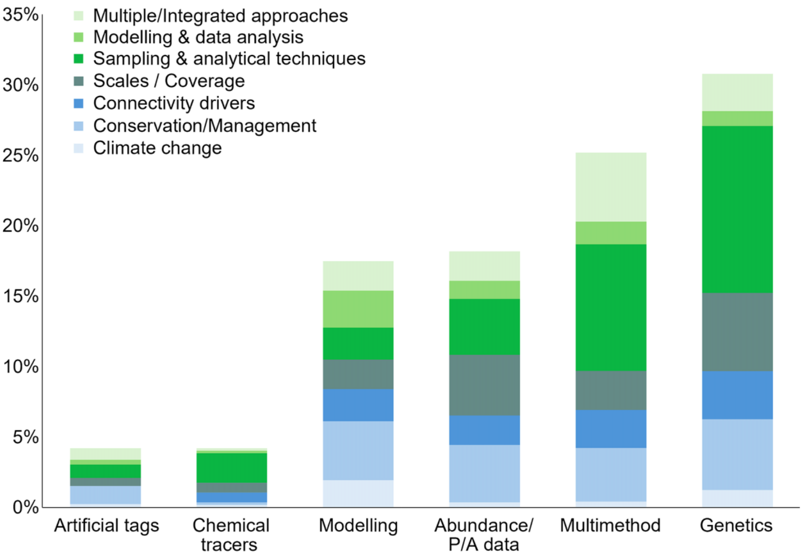

Fig. 10. Subcategories of research priorities suggested in reviews grouped by the different methods used to estimate connectivity and focused on in the reviews (P/A = presence/absence). Note that conceptual reviews and reviews with no information regarding methods (n = 62) are excluded

scales. It is equally important to maintain existing time-series to capture temporal variability and long-term trends, as well as to address geographic biases by strategically shifting attention to less-studied areas. Together, these approaches allow us to understand the factors driving connectivity patterns and assess their implications for population and community resilience. Methodological improvements, particularly in genetics, were frequently highlighted as research priorities (Dawson et al. 2014, Riesgo et al. 2015, Díaz-Ferguson & Hunter 2019, Pazzaglia et al. 2021), along with calls to develop new methods (Boström et al. 2011, Jahnke & Jonsson 2022, Tamaki 2023), improve and validate existing methods (Elsdon et al. 2008, Pickens et al. 2021), and improve and standardize sampling approaches (Clark et al. 2010, Lotterhos 2012, Edmunds et al. 2018). Many reviews also emphasized the need to embrace multidisciplinary (Sale & Kritzer 2003, Pope et al. 2010, von der Heyden et al. 2014, Crook et al. 2015, Starrs et al. 2016, Östman et al. 2017, Edmunds et al. 2018, Manel et al. 2019) and collaborative approaches (Costantini et al. 2018, Kot et al. 2023). Indeed, multidisciplinary approaches are key to achieving a comprehensive understanding of marine connectivity by integrating information across multiple spatiotemporal scales and compensating for limitations within the individual approaches (e.g. Reis-Santos et al. 2018, Brophy et al. 2020). Technological advances were mentioned for improving connectivity modelling and prediction accuracy, for example by enhancing computing and data analysis capacities (Cowen & Sponaugle 2009, Sutton 2013, van Sebille et al. 2018).

Under the 'Ecology and Application' theme, the most prominent and recurring research priority was to increase the application of connectivity data to marine conservation and management. This integration still needs to catch up in practice, partly due to the lack of access to tools and operational frameworks that facilitate collaboration between scientists and managers and promote incorporation of connectivity in marine spatial planning (Balbar & Metaxas 2019). In particular, many reviews highlighted the importance of connectivity in marine spatial planning, MPA design and effectiveness (Green et al. 2014, Umar et al. 2019, Wilson et al. 2020), habitat restoration (Maschinski & Wright 2006, Gilby et al. 2018, Smialek et al. 2021), and monitoring efforts (Jeffery et al. 2022, Swanborn et al. 2022, Liu et al. 2023). Several of these more conservation-focused reviews also emphasized the need for a better understanding of how connectivity influences the survival and capacity of species to adapt to global change (Magris et al. 2014, Bashevkin et al. 2020, Podda & Porporato 2023). This understanding is crucial for predicting the distribution and viability of marine populations, identifying critical habitats, and better understanding the links between connectivity and ecological resilience. Finally, many of the reviews grouped under 'Ecology and Application' highlighted the need to better understand the factors shaping (Miyake et al. 2017, Alzate & Onstein 2022, Ferrera-Rodríguez et al. 2024) and/or disrupting (Procaccini et al. 2007, Lotze et al. 2019) connectivity pathways, and their influence on subsidy dynamics (Hyndes et al. 2014, Zuercher & Galloway 2019).

In summary, spanning the 3 themes was an overall endorsement for building a more integrated research community and developing international networks that foster interdisciplinary collaboration, combine multiple lines of evidence, and harness new technological innovations. Building such a framework will boost our understanding of connectivity patterns and drivers and will also increase our ability to apply this knowledge and data outputs in management and conservation. Ultimately, synthesizing information from various sources is essential to understand and predict connectivity patterns across taxa, ecozones, and regions.

4. CONCLUSIONS

The systematic mapping performed in this paper highlighted large asymmetries in different aspects of marine connectivity research, with author networks dominated by the USA, Australia, and the UK, and a disproportionate interest in certain geographic areas (North Atlantic Ocean and areas around Australia), on iconic ecozones such as coral reefs, and on commercially valuable fishes and ecosystem engineers such as hard corals. Reviews also often focused on a particular method, despite many articles highlighting the importance of embracing multidisciplinary and integrated approaches to estimate connectivity at different spatiotemporal scales (e.g. ontogenetic vs. transgenerational).

Overall, marine connectivity represents a dynamic and rapidly evolving field, requiring transnational cooperation and innovative technologies to meet the growing demand for more accurate connectivity assessments, and more rigorous and holistic management and conservation plans for the ocean and its resources. Indeed, while many reviews highlighted the need to use connectivity data in marine spatial planning, there remains a significant gap between the science and the application in practice (Balbar & Metaxas 2019, Beger et al. 2022). To close this operational gap, there needs to be increased collaboration between scientists and managers, and for so-called 'boundary spanners' (Safford et al. 2017) to facilitate the translation of theoretical knowledge into practical conservation and policy actions. Based on the information synthesized across this review, we compiled 4 key recommendations:

(1) Advance and integrate the methods used to estimate connectivity. This will require increased capacity building — both across countries and research disciplines — as well as harnessing new technological innovations.

(2) Strengthen transnational and transboundary collaboration, particularly at a regional level (e.g. for countries sharing coastlines and marine resources). This will be key to achieving effective management and conservation plans at appropriate spatial scales.

(3) Increase the coverage, scale, and resolution of connectivity studies. This will be key to understanding trends in connectivity and forecasting future impacts of climate change on understudied areas, ecozones, and taxa, such as the South Atlantic and polar regions, in deep sea environments and mudflats, and in important keystone species that are not of commercial interest.

(4) Increase the application of connectivity data into marine management and conservation. With current unprecedented rates of global change, managers need to make informed decisions, particularly around habitat protection and fisheries management. As a community, we need to better support this decision-making process through adopting a unified suite of terms and definitions that support science translation, and developing simpler and more transparent frameworks, software, and tools.

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