



Deposited via The University of York.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/228099/>

Version: Published Version

Article:

Grazia Pennino, Maria, Nachón, D. J., Bamio, D. et al. (2025) A Decade of Mizer:A Systematic Review of Advancements and Applications of Size Spectrum Modeling in Aquatic Ecosystems. *Ecological Modelling*. 111241. ISSN: 0304-3800

<https://doi.org/10.1016/j.ecolmodel.2025.111241>

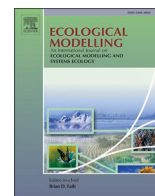
Reuse

This article is distributed under the terms of the Creative Commons Attribution (CC BY) licence. This licence allows you to distribute, remix, tweak, and build upon the work, even commercially, as long as you credit the authors for the original work. More information and the full terms of the licence here:

<https://creativecommons.org/licenses/>

Takedown

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.



A decade of mizer: A systematic review of advancements and applications of size spectrum modeling in aquatic ecosystems

M. Grazia Pennino^{a,*}, D.J. Nachón^b, D. Bamio^b, M. Cousido-Rocha^b, G. Delius^c,
F. Izquierdo^b, A. Paz^b, E. Abad^b, M.A. Torres^d, I. González Herraiz^e, M.P. Sampedro^e,
I.M. Rabanal^f, F. Velasco^f, P. Verisimo^e, Y. Vila^d, S. Cerviño^b

^a Instituto Español de Oceanografía (IEO-CSIC). Sede Central. Calle del Corazón de María, 8 28002 Madrid, Spain

^b Instituto Español de Oceanografía (IEO, CSIC). Centro Oceanográfico de Vigo. Subida a Radio Faro, 50-52 36390, Vigo Pontevedra, Spain

^c Department of Mathematics, University of York, York YO10 5DD, UK

^d Instituto Español de Oceanografía (IEO, CSIC). Centro Oceanográfico de Cádiz. Puerto Pesquero, Muelle de Levante S/N 11006, Cádiz, Spain

^e Instituto Español de Oceanografía (IEO, CSIC). Centro Oceanográfico de A Coruña. Paseo Alcalde Francisco Vázquez, 10 15001, A Coruña, Spain

^f Instituto Español de Oceanografía (IEO, CSIC). Centro Oceanográfico de Santander. Avda. Severiano Ballesteros 16 39004, Santander, Spain

ARTICLE INFO

Keywords:

Bibliometric analysis
Trophic interactions
Size-spectrum models
Ecosystem functioning

ABSTRACT

This systematic review examines the use of the *mizer* R package, a tool for multi-species size-spectrum modeling of marine ecosystems, over the past decade. We analyzed 43 publications, including peer-reviewed articles and academic theses, to highlight its contributions, strengths and limitations across various research domains. We grouped studies into five categories: fisheries management and policy, ecosystem dynamics and species interactions, methodological advances, climate change projections, and broad-scale ecological studies. Geographically, the majority of studies were concentrated in marine ecosystems, particularly in the North Sea and Haizhou Bay, China. Our visualizations, including maps, timelines, Sankey diagrams, and a scientific collaboration network, revealed strong international collaboration, with the UK, Australia, and the USA emerging as central hubs in the global research network. The *mizer* package has evolved through various extensions such as *therMizer*, *MizerShelf* and *MizerEvo*, broadening its application in studying climate impacts and eco-evolutionary dynamics. Overall, *mizer* has proven to be a valuable tool in advancing our understanding of aquatic ecosystems and informing sustainable management practices. Despite its widespread use in theoretical and exploratory studies, direct applications of *mizer*-derived strategies in real-world fisheries management remain limited, underscoring the challenges of integrating complex models into decision-making frameworks. We identify several opportunities to enhance *mizer*'s practical relevance, including the development of validation datasets and benchmarking protocols, comparative evaluation with other ecosystem models, structured sensitivity and uncertainty analyses, and incorporation of socio-environmental feedbacks. We also highlight key technical limitations, such as the absence of automated parameter optimization and the reliance on equilibrium-based model structure, which currently constrain its use in dynamic or data-limited contexts. Addressing these challenges will be critical for advancing the integration of size-spectrum modeling into ecosystem-based management and policy.

1. Introduction

Understanding the intricate dynamics of aquatic ecosystems remains a significant challenge in ecology. Size spectrum models (SSMs) have emerged as essential tools in this context, as they characterize the distribution of biomass across different organism sizes, providing critical insights into energy transfer and trophic interactions that underpin

ecosystem structure and function (Holt et al., 2014; Trebilco et al., 2013). Advancements in computational ecology have led to the development of *mizer* (Multi-Species Dynamic Size Spectrum Modelling in R), an R package designed for implementing and analyzing size spectrum models (Scott et al., 2014). *Mizer* offers a robust and versatile framework for modeling size-based interactions and energy flows in marine ecosystems, supporting both theoretical research and practical applications

* Corresponding author.

E-mail addresses: graziapennino@yahoo.it, grazia.pennino@ieo.csic.es (M.G. Pennino).

<https://doi.org/10.1016/j.ecolmodel.2025.111241>

Received 18 February 2025; Received in revised form 6 June 2025; Accepted 17 June 2025

Available online 26 June 2025

0304-3800/© 2025 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

in fisheries management.

The conceptual foundations of size spectrum models date back to the seminal works of Sheldon et al. (1972) and Dickie et al. (1987), who demonstrated the regularity of size distributions in aquatic communities and established the principles of allometric scaling. Their research revealed the inverse relationship between organism size and abundance, leading to the widespread adoption of size spectrum models in marine ecology (Andersen et al., 2009; Law et al., 2012). This concept, known as allometric scaling, refers to the predictable relationship between an organism's body size and its biological rates—such as metabolism, growth, and reproduction—typically following a power-law function (e. g., metabolic rate scales with body mass to the 3/4 power; West et al., 1997). Over recent decades, these models have been refined with advancements in metabolic theory, trophic dynamics, and ecosystem modeling (Pethybridge et al., 2018).

SSMs are based on the premise that ecological processes such as growth, predation, and mortality are intrinsically linked to organism size (Travers-Trolet et al., 2019). The biomass spectrum, which plots biomass distribution against organism size, generally follows a power-law distribution, reflecting size-dependent metabolic rates and energy transfer efficiencies. *Mizer* builds on this theoretical foundation by offering a comprehensive and user-friendly platform for simulating size-based interactions in aquatic ecosystems. Key features of *mizer* include: (1) modeling populations as continuous size distributions rather than discrete age classes, providing a more accurate representation of growth and mortality processes; (2) incorporating detailed formulations of energy acquisition, assimilation, and allocation to capture the energetic constraints driving trophic interactions and population dynamics; and (3) allowing users to customize model parameters and structures to fit specific ecological contexts and research questions. Additionally, *mizer* supports the integration of empirical data and other ecological processes, such as nutrient cycling and habitat effects.

One of the key aspects that sets SSMs—and particularly *mizer*—apart from other food web or community models is their mechanistic structure based on individual body size, rather than relying on predefined trophic levels or static predator-prey matrices. This differentiates them from frameworks like Ecosim with Ecosim, which are grounded in trophic compartments and mass-balance assumptions, or trophic niche models, which often rely on empirical diet matrices. In contrast, SSMs explicitly link body size to the fundamental drivers of population and community dynamics—growth, reproduction, and mortality—through size-based metabolic scaling. Growth results from energy acquisition via size-structured predation, reproduction emerges from surplus energy once maintenance costs are met, and mortality is governed by size-dependent predation and background processes. *Mizer* operationalizes these principles by simulating populations as continuous size distributions, enabling more flexible and biologically realistic dynamics. Moreover, its modular structure allows for extensions incorporating temperature effects (therMizer), eco-evolutionary change (MizerEvo), and complex benthic-pelagic shelf ecosystems (MizerShelf). These features make *mizer* especially well-suited for investigating emergent ecosystem properties, policy scenarios, and cross-scale ecological questions under a unified, size-based modeling framework.

Since its introduction in 2014, *mizer* has been widely adopted in fisheries science and marine ecology for its capacity to model the impacts of fishing, climate change, and other anthropogenic pressures on marine ecosystems (Hyder et al., 2015). By simulating the size structure and biomass distribution of fish populations, *mizer* aids in assessing ecosystem health and resilience, informing sustainable management strategies and conservation efforts. Furthermore, *mizer* provides a solid framework for exploring theoretical questions about the stability and dynamics of size-structured communities, enhancing our understanding of ecological and evolutionary processes.

This paper presents a systematic review of the literature on the use of the *mizer* package over the past decade, highlighting significant studies and their contributions to the field. By synthesizing findings from

various applications of *mizer*, this review seeks to provide a comprehensive understanding of its capabilities and the insights it has generated regarding aquatic ecological dynamics. As marine ecosystems face increasing pressures from human activities and climate change, the need for robust and adaptable modeling tools like *mizer* is more critical than ever. This systematic review will emphasize the notable contributions made by *mizer*-based research and identify gaps and future directions for further development and application of this valuable tool. Through a thorough analysis of existing literature, we aim to underscore *mizer*'s role in advancing our understanding of marine ecology and informing sustainable management practices.

2. Materials and methods

We conducted a systematic review following the PRISMA 2020 guidelines to synthesize peer-reviewed literature using the *mizer* R package. The search was performed on 18–19 June 2024 using the Web of Science and Scopus databases. We applied combinations of keywords such as "mizer" and "size spectrum models". The goal was to identify original research articles or theses that explicitly employed the *mizer* package as a central modeling framework.

The search yielded an initial pool of 89 records. After removing duplicates and screening titles, abstracts, and full texts, we retained a final set of 43 studies for detailed analysis. Although screening was conducted at both the title/abstract and full-text levels, we did not systematically document excluded records, as our main objective was to characterize the literature that effectively used *mizer*. This selection process is transparently depicted in the PRISMA flow diagram (Supplementary Fig. S1).

We extracted the following metadata from each included study: (i) year of publication, (ii) journal name, (iii) author affiliation country (ies), (iv) geographic area of application, and (v) primary research topic (s). Articles were grouped into five broad research themes: "applications in fisheries management and policy", "modeling ecosystem dynamics and species interactions", "methodological advances and model validation", "climate change and environmental impact projections", and "broad-scale ecological and theoretical studies". When articles fit more than one category, multiple assignments were allowed; accordingly, results are presented in relative proportions (%).

These five categories were identified through an iterative coding process during the full-text review. Each study was evaluated based on its research aims, methodologies, and main findings. The resulting themes reflect both the major areas of application of the *mizer* framework and the evolution of the package itself. Our goal was to capture the full range of uses, from applied management tools to theoretical model development, in a structure that balances comprehensiveness with interpretability.

To enrich our synthesis, we additionally recorded whether each study (i) calibrated the model to empirical data, (ii) employed any official *mizer* extensions (e.g., therMizer, MizerEvo, MizerShelf), and (iii) focused on a specific ecosystem type (e.g., shelf, open ocean, estuary, or inland system). This information is compiled in Supplementary Table S1.

Results were visualized through maps, bar plots, and Sankey diagrams to illustrate article frequencies and thematic trends. We also constructed a country-level collaboration network, where nodes represent countries and edges indicate co-authorship relationships. The network layout was optimized using the Fruchterman–Reingold algorithm to spatially group countries based on collaboration intensity.

Finally, we applied snowballing techniques (reviewing citations within the included studies) and examined conference materials and academic theses to capture additional relevant works.

All analyses and visualizations were performed in R version 4.2.0 (R Core Team, 2023), using the packages: "ggplot2" (Wickham et al., 2016), "mapdata" (Deckmyn, 2018), "networkD3" (Allaire et al., 2017), and "igraph" (Csardi & Nepusz, 2006).

All R-code used for the analysis is openly available at: <https://github.com/graziapennino/A-Decade-of-Mizer-A-Systematic-Review-git>

3. Results

In this section, we provide the results of the bibliometric analysis of *mizer*-related literature (section 3.1) and an overview of the key contributions of this literature by research topic (section 3.2).

3.1. Bibliometric analysis

A total of 43 studies were retained for review, all published between 2014 and 2024 (see Supplementary Material, Table S1). Among them, one was a master dissertation and two were doctoral theses that used *mizer* as primary tool for their studies (Supplementary Material, Table S1). The number of publications has increased steadily over the decade, with an average of approximately four articles per year, peaking in 2022 (Fig. 1).

The majority of studies focused on applications in fisheries management and policy (23 %) and modeling ecosystem dynamics and species interactions (23 %). These were followed by research on methodological advances and model validation (19 %), and climate change and environmental impact projections (19 %). Broad-scale ecological and theoretical studies comprised 16 % of the articles (Fig. 1).

Geographically, most studies concentrated on marine ecosystems, with only three focusing on freshwater realms. The North Sea (Northern Europe) emerged as the most studied region ($n = 9$), followed by Haizhou Bay, China ($n = 5$) (Fig. 2).

The Sankey diagram (Fig. 3) illustrates the distribution of research topics across different countries, providing insights into international collaboration and research focus areas. Notably, the United Kingdom (UK) and Australia are prominently involved in multiple research categories, particularly in “Applications in Fisheries Management and Policy” and “Methodological Advances and Model Validation”. China and the United States also exhibit substantial contributions, especially in “Modeling Ecosystem Dynamics and Species Interactions” and “Climate Change and Environmental Impact Projections”. Other countries, such as Denmark, Sweden, and Canada, show more specialized involvement,



Fig. 1. Yearly and cumulative number of publications applying the *mizer* R package, categorized by primary research focus. The cumulative curve represents the total number of studies published from 2014 through each year.

often contributing to specific categories such as “Broad-Scale Ecological and Theoretical Studies” and “Applications in Fisheries Management and Policy”. This visualization highlights both the diverse geographical scope of research in these fields and the overlap in research categories across different countries. Countries with a broader scope of collaboration, such as the UK and Australia, are involved in a wide array of research topics, suggesting leadership in interdisciplinary research within ecosystem management and environmental studies.

The collaboration network included 22 nodes (countries) and 104 unique edges (collaborations) (Fig. 4). The average node degree was 9.45, indicating that each country collaborated with about four others on average. The edge density was 0.45, suggesting a moderately connected network. The global clustering coefficient was 0.72, indicating a moderate tendency for countries to form collaborative clusters. The diameter of the network was 3, reflecting the longest minimum path between any two countries. Together, these metrics indicate a moderately cohesive and collaborative global network of researchers using the *mizer* package. In particular, the UK, Australia, and the US emerged as central nodes in the network, demonstrating the highest number of collaborations and contributions to literature. These countries are connected by numerous edges, reflecting repeated co-authorship across multiple publications. China, Denmark, and Canada also play significant roles in the network, particularly in collaboration with larger hubs such as the UK and the USA. The size of the nodes represents the number of publications from each country, with the UK, Australia, and the USA contributing the most. The edge thickness corresponds to the frequency of collaborations, highlighting strong links between the UK and Australia, as well as between the USA and China. This network visualization underscores the global and collaborative nature of research using size spectrum modeling, with several countries playing pivotal roles in advancing the field.

Mizer was utilized in publications across 23 different journals. The journals Fisheries Research, Fish and Fisheries, Ecological Modelling, and Marine Ecology Progress Series each had the highest number of publications ($n = 4$). Several journals, including Journal of Applied Ecology, ICES Journal of Marine Science, and Canadian Journal of Fisheries and Aquatic Sciences, featured two papers each, while others like PLoS ONE, Marine Policy, and Ecological Indicators each published one paper. This distribution highlights a preference for journals specializing in fisheries science and marine ecology (Fig. 5).

3.2. *Mizer* contributions overview

An overview of the main literature contributions by research topic is provided in this section. First, contributions related to “fisheries management and policy applications” are reviewed, and then key aspects of the literature on “modeling ecosystem dynamics and species interactions” are discussed, followed by a review of the literature on “climate change”. Next, relevant contributions from the literature classified as “broad ecological and theoretical studies” are also described. Finally, an overview of methodological advances and model validation, along with a summary of major updates to the *mizer* package, are provided.

3.2.1. Applications in fisheries management and policy

The application of *mizer* in fisheries management and policy has proven its utility across various decision-making contexts (Fig. 6). Blanchard et al. (2014) were pioneers in demonstrating how *mizer* could evaluate trade-offs between fisheries yield and conservation goals. Their work emphasized the potential conflicts between different management objectives and highlighted the value of size-spectrum models in balancing these competing interests. Expanding on this, Zhang et al. (2016a) utilized *mizer* to assess the long-term implementation of Maximum Sustainable Yield (MSY) in an ecosystem-based framework. By incorporating trophic interactions and uncertainties, they revealed that traditional single-species MSY strategies might be inadequate for

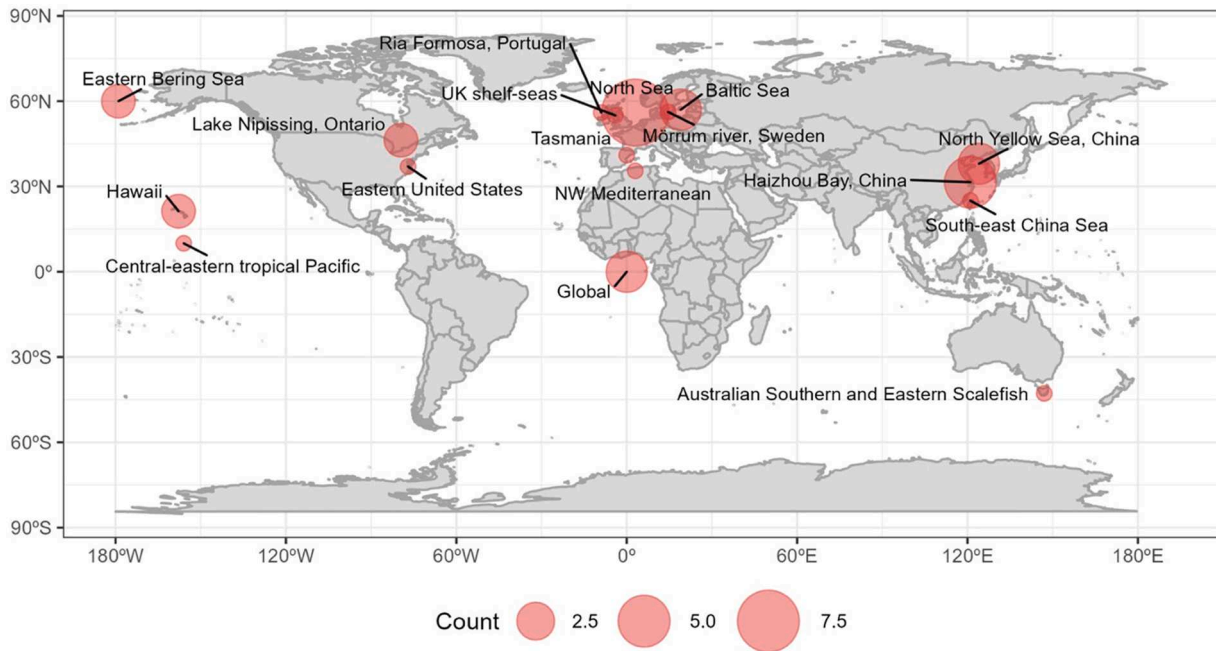


Fig. 2. Geographic distribution of case studies using the mizer R package. Circle size indicates the total number of studies conducted in each region. Colors denote the dominant research theme assigned to each study site.

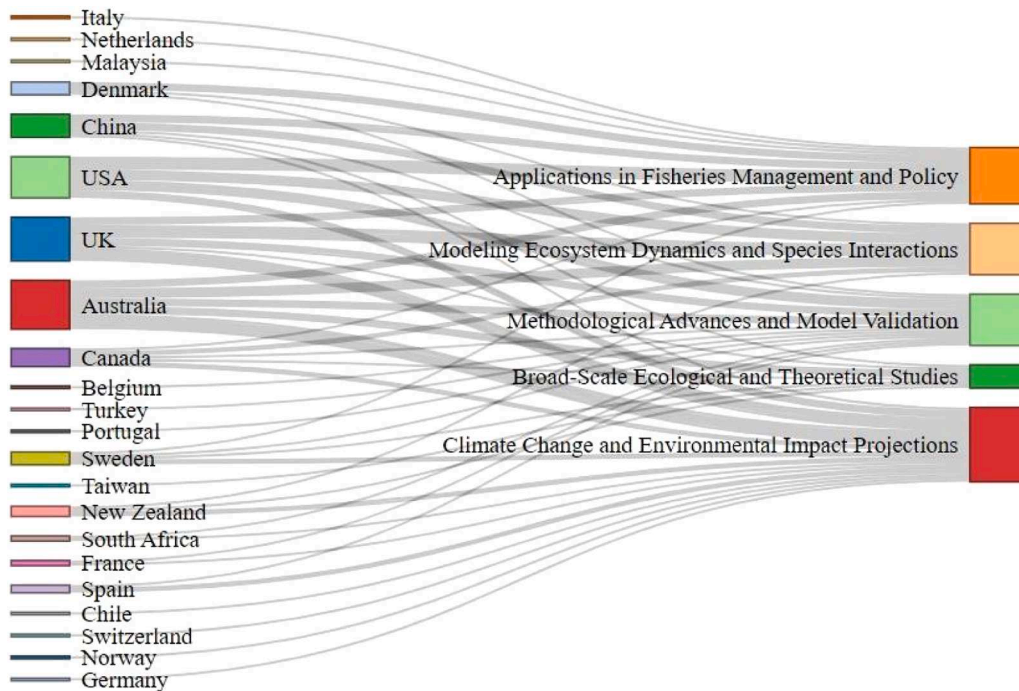


Fig. 3. Sankey diagram between the countries and research topics.

sustainability in complex ecosystems. In a related study, Zhang et al. (2016b) showed how fisheries closures, implemented within a size-spectrum model, could successfully rebuild depleted stocks. Jacobsen et al. (2017) further extended the use of *mizer* by investigating fisheries efficiency at the ecosystem level, finding an increase in efficiency, which raised concerns about its effects on ecosystem resilience. Likewise, Zhang et al. (2018) explored the destabilizing impact of intensive fishing on fish communities, particularly when top predators are removed, further demonstrating the ecosystem-wide implications of fishing pressure. Spence et al. (2018) proposed a general framework that

integrates different ecosystem models, including *mizer*, to enhance ecosystem-based management. Their approach enabled more robust predictions, improving the quality of fisheries management decisions. Robinson et al. (2022) introduced a novel concept of managing fisheries for maximum nutrient yield, rather than focusing solely on biomass, proposing that this method could promote more holistic management strategies aligned with human health objectives.

In the context of mixed fisheries, Wo et al. (2022) advocated for a multispecies Total Allowable Catch (TAC) strategy, showing how size-spectrum models can address the complexities inherent in

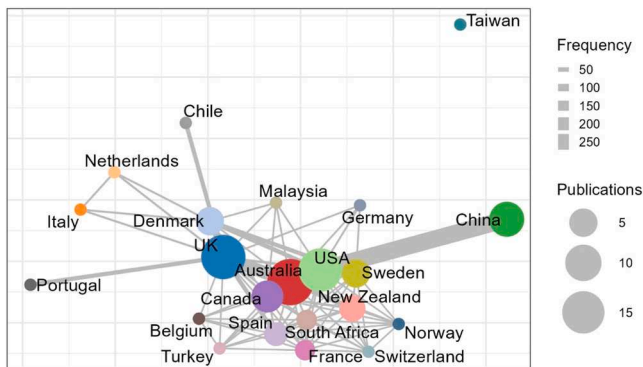


Fig. 4. Country-level collaboration network of studies using the *mizer* package. Node size is proportional to the number of publications from each country. Edges represent co-authored publications between countries, with edge thickness indicating the frequency of collaborations—thicker edges denote more frequent co-authorships.

multispecies fisheries. De Juan et al. (2023) applied *Mizer* to Mediterranean mixed demersal fisheries to examine how improving selectivity and reducing discards could benefit both ecological sustainability and

economic outcomes. Finally, Wo et al. (2024) proposed the use of species portfolio schemes as a strategy to mitigate the risks of over-exploitation, highlighting the importance of diversifying fisheries portfolios to enhance stock resilience.

3.2.2. Modeling ecosystem dynamics and species interactions

Equally prominent is the use of *mizer* for modeling ecosystem dynamics and species interactions (Fig. 7). Studies have shown that *mizer* effectively captures the complexities of consumer biomass, size structure, and production across global marine ecosystems (Jennings & Collingridge, 2015). This broad applicability is further supported by Zhang et al. (2015), who emphasized the role of uncertainty in multi-species models, underscoring the importance of incorporating uncertainties in predictions. Andersen et al. (2016) provided a theoretical foundation for size spectrum models, which Datta and Blanchard (2016) extended by highlighting the impact of seasonal variability on size spectrum dynamics. Spence et al. (2016) addressed parameter uncertainty, offering insights into improving model accuracy, while Zhang et al. (2016c) demonstrated *mizer*'s adaptability in data-poor environments. Additionally, empirical studies by Szuwalski et al. (2017) and Wo et al. (2020) revealed the model's capacity to analyze trophic cascades and regional fisheries dynamics, respectively. Sensitivity analyses by Benoit et al. (2021) further refined our understanding of influential

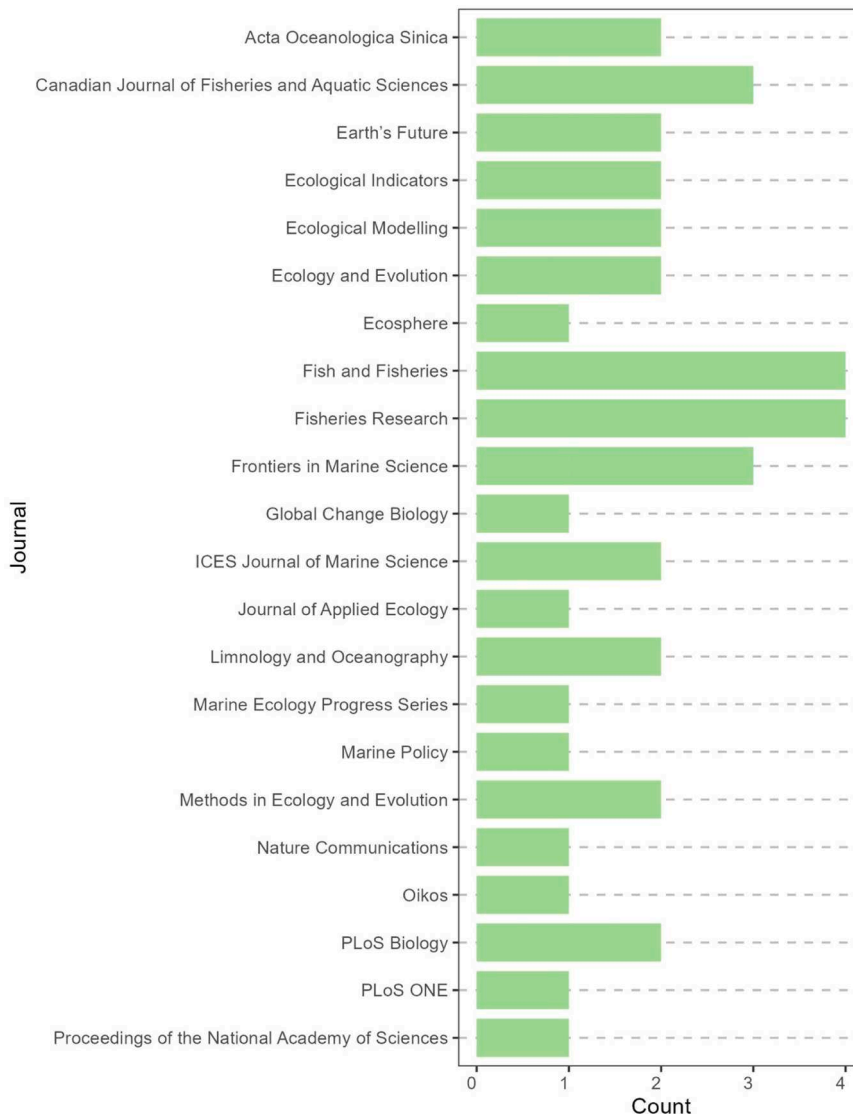


Fig. 5. Number of articles applying the *mizer* package published in each journal.

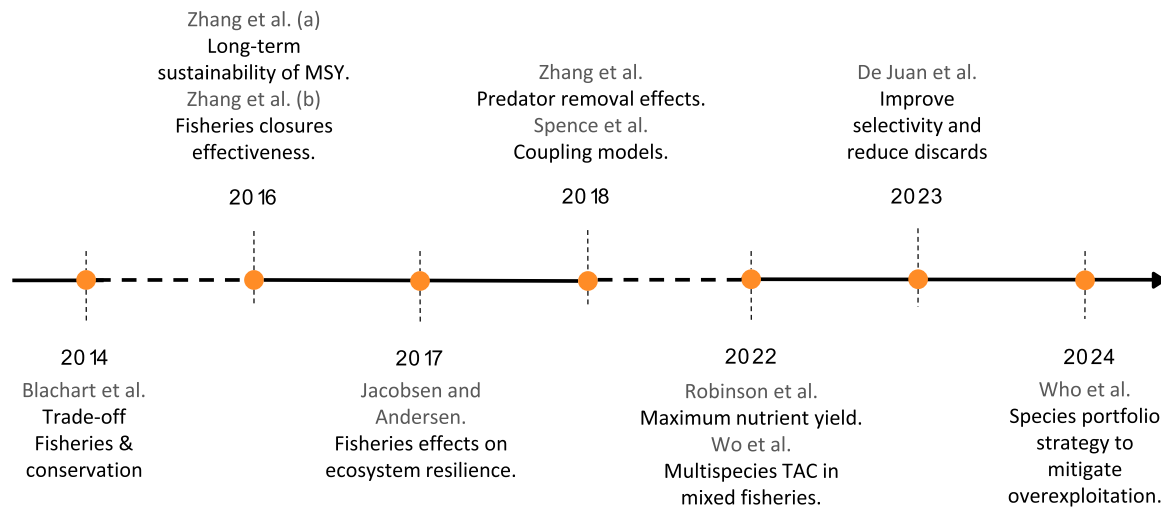


Fig. 6. Timeline of studies applying the mizer package in fisheries management and policy. Each point represents a publication, colored by research category. Dashed lines indicate non-consecutive years to accurately reflect the temporal distribution of publications.

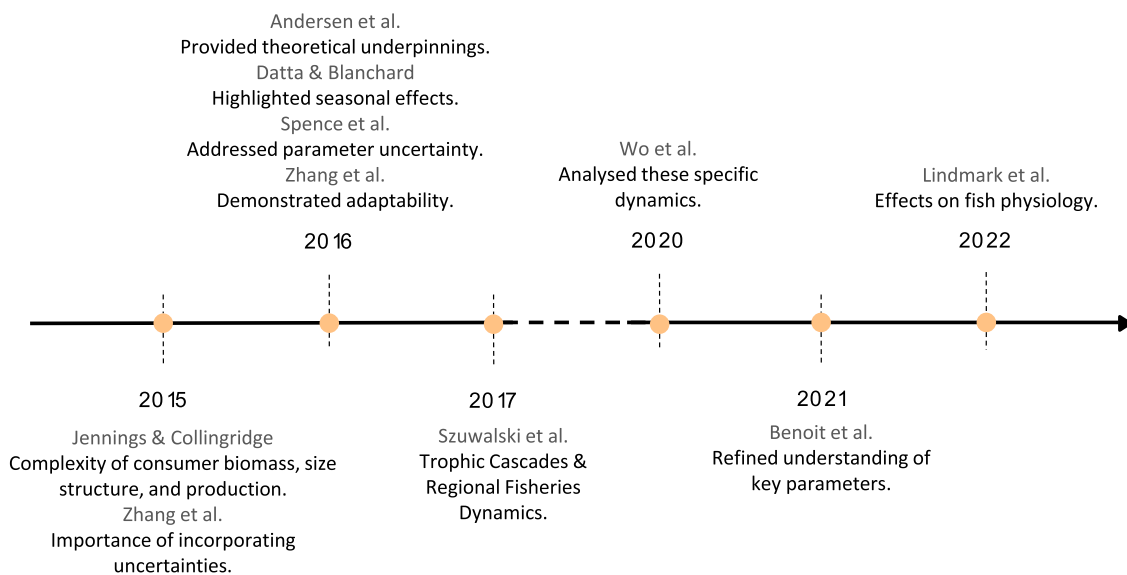


Fig. 7. Timeline summarizing studies that applied mizer to model ecosystem dynamics and species interactions. Dashed lines indicate non-consecutive years to accurately reflect the temporal distribution of publications.

parameters in ecosystem models, and Lindmark et al. (2022) highlighted the implications of climate change on fish physiology and resource abundance. Collectively, these studies illustrate *mizer*'s robust ability to model complex ecosystem interactions and environmental impacts, while also acknowledging challenges such as parameter uncertainty and data limitations.

3.2.3. Climate change and environmental impact projections

The application of the *mizer* model to study the impact of climate change on marine ecosystems has provided valuable insights into how future environmental changes may influence fish communities and ecosystem dynamics. Woodworth-Jefcoats et al. (2019) highlighted the significance of considering cumulative stressors, such as warming temperatures and overfishing, in predicting future ecosystem states. Reum et al. (2019) demonstrated that species-specific diet shifts due to warming could mitigate some negative impacts of climate change by potentially lengthening food chains and buffering trophic cascades. Forestier et al. (2020) investigated the interplay between predation, fishing pressures, and climate-induced changes in predator-prey

dynamics, revealing potential shifts in species maturation sizes and reproductive strategies. Reum et al. (2020) further assessed future climate impacts on the Eastern Bering Sea food web, identifying potential shifts in species composition and biomass distribution under different climate scenarios. Lindmark (2020) contributed to understanding how temperature affects growth rates and size structures, emphasizing the need to consider these changes across trophic levels. Hansen et al. (2023) explored the effects of dam removal on fish communities, highlighting varying impacts based on environmental conditions and species characteristics. Ortega-Cisneros et al., 2025 developed an integrated approach for simulating climate change impacts at both global and regional scales, bridging the gap between broad-scale projections and local management needs. Finally, Reum et al. (2024) underscored the sensitivity of climate impact projections to temperature-dependent assumptions, stressing the importance of carefully considering these factors in model projections.

3.2.4. Broad-scale ecological and theoretical studies

Mizer has been employed in broader ecological and theoretical

studies, constituting 16 % of the reviewed articles. These studies, including those by Hyder et al. (2015) and Canales et al. (2020), explore fundamental ecological questions and theoretical dynamics, expanding our understanding of long-term ecosystem changes and fisheries management. Theoretical studies by Forestier (2021) and Audzijonyte et al. (2023) explored eco-evolutionary dynamics and sea floor productivity, respectively. The integration of fleet dynamics by Novaglio et al. (2022a and 2022b) represents a novel approach, offering new perspectives on mixed fisheries management.

3.2.5. Methodological advances and model validation

The methodological advances and model validation efforts in the application of *mizer* have substantially enhanced its accuracy, applicability, and utility in ecosystem modeling. Edwards et al. (2017) and Edwards et al. (2020) have made significant contributions by refining techniques for fitting size spectra to empirical data, improving the precision of model estimates and addressing biases associated with data bin structures. Fu et al. (2019) advanced the development of ecological indicators tailored for management purposes, ensuring that these indicators are sensitive and specific enough to capture ecosystem responses effectively. West (2019) provided a comparative analysis of *mizer* and Ecopath models, offering insights into their respective strengths and limitations for different management scenarios. Clements et al. (2019) utilized *mizer* to identify early warning signals of ecosystem recovery, contributing to proactive management strategies for over-exploited systems. Spence et al. (2021) demonstrated through ensemble modeling that sustainable fishing practices could significantly improve marine ecosystem health, supporting the case for ecosystem-based fisheries management. Benoit et al. (2022) extended the application of size-spectrum models to freshwater ecosystems, broadening their relevance and demonstrating their versatility. Falciani et al. (2022) linked size-spectrum models to blue carbon management, illustrating how these models can integrate fisheries management with climate change mitigation efforts.

3.2.6. *Mizer* evolution and extensions

The core *mizer* package was introduced as an R package for implementing size-spectrum models in 2014, allowing for the simulation of marine ecosystems by modeling size-based predator-prey interactions and the impacts of fishing (Fig. 8). In 2016, significant updates were made to the *mizer* package, refining its capacity to model multiple species and size classes, thereby improving the accuracy and flexibility of ecosystem simulations. In 2019, Woodworth-Jefcoats et al. (2019), developed the *therMizer* extension that integrates the effects of temperature on metabolic rates and, consequently, on the growth and survival of marine species. This addition is particularly relevant in the context of climate change, as it allows researchers to model the impacts of varying temperature regimes on marine ecosystems.

In 2020, Forestier et al. (2020) developed the *MizerEvo* extension to incorporate eco-evolutionary dynamics into the *mizer* framework. This extension enabled the modeling of evolutionary changes in species

traits, such as maturation size, in response to selective pressures like fishing and predation. In the same year, Edwards et al. (2020) contributed to methodological improvements by addressing biases related to the bin structure of data within size-spectrum models, enhancing the accuracy of model fitting processes. Forestier (2021) further developed *MizerEvo*, emphasizing the importance of eco-evolutionary processes in size-structured ecosystems, and demonstrated how this extension could be applied to study species' traits evolution. The *MizerShelf* extension was developed as part of the study by de Juan et al. (2023). This extension allows for the application of size-spectrum models to shelf ecosystems, which are characterized by high species diversity and complex food webs.

4. Discussion

The review of the literature on the use of the *mizer* R-package reveals a substantial and growing body of work that underscores its versatility and impact across various ecological and fisheries management contexts. A total of 43 studies published between 2014 and 2024 demonstrate a steady increase in the application of *mizer*, with peaks in publication frequency highlighting its rising importance in research. *Mizer* has been widely adopted for various applications, including fisheries management and policy, modeling ecosystem dynamics and species interactions, and climate change impact projections. Geographically, the majority of research has concentrated on marine ecosystems, with notable contributions from regions such as the North Sea and Haizhou Bay, China. International collaboration is evident, with the UK, Australia, and the US emerging as central nodes in the research network, reflecting their significant roles in advancing the field. The wide range of journals publishing *mizer*-related research further underscores its broad applicability, particularly within the domains of fisheries science and marine ecology.

In light of this growing body of work, and in response to recent advances in ecological modeling, we contextualize our review within the landscape of individual- and size-based approaches. We position our work in contrast to complementary studies such as those by Woodson et al. (2024) and Duskey (2023). While Woodson et al. developed an individual-based model (IBM) to explore population and stock dynamics at fine physiological and behavioral resolution, and Duskey integrated metabolic modeling to simulate fish responses under hypoxic stress, our work takes a broader, synthetic approach. We offer a systematic review of the *mizer* R package, a tool specifically designed for multi-species size-spectrum modeling at the population and community level. This allows for efficient simulation of trophic dynamics, energy flow, and anthropogenic pressures across aquatic ecosystems, offering insights at spatial and temporal scales relevant to ecosystem-based management.

Unlike IBMs, which capture individual variability and physiological detail, size-spectrum models like *mizer* rely on mechanistic rules linked to body size and metabolic scaling to model emergent patterns in community structure and function. This makes them particularly suited for exploring general ecological principles, projecting ecosystem

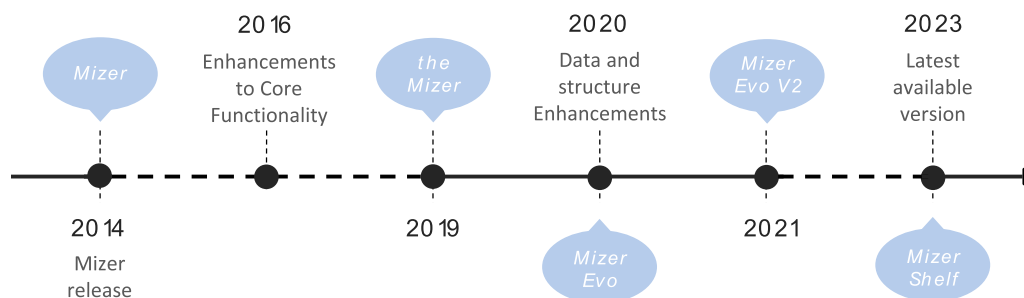


Fig. 8. Timeline of methodological developments and extensions of the *mizer* package over the past decade. Dashed lines indicate non-consecutive years to accurately reflect the temporal distribution of publications.

responses to external drivers, and informing fisheries and conservation policy.

Furthermore, our review highlights the evolution of *mizer* through recent extensions, such as *MizerEvo* and *therMizer*, which incorporate eco-evolutionary processes and temperature dependence, respectively. These developments illustrate how size-spectrum modeling is progressively bridging the gap between individual-based physiology and ecosystem-level dynamics. We also identify opportunities for integrating *mizer* with IBMs and physiologically structured models, such as those explored by [Duskey \(2023\)](#), to enhance ecological realism and improve the prediction of complex responses to climate and anthropogenic stressors.

Finally, we align our synthesis with the conceptual gaps outlined by [Jakeman et al., \(2024\)](#). Our work contributes directly to the research agenda proposed in [Section 4](#) of that publication by showcasing how structured literature reviews can support model transferability, good practices, and cross-disciplinary dialogue.

The review of the *mizer* package highlights its significant strengths and limitations across various applications, including fisheries management, climate change impacts, and theoretical studies. One of *mizer*'s key strengths is its flexibility and robust theoretical foundation, which enable detailed modeling of size-based predator-prey interactions and energy flows within marine ecosystems. This versatility allows *mizer* to simulate the impacts of fishing, environmental changes, and other anthropogenic pressures effectively ([Hyder et al., 2015](#); [Scott et al., 2014](#)).

In fisheries management, *mizer* has proven its utility by evaluating trade-offs between yield and conservation goals, assessing Maximum Sustainable Yield (MSY) strategies, and managing fisheries closures to rebuild depleted stocks ([Blanchard et al., 2014](#); [Zhang et al., 2016a, 2016b](#)). The model's adaptability extends to ecosystem-level considerations, with applications exploring fisheries efficiency and the impacts of fishing pressure on fish communities ([Jacobsen & Andersen, 2017](#); [Zhang et al., 2018](#)). However, challenges persist, particularly in managing multispecies interactions and integrating innovative approaches such as nutrient yield management and species portfolio schemes ([Robinson et al., 2022](#); [Wo et al., 2022](#); [Wo et al., 2024](#)). The model's complexity can hinder its use for tactical advice in stock status assessment and management actions, indicating a need for further integration and validation efforts. The insights generated by *mizer* are invaluable for conditioning operating models (OMs) within Management Strategy Evaluations (MSEs), where they can inform the development of more robust and resilient management strategies ([Edwards et al., 2020](#); [Reum et al., 2020](#)).

The category of modeling ecosystem dynamics and species interactions benefits from *mizer*'s ability to predict consumer biomass, size structure, and production across diverse environments ([Jennings & Collingridge, 2015](#)). The model's ability to incorporate uncertainties and adapt to data-scarce environments enhances its reliability ([Zhang et al., 2015, 2016c](#)). However, challenges such as parameter uncertainty and environmental variability continue to pose limitations ([Benoit et al., 2021](#); [Spence et al., 2016](#)). Addressing these issues through ongoing refinement is crucial for maximizing *mizer*'s effectiveness in understanding complex ecosystem interactions.

In terms of climate change projections, *mizer* excels at integrating multiple stressors and providing nuanced predictions of ecosystem states under various climate scenarios ([Reum et al., 2019](#); [Woodworth-Jefcoats et al., 2019](#)). The model's flexibility in exploring species-specific responses and scaling relationships under climate pressures further demonstrates its utility ([Forestier et al., 2020](#); [Lindmark, 2020](#)). Nonetheless, projections can vary significantly based on assumptions and environmental conditions ([Hansen et al., 2023](#); [Reum et al., 2024](#)), emphasizing the need for careful consideration of model inputs to ensure accuracy. Future work could focus on incorporating more detailed climate models and exploring a wider range of climate scenarios ([Reum et al., 2020](#)). This will enable researchers and policymakers to better

understand and anticipate the impacts of climate change on marine and freshwater ecosystems.

Theoretical studies employing *mizer* have advanced our understanding of fundamental ecological dynamics and long-term changes, providing valuable insights into eco-evolutionary processes and species interactions ([Canales et al., 2020](#); [Forestier, 2021](#); [Hyder et al., 2015](#)). The integration of novel concepts like fleet dynamics ([Novaglio et al., 2022a](#)) illustrates *mizer*'s adaptability to new research questions. However, integrating complex variables and translating theoretical advancements into practical applications remain challenges that require further validation and refinement.

Methodological advances, including the development of extensions like *MizerEvo* and *therMizer*, have enhanced *mizer*'s utility by addressing biases, refining parameter estimation, and integrating temperature effects ([Edwards et al., 2017, 2020](#); [Forestier et al., 2020](#); [Woodworth-Jefcoats et al., 2019](#)). Despite these improvements, challenges persist in model calibration and data quality, which can impact prediction accuracy ([Edwards et al., 2020](#)). Future research should focus on expanding *mizer*'s applications, integrating emerging technologies, and fostering interdisciplinary collaboration to address complex ecological and management questions.

Looking ahead, several promising and actionable directions for future research emerge from this review. First, applying *mizer* to underrepresented systems, such as tropical marine and freshwater environments, should not be viewed as a simple spatial extension, but rather as a critical strategy for testing the model's transferability, robustness, and adaptability across contrasting ecological contexts. Exploring biogeographic variation allows researchers to evaluate how the model performs under differing environmental regimes, trophic structures, and life-history traits, thereby identifying both its strengths and potential limitations in generalization. Second, integrating emerging technologies, including environmental DNA (eDNA), satellite remote sensing, and high-resolution environmental monitoring, could enhance the accuracy and resolution of model parameterization and validation. Another priority is the development of standardized libraries of life-history traits and feeding parameters for key ecosystem types, which would facilitate model comparability, transferability, and reproducibility across studies. Finally, coupling *mizer* with complementary frameworks, such as individual-based models, trophic network models, or spatially explicit approaches, offers an opportunity to capture cross-scale ecological dynamics and improve the ecological realism of simulations.

There is also potential for developing new features and extensions to address specific ecological and management questions, including the impacts of invasive species and habitat degradation. Increasing interdisciplinary collaboration will be essential to tackling complex environmental challenges. By combining expertise from fields such as economics, biology, sociology, and climate science with ecological modeling, researchers can develop more holistic and effective strategies for managing and conserving ecosystems. Countries such as the UK and Australia, which are central to *mizer* research, can lead these efforts by facilitating international collaborations and expanding the model's applications beyond traditional fisheries contexts.

Opportunities for model improvement and testing

In addition to the research directions discussed above, our review identifies several actionable opportunities for improving and rigorously testing the *mizer* modeling framework. First, there is a clear need to develop standardized validation datasets and evaluation protocols that enable benchmarking of model outputs against empirical observations. Such efforts would enhance transparency and foster comparability across studies. Second, conducting systematic comparisons between *mizer* and other well-established ecosystem modeling platforms, such as *Ecopath* with *Ecosim* or *Atlantis*, could help assess relative performance, clarify model assumptions, and identify complementary strengths. Third, further efforts are required to quantify uncertainty propagation and assess model sensitivity to both biological parameters and scenario

assumptions. Implementing structured sensitivity analyses across trophic levels and environmental gradients would provide valuable insights into the robustness of predictions. Lastly, future extensions of mizer could benefit from the inclusion of feedback mechanisms, such as those linking environmental drivers or socio-economic processes to species dynamics and fishing effort. These improvements would not only enhance the model's ecological realism but also increase its relevance for management applications under real-world complexity.

One important technical limitation of the current mizer framework is the lack of an automated optimization routine for estimating model parameters, even in single-species contexts. Currently, parameters such as feeding rates, reproductive efficiency, or mortality must be manually specified based on literature or expert knowledge, which can limit reproducibility and calibration quality, especially in data-limited systems. Ongoing development efforts are working toward implementing optimization procedures that allow users to estimate unknown parameters, while fixing others, by fitting model outputs to empirical observations of biomass and yield. In parallel, a second key limitation is that mizer is currently structured as a static equilibrium model, which constrains its ability to explore transient ecosystem dynamics and temporal responses to perturbations. While dynamic implementations are reportedly under development, further work is needed to make them broadly available and tested. These technical enhancements would substantially improve mizer's flexibility, facilitate model calibration, and extend its utility for simulating real-world ecological dynamics.

In conclusion, this systematic review provides a comprehensive synthesis of how the mizer package has been applied and evolved over the past decade. By identifying five core research domains and outlining key methodological and conceptual developments, we highlight mizer's versatility as a tool for ecosystem-based modeling. As environmental and policy challenges grow increasingly complex, advancing size-spectrum modeling through interdisciplinary integration, technological innovation, and broader application will be crucial. Our review offers a roadmap for future research and practical implementation, contributing to more effective and adaptive management of aquatic ecosystems.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used ChatGPT in order to improve the readability and correct grammatical and stylistic errors in the English language of the manuscript. After using this tool, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

CRediT authorship contribution statement

M. Grazia Pennino: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **D.J. Nachón:** Writing – review & editing, Writing – original draft, Data curation. **D. Bamio:** Writing – review & editing, Data curation. **M. Cousido-Rocha:** Writing – review & editing, Writing – original draft, Conceptualization. **G. Delius:** Writing – review & editing, Writing – original draft. **F. Izquierdo:** Writing – review & editing, Writing – original draft, Visualization. **A. Paz:** Writing – review & editing, Writing – original draft. **E. Abad:** Writing – review & editing, Writing – original draft. **M.A. Torres:** Writing – review & editing, Writing – original draft. **I. González Herraiz:** Writing – review & editing, Writing – original draft. **M.P. Sampedro:** Writing – review & editing, Writing – original draft. **I.M. Rabanal:** Writing – review & editing, Writing – original draft. **F. Velasco:** Writing – review & editing, Writing – original draft. **P. Verísimo:** Writing – review & editing. **Y. Vila:** Writing – review & editing. **S. Cerviño:** Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Maria Grazia Pennino reports financial support was provided by Spain Ministry of Science and Innovation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This publication is part of the FRESKO research project PID2022-140290OB-I00 funded by MCIN/AEI/10.13039/501100011033/ and by “ERDF A way of making Europe”.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2025.111241](https://doi.org/10.1016/j.ecolmodel.2025.111241).

Data availability

Data will be made available on request.

References

- Allaire, J., Gandrud, C., Russell, K., Yetman, C., 2017. networkD3: D3 JavaScript network graphs from R. In: R package version 0, 4. <https://CRAN.R-project.org/package=networkD3>.
- Andersen, K.H., Farnsworth, K.D., Pedersen, M., Gislason, H., Beyer, J.E., 2009. How community ecology links natural mortality, growth, and production of fish populations. *ICES J. Mar. Sci.* 66, 1978–1984.
- Andersen, K.H., Beyer, J.E., 2016. Size-dependent changes in marine ecosystems: theoretical insights and their empirical implications. *J. Mar. Syst.* 159, 1–13.
- Audzijonyte, A., et al., 2023. Eco-evolutionary dynamics in marine systems: insights from size-based modeling. *Ecol. Lett.* 26 (4), 527–542.
- Benoit, H.P., et al., 2021. Modeling freshwater fisheries dynamics using size-spectrum models: insights and applications. *Freshw. Biol.* 66 (12), 2267–2281.
- Benoit, H.P., et al., 2022. Optimizing fisheries for blue carbon management: advances and challenges. *Glob. Change Biol.* 28 (6), 1510–1525.
- Blanchard, J.L., et al., 2014. Balancing fisheries and conservation objectives: a multispecies size-spectrum model approach. *Mar. Ecol. Prog. Ser.* 505, 1–15.
- Canales, A., et al., 2020. Fish stock regulation and size-spectrum models: insights from theoretical studies. *Ecol. Model.* 425, 1080–1093.
- Clements, C.F., McCarthy, M.A., Blanchard, J.L., 2019. Early warning signals of recovery in complex systems. *Nat. Commun.* 10 (1), 1681.
- Core Team, R., 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research. *Inter J. Complex Syst.* 1695, 1–9.
- Datta, A., Blanchard, J.L., 2016. Seasonal processes and parameter uncertainties in size-spectrum models: theoretical insights. *Mar. Ecol. Prog. Ser.* 558, 1–13.
- Deckmyn, M. A. (2018). Package ‘mapdata’.
- de Juan, S., et al., 2023. Improving fisheries selectivity and reducing discards: a size-spectrum modeling approach for Mediterranean mixed demersal fisheries. *Fish. Res.* 254, 106676.
- Dickie, L.M., et al., 1987. Size distributions and the structure of aquatic communities. *J. Theor. Biol.* 124 (3), 363–374.
- Duskey, E., 2023. Metabolic prioritization of fish in hypoxic waters: an integrative modeling approach. *Front. Mar. Sci.* 10, 1206506.
- Edwards, C., et al., 2017. Standardizing methods for fitting size spectra to data: an application of the mizer package. *Ecol. Appl.* 27 (4), 1025–1036.
- Edwards, A.M., Robinson, L.A., Plank, M.J., 2020. A size spectrum model for exploring the combined effects of fishing and climate change on the North Sea community. *Mar. Ecol. Prog. Ser.* 635, 1–24.
- Falciani, A., et al., 2022. Blue carbon management and fisheries optimization using size-spectrum models. *Environ. Manag.* 70 (3), 421–432.
- Forestier, M., Chifflet, M., Cresson, P., 2020. Size-based indicators show temporal changes in the fish community of a temperate marine protected area. *Estuar. Coast. Shelf Sci.* 235, 106576.
- Forestier, L., 2021. Long-term ecological changes and eco-evolutionary dynamics in marine systems: a modeling perspective. *J. Theor. Biol.* 525, 1108–1120.
- Fu, C., Xu, Y., Bundy, A., Grüss, A., Coll, M., Heymans, J.J., Shin, Y.J., 2019. Making ecological indicators management ready: assessing the specificity, sensitivity, and threshold response of ecological indicators. *Ecol. Indic.* 105, 16–28.
- Hansen, H.H., Andersen, K.H., Bergman, E., 2023. Projecting fish community responses to dam removal—data-limited modeling. *Ecol. Indic.* 154, 110805.

- Hyder, K., et al., 2015. Ecosystem models in policy development: the role of size-spectrum models in fisheries management. *Mar. Policy* 56, 88–96.
- Holt, R.D., et al., 2014. Size-spectrum models in ecology: applications and advances. *Annu. Rev. Ecol. Evol. Syst.* 45, 55–80. <https://doi.org/10.1146/annurev-ecolsys-110213-112051>.
- Jacobsen, N.S., Burgess, M.G., Andersen, K.H., 2017. Efficiency of fisheries is increasing at the ecosystem level. *Fish Fish.* 18 (2), 199–211.
- Jakeman, A.J., Elsworth, S., Wang, H.H., Hamilton, S.H., Melsen, L., Grimm, V., 2024. Towards normalizing good practice across the whole modeling cycle: its instrumentation and future research topics. *Socio-Environ. Syst. Model.* 6, 18755–18755.
- Jennings, S., Collingridge, K., 2015. Predicting consumer biomass and size structure in marine ecosystems: challenges and advancements. *J. Fish Biol.* 87 (2), 280–296.
- Law, R., et al., 2012. Size spectrum modeling in marine ecology: a review and future directions. *Mar. Ecol. Prog. Ser.* 448, 101–113.
- Lindmark, M., Huss, M., Ohlberger, J., Gårdmark, A., 2020. Size-based ecological interactions drive food web responses to climate warming. *Ecol. Lett.* 23 (4), 705–715.
- Lindmark, J., et al., 2022. Temperature changes and their effects on fish physiology and resource abundance: a size-spectrum modeling approach. *J. Mar. Syst.* 232, 103560.
- Novaglio, C., et al., 2022a. Integrating fleet dynamics into size-spectrum models: new perspectives on mixed fisheries management. *Fish Fish.* 23 (5), 1124–1142.
- Novaglio, C., Blanchard, J.L., Plank, M.J., van Putten, E.I., Audzijonyte, A., Porobic, J., Fulton, E.A., 2022b. Exploring trade-offs in mixed fisheries by integrating fleet dynamics into multispecies size-spectrum models. *J. Appl. Ecol.* 59 (3), 715–728.
- Ortega-Cisneros, K., Fierros-Arcos, D., Lindmark, M., Novaglio, C., Woodworth-Jefcoats, P., Eddy, T.D., Blanchard, J.L., 2025. An integrated global-to-regional scale workflow for simulating climate change impacts on marine ecosystems. *Earth's Fut.* 13 (2), e2024EF004826.
- Pethybridge, H.R., et al., 2018. Advancements in metabolic theory and size-spectrum models: implications for ecosystem modeling. *Ecol. Model.* 368, 49–58.
- Reum, J.C., Blanchard, J.L., Holsman, K.K., Aydin, K., Punt, A.E., 2019. Species-specific ontogenetic diet shifts attenuate trophic cascades and lengthen food chains in exploited ecosystems. *Oikos* 128 (7), 1051–1064.
- Reum, J.C., et al., 2020. Ensemble projections of climate change impacts on the Eastern Bering Sea food web using size-spectrum models. *Mar. Ecol. Prog. Ser.* 637, 69–86.
- Reum, J.C.P., Woodworth-Jefcoats, P., Novaglio, C., Forestier, R., Audzijonyte, A., Gårdmark, A., Blanchard, J.L., 2024. Temperature-dependence assumptions drive projected responses of diverse size-based food webs to warming. *Earth's Fut.* 12 (3), e2023EF003852.
- Robinson, J.P.W., et al., 2022. Managing fisheries for maximum nutrient yield. *Fish Fish.* 23, 800–811.
- Scott, F., et al., 2014. The mizer package: a framework for size-spectrum modeling in R. *J. Stat. Softw.* 58 (5), 1–23.
- Sheldon, R.W., Prakash, A., Sutcliffe, W.H., 1972. The size distribution of particles in the ocean. *Limnol. Oceanogr.* 17 (3), 327–340.
- Spence, M., Blackwell, P., Blanchard, J.L., 2016. Parameter uncertainty of a dynamic multispecies size spectrum model. *Can. J. Fish. Aquat. Sci.* <https://doi.org/10.1139/cjfas-2015-0022>.
- Spence, M.A., et al., 2018. A general framework for combining ecosystem models. *Fish Fish.* 19, 1031–1042.
- Szuwalski, C.S., Burgess, M.G., Costello, C., Gaines, S.D., 2017. High fishery catches through trophic cascades in China, 114. *Proceedings of the National Academy of Sciences of the United States of America*, pp. 717–721.
- Spence, M.A., et al., 2021. Sustainable fishing and marine ecosystem status: insights from ensemble-model approaches. *Ecol. Evol.* 11 (10), 2033–2048.
- Trebilco, R., et al., 2013. Size-based models of marine ecosystems: insights into energy transfer and trophic interactions. *Ecol. Evol.* 3 (3), 736–748.
- Travers-Trolet, M., et al., 2019. Ecological processes and size-dependence: implications for growth, predation, and mortality. *J. Appl. Ecol.* 56 (3), 573–584.
- West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276 (5309), 122–126.
- West, M., 2019. Comparing the performance of size-spectrum models: a case study with mizer and Ecolpath. *Fish. Res.* 211, 139–149.
- Wickham, H., Wickham, H., 2016. Programming with ggplot2. *Ggplot2: Elegant Graph. Data Anal.* 241–253.
- Woodworth-Jefcoats, P.A., et al., 2019. Projecting future climate impacts on the food web of the Eastern Bering Sea using size-spectrum models. *PLOS ONE* 14 (7), e0219156.
- Wo, S., et al., 2020. Modeling multispecies fisheries dynamics in the North Yellow Sea using mizer: insights and applications. *Mar. Ecol. Prog. Ser.* 645, 87–100.
- Wo, J., Zhang, C., Ji, Y., Xu, B., Xue, Y., Ren, Y., 2022. A multispecies TAC approach to achieving long-term sustainability in multispecies mixed fisheries. *ICES J. Mar. Sci.* 79 (1), 218–229.
- Wo, S., et al., 2024. Species portfolio schemes and overexploitation risk: applications of size-spectrum models in fisheries management. *Can. J. Fish. Aquat. Sci.* 81 (4), 523–537.
- Woodson, C.B., Litvin, S.Y., Schramski, J.R., Joye, S.B., 2024. An individual-based model for exploration of population and stock dynamics in marine fishes. *Ecol. Model.* 498, 110842.
- Zhang, C., et al., 2015. Uncertainty in multispecies size-spectrum models due to process and observation errors. *Mar. Ecol. Prog. Ser.* 531, 1–13.
- Zhang, C., et al., 2016a. Ecosystem context of maximum sustainable yield: a size-spectrum modeling approach. *Fish. Res.* 175, 114–127.
- Zhang, C., Chen, Y., Ren, Y., 2016b. The efficacy of fisheries closure in rebuilding depleted stocks: lessons from size-spectrum modeling. *Ecol. Model.* 332, 59–66, 2016 Jul 24.
- Zhang, C., Chen, Y., Thompson, K., Ren, Y., 2016c. Implementing a multispecies size-spectrum model in a data-poor ecosystem. *Acta Oceanol. Sin.* 35 (4), 63, 2016 Apr 1.
- Zhang, C., Chen, Y., Xu, B., Xue, Y., Ren, Y., 2018. Evaluating fishing effects on the stability of fish communities using a size-spectrum model. *Fish. Res.* 197, 123–130.