

Advances in Ecological Modeling: Tools, Approaches, and Future Perspectives

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ABSTRACT

An ecological model serves as a simplified representation of a real-world system, aiming to capture our current understanding of its functioning through the use of mathematical relationships, computer code, and rules. Ecological modeling gained remarkable popularity as a tool in environmental management during the 1970s. Over time, various tools and approaches for ecological modeling have been invented and developed. Ecological models are crucial in supporting environmental decision-making by predicting ecological consequences and helping achieve societal objectives. This paper aims to review recent model types, approaches, and tools used by ecologists by consolidating peer-reviewed research articles published from 1984 to 2023. The results revealed that researchers employ unique model types to address specific ecosystem situations. These model types include dynamic, population dynamic, static, structurally dynamic, artificial neural networks, fuzzy, individual-based, and cellular automata, ecotoxicological, spatial, stochastic, and hybrid/integrated models. Each model has limitations in its application and is suitable for specific situations. However, integrated/hybrid models are recommended as they combine multiple model types, enhancing their effectiveness. Different model approaches such as Ecopath, Ecosim, Ecospace, Ecotroph, and Ecopath with Ecosim are utilized for modeling ecosystems and predicting outcomes amidst disturbances caused by anthropogenic factors, fishing impacts, and climate change. These model approaches greatly contribute to our understanding of ecosystems. However, despite the variety of methods available, authors still encounter challenges when using these methods, leading to the evolution and refinement of additional approaches and tools that will continue to emerge in the future. Future ecologists should devise a general model that will serve as a tool to represent the ecological state of an area.

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1. INTRODUCTION

The sea is an exceptionally delicate system, vulnerable to even minor environmental changes (BFAR, 2010). Recently, a combination of human-induced factors, including climate change, habitat loss, and degradation, has exerted significant pressure on ecosystems worldwide (Travis, 2003). The consequence of this has been the worldwide depletion of fishery resources and the deterioration of marine ecosystems (Worm *et al.*, 2009; Pitcher and Cheung, 2013). The ongoing challenge faced by fisheries, conservation managers, and society is to find a balance between the inherent value of natural resources and their utilization (Thrush and Dayton, 2010). The importance of Earth's ecology for human health, well-being, and the economy is evident. However, our understanding of the services provided by ecosystems remains limited (Millennium Ecosystem Assessment, 2005; Hindmarch *et al.*, 2006). It is crucial to

adopt a broader perspective that considers ecosystem function and interactions, including critical food web relationships, to ensure the vitality and resilience of valued ecosystems (Thrush and Dayton, 2010). Acknowledging the growing importance of comprehending and foreseeing the ecological outcomes resulting from various management approaches. Schuwirth *et al.* (2019) underscore the significance of bolstering decisions related to environmental management. In light of the existing perils faced by the marine environment, the proposition of an ecosystem-based approach to marine resource management has emerged. This approach entails safeguarding the integral processes and elements within the ecosystem that contribute to its structure and functionality, ultimately ensuring the provision of ecosystem goods and services to humanity (Pikitch *et al.*, 2004; Arkema *et al.*, 2006).

The Ecosystem-based Approach to Fisheries (EAF) framework has garnered substantial attention among the scientific community, resulting in the emergence of novel tools, including ecological models and indicators, in recent years (Link, 2011; Plagányi, 2007). These tools play a pivotal role in incorporating ecological and ecosystem factors into management initiatives. By facilitating the evaluation of species-fisheries interactions and their repercussions for marine fisheries management, they provide valuable support for the implementation of efficient strategies based on ecosystem considerations (Corrales *et al.*, 2015; Thrush and Dayton, 2010). Ecologists often utilize models to simulate and study the systems they investigate, providing insights into system operations, data requirements, and knowledge gaps (Jackson *et al.*, 2000). Ecological models not only contribute to our understanding and prediction of ecological consequences (Schuwirth *et al.*, 2019) but also help estimate ecological risks, as demonstrated by numerous existing studies. For instance, Ni *et al.* (2019) developed a hybrid model called a multi-cloud-fuzzy support vector machine (MC-FSVM) to assess risks in various regions across five countries. Their study highlighted the influence of certainty levels on risk grading, making their framework a valuable alternative for ecological risk estimation. Similarly, Sajid *et al.* (2020) employed a model to evaluate the ecological risk of oil spills in Arctic waters, while Gribble (2003) focused on assessing the impacts of major fisheries and management plans on different ecosystems, including mangroves, lagoon-seagrass, as well as coral reefs. In addition to the aforementioned research, Christensen *et al.* (2015) developed a sophisticated model that predicts the combined influence of environmental factors and fisheries on worldwide seafood production. To evaluate its performance, they conducted a retrospective analysis of the global ocean, encompassing primary producers, top predators, and fisheries. This model represents a significant advancement in assessing the global impact of various fisheries management approaches in mitigating the impacts of climate change. Furthermore, Bacalso and Wolff (2014) conducted a study in the Danajon Bank area, constructing a trophic model of the fishery system to understand its trophic structure, dynamics, and ecological interactions. Their model provided crucial initial insights into how the fishery influences the structure and functioning of the ecosystem. Thus, models are employed for decision-making under uncertainty and optimizing those decisions (Tixier *et al.*, 2013), further highlighting their versatility and usefulness in various contexts.

As mentioned earlier, ecosystem modeling plays a crucial role in marine conservation by examining the implications of various management strategies and temporal

and spatial changes in ecosystems (Shannon *et al.*, 2010; Christensen, 2013). Ecologists are continually developing and utilizing diverse methods to create models that closely represent ecosystems, enabling them to understand and address potential impacts more effectively. Recognizing the significance of ecological modeling, this paper aims to provide a comprehensive review and discussion of the concept, applications, and contributions of ecosystem modeling. The paper offers an overview of ecological modeling, including the identification of different types, tools, approaches, and their importance. It also addresses the challenges faced in ecological modeling and proposes potential solutions. Additionally, the future directions of ecological modeling are discussed. To illustrate the importance of ecological modeling, the paper includes examples of published studies that demonstrate its practical applications and provide further insights. This review paper serves as a valuable resource for students and aspiring ecological modelers, offering them an overview of ecological modeling and guiding them on the right path to begin their journey. It provides essential information that beginners will find useful and educational.

2. OVERVIEW OF ECOLOGICAL MODELING

The aim of fisheries management is not to halt fishing altogether, but rather to prevent it from being destructive, excessive, and wasteful. The primary objective is to ensure sustainable fishing practices (BFAR, 2010). Modern fishing activities significantly alter the ocean environment by disturbing the sea floor, modifying food webs, and disrupting vital ecosystem functions (Thrush and Dayton, 2010). However, environmental management decisions should be grounded in the latest scientific knowledge while also considering diverse societal objectives with varying degrees of importance for different stakeholders (Schuwirth *et al.*, 2019). Ecological models serve as abstractions of real-world systems (Jeffers, 1988), utilizing mathematical relationships, rules, and computer code to encapsulate our current understanding of system functioning. Models serve as simplified representations of real-world phenomena, enabling us to gain a deeper understanding of those phenomena (Weisberg, 2007; Sutherland, 2006). Ecological modeling is the use of systems analysis and simulation to mimic complex ecological systems by summarizing available relevant information. The process includes the development of conceptual and quantitative models, and the evaluation and use of the model to answer the specific questions for which the model was built (Pittroff and Pedersen, 2005). Interestingly, even ecologists who lack expertise in mathematical modeling or coding can still benefit from existing ecological models as virtual laboratories. These models

enable the examination of different hypotheses, assist in experimental planning, provide predictions about future system states, facilitate scenario analyses, and contribute to decision-making processes concerning environmental and resource management. By leveraging ecological models, researchers can explore and navigate the complexities of ecological systems more effectively (Pittroff and Pedersen, 2005; Kennedy, 2019). The more knowledge exists about the system, the better we can predict its response. Such knowledge can consist of mechanistic understanding and of empirical data (Schuwirth *et al.*, 2019).

Numerical models of ecological systems are increasingly used to address complex environmental and resource management questions (Planque *et al.*, 2022). In this type of field, models commonly take the form of mathematical constructs (Weisberg, 2007). Ecological models are essential for the development of future safeguards for our life support systems (Pittroff and Pedersen, 2005). Models are assuming a growing significance in diverse fields, such as providing inputs for regulatory guidelines (National Research Council, 2007), assisting in the management of conservation and natural resources (Fieberg and Ellner, 2001), and predicting the ecological ramifications of climate change (Keane *et al.* 2001). The utilization of ecological models has tangible implications as it advances ecological theory, facilitates science-driven decision-making, and informs policymaking processes. Consequently, it becomes imperative that the insights derived from ecological models rest upon robust quantitative foundations that are both credible and reliable (Kennedy, 2019). In the realm of ecological understanding, the concept of resilience recognizes and embraces uncertainty, emphasizing the importance of employing multiple approaches to managing human activities to ensure the maintenance of ecosystem functions (Thrush and Dayton, 2010). As human interactions continue to shape biological systems, the demand for robust and comprehensive tools to assess the sustainability of these systems has grown. This has led to a recent increase in the use of ecological models, as they offer valuable support in evaluating the long-term viability of ecosystems impacted by human influences (Rawlings *et al.*, 2020).

Ecological modeling has a rich history, gaining significant popularity as a tool in environmental management during the 1970s. At that time, three primary types of models were commonly used. The first involved population dynamic models, which represented age structure using matrices. The second category comprised dynamic models based on biogeochemical or bioenergetic principles, utilizing differential equations. On the other hand, static models, where all differential equations equated to zero, were employed to

depict extreme or average scenarios (Jørgensen and Swannack, 2019). In recent times, numerous models have been proposed to enhance our comprehension of the dynamic interactions occurring within ecosystems. Socio-economic-ecological models are a noteworthy example that analyzes the complex relationship between the environment, natural predators, and human populations as they utilize ecological systems to meet the demands of industrial and energy sectors (Rawlings *et al.*, 2020). Furthermore, Jørgensen (2011), as cited by Guo *et al.* (2015), identified five distinct generations in the historical progression of ecological models. These generations represent significant advancements in the field and are illustrated in Figure 1, showcasing the evolution of this scientific approach. Ecological modeling has long been pursued by scientists seeking to understand and assess the state of the environment.

To offer a comprehensive overview of ecological models, Jørgensen and Swannack (2019) presented five distinct classifications that can be used to categorize these models:

1. What is modeled: matter, energy, or population;
2. Classification of all the models in nine different pairs of models (this classification involves as much as $2^9 = 512$ classes);
3. Type of model employed (11 types given);
4. Type of system modeled; and
5. Type of problem modeled.

Jørgensen and Swannack (2019) show in Table 1 what is modeled, the organization, and the pattern.

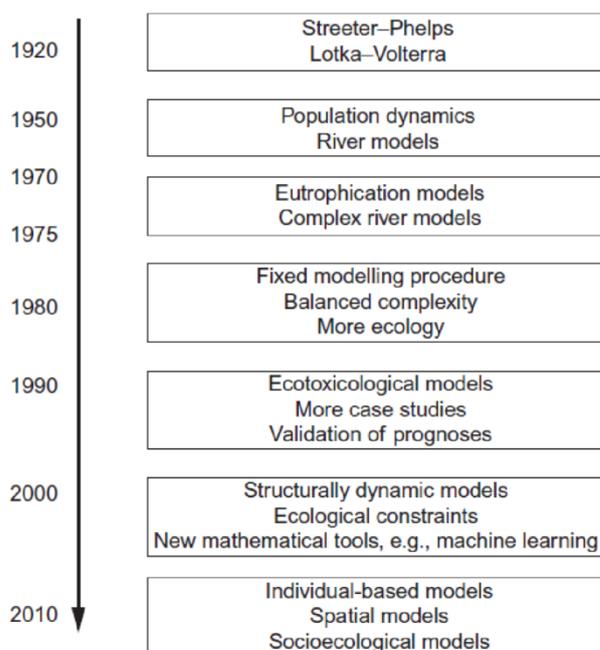


Figure 1. Schematic representation of the development of ecological and environmental models (Jørgensen, 2011).

Models can be characterized by three common aspirations. Firstly, they can be general, which means their conclusions apply to a broad-spectrum of real-life systems, capturing essential principles that apply to various scenarios. Secondly, models can be realistic, accurately reflecting the functioning of a specific system and closely aligning with real-life observations. Lastly, models can strive for precision, providing predictions for specific circumstances with minimal uncertainty (Evans, 2012). Table 2 presents a classification of models based on nine pairs of model types. This classification suggests that all models fall into one of 512 classes,

encompassing all possible combinations of these nine pairs. For instance, a model could be classified as a research model, which means it is deterministic while also being a compartment model that is dynamic, causal, nonlinear, distributed, spatial, and holistic (Jørgensen and Swannack, 2019). Alternatively, the model could be classified as a stochastic management model that is dynamic, linear, compartmentalized, lumped, non-spatial, and holistic in nature. This classification framework helps to understand the diverse characteristics and attributes of different models.

Table 1. Classification of models (Jørgensen and Swannack, 2019).

Modeled/Measured	Organization	Pattern	Model Type
Number of individuals	Conservation of genes	Life cycles	Biodemographic
Energy	Conservation of energy	Energy flow	Bioenergetic
Mass or concentration	Conservation of mass	Element flow	Biogeochemical

Table 2. Classification by model pairs (Jørgensen and Swannack, 2019).

Pair 1: Is the model applied for research or management?
Research models
Management models
Pair 2: Is the model deterministic or stochastic?
Deterministic models
Stochastic models
Pair 3: Does the model apply matrices or differential equations?
Matrix models
Compartment models
Pair 4: Are the variables dependent or not on time?
Dynamic models
Static models
Pair 5: Are the equations linear or nonlinear?
Linear models
Nonlinear models
Pair 6: Is the model based on casualty, or is no casualty included?
Casual models
Black box models
Pair 7: Are the parameters (the properties of the state variables) dependent on time and/or space or constant?
Distributed models
Lumped models
Pair 8: Is a reductionistic or holistic model approach applied?
Reductionistic models
Holistic models
Pair 9: Is the model considering spatial distribution?
Spatial models
Nonspatial models
Pair 10: Are the equations solved numerically or analytically?
Numerical models
Analytical models
Pair 11: Are the model results discrete or continuous?
Discrete models Continuous models

Furthermore, Evans (2012) emphasizes that when developing a model, it is crucial for the modeler to determine the specific characteristics they wish to emphasize. It is important to note that it is not feasible to maximize all desirable characteristics simultaneously, as philosophical considerations suggest (Evans, 2012). Therefore, during the modeling process, sacrifices need to be made in terms of certain points or parameters in order to prioritize the desired prediction. This process is commonly referred to as modeling trade-offs. Figure 2 illustrates the schematic representation of how these trade-offs occur.

In recent ecological studies, a plethora of innovative modeling techniques have been proposed and regularly employed (Guo *et al.*, 2015). When it comes to modeling, a selection of a scale and form that aligns with the specific questions being solved is a fundamental principle (Ainsworth and Walters, 2015). In terms of form, various model types are worth considering, such as individual-based models (Shin and Cury, 2004; Poloczanska *et al.*, 2013), size-based models (Jennings *et al.*, 2008; Smith *et al.*, 2010), as well as models for trophic food web (Christensen and Pauly, 1992). To provide a comprehensive overview, Table 3 presents eleven distinct model types utilized in the modeling of ecological systems, along with their corresponding descriptions, advantages, and disadvantage.

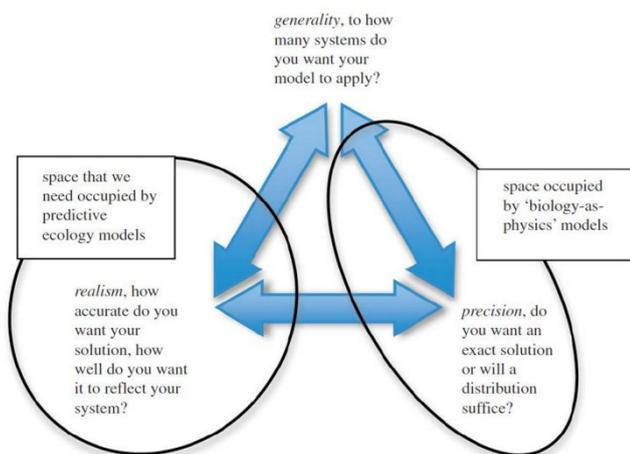


Figure 2. Schematic of modeling trade-offs (Evans, 2012).

From 2000 onwards, there was a greater utilization of Structurally Dynamic Models (SDMs), Artificial Neural Networks (ANN), and Individual-Based Models (IBMs) in environmental applications. This trend was driven by the increased availability of modeling software and the growing demand for these types of models. The accessibility of software for running large, intricate simulations in a relatively

short time period has led to the widespread utilization of static models such as food web models. These models are particularly valuable for studying fisheries as well as numerous aquatic ecosystems (Jørgensen and Swannack, 2019). Leroy (2022) reviewed thoroughly the SDMs on his paper which highlighted in addressing the gap in choosing this type of model. In recent years, the use of ecological niche models (ENMs) and SDMs to explore the patterns and processes behind observed distribution of species has experienced an explosive growth. Although the use of these methods has been less common and more recent in marine ecosystems than in a terrestrial context, they have shown significant increases in use and applications. Herein, Melo-Merino *et al.* (2020) made a systematic review of 328 articles on marine ENMs and SDMs published between 1990 and 2016, aiming to identify their main applications and the diversity of methodological frameworks in which they are developed, including spatial scale, geographic realm, taxonomic groups assessed, algorithms implemented, and data sources. Their study also indicates that marine ENMs and SDMs have been widely applied across a range of taxonomic groups and geographic regions. They noted biases toward certain species and regions with better data availability and identified challenges such as inconsistent methodologies and data gaps in underrepresented areas and emphasized the need for standardized approaches, expanded data collection, and interdisciplinary tools to improve the effectiveness of marine ENMs and SDMs. Despite the growth in the field, the study highlights the need for more standardized methods and better integration of diverse data sources to improve the accuracy and applicability of ENMs and SDMs in marine ecology. Additionally, a research by AlAdwani and Saavedra (2019) has demonstrated that incorporating higher-order terms in population dynamics models can promote diversity, enhance stability, and improve the understanding of ecological system dynamics. However, the authors proposed that while including higher-order interactions in ecological models may enhance predictive capabilities, it does not offer additional explanatory power unless the model parameters are ecologically constrained. Moreover, in addition to the eleven models presented in Table 3, there has been a development of several new model types such as Integrated/Holistic Models, Stochastic Models, Multi-scale Models, Agent-based Models, Adaptive Management Models and Coupled Human-Natural System Models. This is due to the increasing requirement to model complex environments, the integration of different disciplines, as well as remarkable advancements in computing power (Jørgensen and Swannack, 2019).

Table 3. Different model types used in ecological modeling (Jørgensen and Swannack, 2019).

Model type	Model Descriptions	Advantages	Disadvantages
1. Dynamic Models Biogeochemical and bioenergetics models	The model relies on conservation principles, where changes in state variables are determined by the difference between incoming and outgoing substances. This model type has found widespread application in environmental management, serving as a powerful tool to comprehend ecosystem responses to pollutants and make predictions for the future.	<ul style="list-style-type: none"> ✓ Typically grounded in causality ✓ Rooted in the principles of mass or energy conservation ✓ Straightforward to comprehend, interpret, and construct ✓ Software, such as system dynamics software, is readily accessible ✓ User-friendly for making predictions 	<ul style="list-style-type: none"> ✓ Challenging to develop and parameterize with diverse data sources ✓ Relies on relatively high-quality data ✓ Complex and parameter-rich models are difficult to calibrate ✓ Unable to consider adaptation and shifts in species composition
2. Static Models	The model used is a biogeochemical or bioenergetic dynamic model in which all the differential equations are set to zero, resulting in static values for the state variables that represent a snapshot of the system. This model provides a static view of the system at a specific moment and does not involve predicting or projecting future dynamics. Such a model is commonly employed when a static representation adequately describes an ecological system or when making environmental management decisions.	<ul style="list-style-type: none"> ✓ Requires smaller databases compared to other model types ✓ Excellent for portraying a worst-case or average scenario ✓ Results can be easily validated and verified 	<ul style="list-style-type: none"> ✓ Does not provide any information about dynamics and temporal changes ✓ Unable to make predictions with time as an independent variable ✓ Limited to providing average or worst-case scenarios
3. Population Dynamic Models	<p>This model type is based on the Lotka-Volterra model, which originated in the 1920s.</p> <p>Population dynamic models often incorporate age structure, commonly calculated using matrices.</p> <p>Population dynamics models can be classified into various types, such as individual-based, matrix-based, statistical, population viability analyses, and analytical models.</p> <p>This model type is commonly employed to monitor population development.</p> <p>The model type finds widespread application in the management of fisheries, in formulating biological opinions for threatened and endangered species, and in national park management.</p>	<ul style="list-style-type: none"> ✓ Designed to track the progression of a population ✓ Allows for the incorporation of age structure and consideration of influential factors ✓ Characterized by its simplicity of understanding, interpretation, and development ✓ Predominantly based on causality 	<ul style="list-style-type: none"> ✓ May not always be applied in this model type ✓ Limited scope to population dynamics ✓ Robust database is necessary for its implementation ✓ Can be challenging in certain scenarios in terms of calibration ✓ Requires a relatively homogeneous database

<p>4. Artificial Networks (ANN)</p>	<p>Neural</p>	<p>These model types establish relationships between state variables and forcing functions using a diverse database.</p> <p>Although they are black box models and lack causality, they often yield valuable models that can be used for making predictions. However, it is crucial that these models are built upon a sufficiently large database to establish and test relationships, ideally using an independent dataset.</p>	<ul style="list-style-type: none"> ✓ Can be employed when other methods reach their limitations ✓ Straightforward to utilize ✓ Provide a reliable assessment of certainty through the use of a test set ✓ Compatible with heterogeneous datasets ✓ Allow for near-optimal utilization of the available data set ✓ 	<ul style="list-style-type: none"> ✓ Lacks causality unless algorithms are introduced or a hybrid model combining ANN and a traditional model is employed ✓ Cannot substitute biogeochemical models that rely on conservation principles ✓ Predictive accuracy is occasionally constrained
<p>5. Individual-Based Models (IBMs) and Cellular Automata</p>		<p>This model type can be seen as a reductionistic approach, where system-level properties arise from the interactions among individual agents (such as individuals within a population).</p> <p>The development of this model type aimed to investigate how ecosystem properties emerge through interactions among individuals, whether within the same species or between different species, within the system.</p>	<ul style="list-style-type: none"> ✓ Capable of accommodating individuality ✓ Capable of incorporating adaptation within a range of properties ✓ Software options are available, although the selection may be more limited compared to biogeochemical dynamic models ✓ Can encompass spatial distribution 	<ul style="list-style-type: none"> ✓ Models become highly intricate when numerous properties are taken into account. ✓ Substantial volume of data is necessary to calibrate and validate the models. ✓ Thorough evaluation is required, and communicating the models to individuals without modeling expertise can be challenging.
<p>6. Spatial Models</p>		<p>Geographic Information System (GIS) is an alternative approach that can be deemed a convenient method for presenting model outcomes. In the context of aquatic ecosystems, an ideal spatial model would provide a comprehensive three-dimensional (3-D) depiction of processes, forcing functions, and state variables. Often, the focus is on accurately describing hydrodynamics. Spatial models are employed when it is essential for the results to incorporate spatial distribution. This is particularly crucial when the spatial arrangement significantly influences the model outcomes.</p>	<ul style="list-style-type: none"> ✓ Spatial distribution, which is often crucial in ecology, can be covered. ✓ The results can be presented in various informative formats, such as using GIS. ✓ 	<ul style="list-style-type: none"> ✓ Typically, a vast database is required to obtain information on spatial distribution. ✓ Calibration and validation processes are challenging and time-consuming. ✓ Providing an accurate description of spatial patterns often necessitates the use of a highly intricate model.

<p>7. Ecotoxicological Models</p>	<p>Ecotoxicological models, unlike biogeochemical models or population dynamic models widely used in ecotoxicology, do not represent a distinct model type in principle. However, it is advisable to consider ecotoxicological models as a separate model type due to the following reasons:</p> <ul style="list-style-type: none"> a) Limited knowledge of parameters necessitates the use of estimation methods, which have been developed to overcome this limitation. b) Ecotoxicological models tend to be simple due to the incorporation of safety factors and the restricted knowledge of parameters. This is particularly evident in fugacity models. c) Ecotoxicological models often include an effect component. 	<ul style="list-style-type: none"> ✓ These models are specifically designed to address ecotoxicological issues. ✓ In most cases, they are user-friendly and straightforward to use. ✓ They frequently incorporate an effect component or can be readily interpreted to quantify the effect. 	<ul style="list-style-type: none"> ✓ The development of models for all toxic substances requires a vast number of parameters, of which only a maximum of 1% is currently known. ✓ Estimation methods are necessary but inherently come with high uncertainty. ✓ Consequently, the model results also possess a high level of uncertainty. ✓ Incorporating an effect component in the models necessitates knowledge of the effect, which is also limited.
<p>The purpose of these models is evident: to address ecotoxicological research and management challenges, as well as to conduct environmental risk assessments for chemical applications.</p>			
<p>8. Stochastic Models</p>	<p>This model category exhibits a component of randomness.</p> <p>This randomness can manifest in various forms, such as the forcing functions, particularly the climatic forcing functions, or the model parameters. A stochastic model can encompass biogeochemical/bioenergetic models, spatial models, structural dynamic models, Individual-Based Models (IBM), or population dynamic models.</p>	<ul style="list-style-type: none"> ✓ These models have the capability to account for the randomness associated with forcing functions or processes. ✓ The uncertainty of the model results can be readily obtained by running the model multiple times. 	<ul style="list-style-type: none"> ✓ Understanding the distribution of the random elements within the model is essential. ✓ The model exhibits a high level of complexity and demands significant computational resources and time.
<p>9. Integrated/Hybrid Models</p>	<p>In principle, hybrid or integrated models can be created by combining any two of the ten previously mentioned model types.</p>	<ul style="list-style-type: none"> ✓ The combination of models from diverse disciplines allows for the integration of the unique strengths and capabilities of each model within the modeling suite. 	<ul style="list-style-type: none"> ✓ It diminishes the necessity to create new models for every specific scenario. ✓ Disciplinary-specific approaches can be employed to handle spatio-temporal dynamics. ✓ The underlying assumptions of each model may be incompatible. ✓ Communicating across disciplines can be time-consuming. ✓ It is crucial to prioritize the design of input/output requirements.

Back in 1984, a pioneering marine ecosystem model named Ecopath was developed by Dr. Jeffrey Polovina and his team at the National Marine Fisheries Service, Honolulu Laboratory (Polovina, 1984). This model revolutionized the field of marine ecology by introducing statistical "path analysis" techniques to effectively portray ecological relationships (Christensen, 2013). Recognizing its significance, the United States National Oceanographic and Atmospheric Administration (NOAA) officially acknowledged Ecopath as one of their top ten scientific breakthroughs in 2010 (Coll *et al.*, 2015). Ecopath focuses on modeling the instantaneous flow of biomass within functional groups, which are clusters of species categorized based on their niche similarities (Polovina, 1984; Christensen and Pauly, 1992). What makes Ecopath truly exceptional is its simplicity, modest data requirements, and adaptability to future updates, making it an invaluable tool for ecosystem modeling. By utilizing Ecopath, researchers gain valuable insights into the structure and functioning of diverse marine ecosystems, especially in regions where comprehensive fisheries data is limited (Bacalso and Wolff, 2014). Furthermore, the application of trophic modeling using Ecopath, pioneered by Christensen and Pauly (1992) and Walters *et al.* (1997), has empowered fisheries managers to examine the intricate trophic interactions between exploited and non-exploited functional groups within ecosystems. This approach enables a comprehensive investigation into the direct and indirect impacts of fisheries on all biological components of the system, leading to a deeper understanding of system productivity (Christensen *et al.*, 2004; Pauly *et al.*, 2002).

However, according to Walters *et al.* (1997), Ecopath renders only a static representation of the trophic structure in an ecosystem. It focuses on answering the question of what trophic flows are necessary to aid the recent trophic structure as well as align with recorded mortality and growth patterns. Consequently, its results cannot be used to address hypothetical scenarios or policy changes that could cause shifts in trophic interactions. To overcome this limitation, the authors introduced Ecosim. The objective of Ecosim was to develop a straightforward model for biomass dynamics. This modeling approach can provide insights into the potential changes in biomass direction across numerous trophic groups under gradual experimental policies designed at enhancing ecosystem management. Therefore, Ecosim has established itself as an invaluable instrument for the design and implementation of adaptive management experiments at the ecosystem level (Walters *et al.*, 1997).

In addition to Ecopath and Ecosim, another model framework called Ecospace was introduced by Walters *et al.* (1999). Ecospace incorporates spatial dynamics into trophic

mass-balanced models using Ecopath (Christensen and Pauly, 1992) and dynamic simulations from Ecosim (Walters *et al.*, 1997). It operates within a two-dimensional grid of interconnected cells, incorporating habitat and habitat affinities. This spatially explicit model facilitates the evaluation of policies, specifically considering the impact of Marine Protected Areas (MPAs) within an ecosystem context. Ecospace relies on the Ecopath mass-balance approach for parameterization. An application example of Ecospace is presented, showcasing the effect of an MPA and validation using trawl survey data. The results are illustrated through a color map depicting biomass patterns on the shelf of Brunei Darussalam, Southeast Asia. A significant finding of Ecospace is the occurrence of spatial "cascade" effects, where prey densities are low in predator-rich areas, such as protected areas or regions with high fishing costs. The model also highlights that the potential benefits of local protection can be diminished by high movement rates and concentrated fishing efforts at the edges of MPAs, where prey gradients attract predators out of the protected areas. Although Ecospace has some limitations, such as the absence of explicit consideration for seasonal changes or directed migration, its user-friendly interface and informative graphs make it likely to be widely adopted. The increasing availability of Ecopath files further supports its application. According to Walters *et al.* (1999), Ecospace can be utilized to generate hypotheses about ecosystem function and assess policy choices. Instead of providing precise quantitative predictions, the authors view Ecospace as a method for "policy screening," helping identify policy alternatives that warrant further detailed analysis and experimental field testing. Additionally, Walters *et al.* (1999) noted that Ecospace serves as an effective teaching tool, facilitating the exploration of trophic and spatial relationships. The program interface enables users to sketch topographic features, primary productivity areas, habitat types, and preferences on a computer screen using a mouse. They can then observe the development of spatial biomass patterns over time through color-coded density maps.

Next that we will discuss is EcoTroph, a trophic model that focuses on marine ecosystems and assesses the impacts of fisheries by considering the distribution of biomass or related quantities across continuous trophic levels (TLs) (Gascuel, 2005; Gascuel and Pauly, 2009). In an EcoTroph representation, ecosystem parameters such as biomass, production, catch, and fishing mortality are displayed along trophic spectra (Gascuel, 2005). The model incorporates fractional TLs to account for the fact that marine animals often feed on species from multiple TLs (Odum *et al.*, 1975). A key advantage of EcoTroph is its ability to provide an overview of the entire ecosystem, considering the complete trophic

spectrum instead of focusing solely on individual species. Comparing ecosystems using EcoTroph is valuable for highlighting differences in ecosystem functioning. However, there are limitations associated with data availability, potential underestimation of overfishing effects in certain TLs, estimation of catches, and the level of aggregation of Ecopath groups when constructing EcoTroph models (Halouani *et al.*, 2015). EcoTroph is useful for developing ecosystem-based indicators, which are essential for effective ecosystem management (Rombouts *et al.*, 2013). It is relevant for comparing trophic structures and analyzing trophic flows in marine ecosystems from ecological and fisheries perspectives, as it does not focus specifically on individual species (Gascuel and Pauly, 2009). Additionally, EcoTroph shows promise as a tool for exploring different levels of fishing pressure and understanding food web properties such as sensitivity to fishing, intensity of top-down control, and ecosystem stability (Halouani *et al.*, 2015).

Another trophic model widely employed by ecologists is Ecopath with Ecosim (EwE). It is a trophic model frequently employed by ecologists, offering a comprehensive representation of ecosystems that accounts for the complexities of the food web (Christensen *et al.*, 2004; Walters *et al.*, 1999). EwE is well-known as desktop software designed for the Microsoft Windows platform (Steenbeek *et al.*, 2016) and has found applications in ecological studies, ecosystem-based management, and environmental impact assessments (Christensen and Maclean, 2011; Canadian Environmental Assessment Agency, 2015; Link, 2011). The EwE modeling approach consists of three interconnected routines: Ecopath, Ecosim, and Ecospace (Steenbeek *et al.*, 2016). It has been utilized in various fields, including the analysis of fishing and climate change impacts on ecosystems, the understanding of emergent ecosystem dynamics, ecosystem-based management, marine conservation, and spatial planning. Beyond fishing impact assessments, the scientific community employs EwE for a wide range of purposes such as providing scientific advice for management, investigating conservation issues, and evaluating cumulative impacts of environmental and human activities on marine food webs, including habitat modification and the invasion of alien species (Coll *et al.*, 2015). EwE currently stands as the most widely used ecosystem modeling platform globally (Ainsworth and Walters, 2015). Over the past three decades, the Ecopath approach has evolved into a comprehensive modeling suite referred to as "Ecopath with Ecosim and Ecospace" or the EwE toolbox (Coll *et al.*, 2015).

In the Mediterranean Sea, researchers have developed numerous ecological models using the Ecopath with Ecosim approach (Christensen *et al.*, 2004; Coll and

Libralato, 2011). These models have been applied in various domains, including the assessment of fishing impacts (Coll *et al.*, 2006), the comparison of ecosystem structure and functioning traits (Hattab *et al.*, 2013; Tsagarakis *et al.*, 2010), exploration of management options (Fouzai *et al.*, 2012), evaluation of aquaculture impacts (Forestal *et al.*, 2012), analysis of environmental effects (Coll *et al.*, 2008; Piroddi *et al.*, 2010), and investigation of the effects of invasive species on the food web (Daskalov, 2002).

3. CASE STUDIES IN DIFFERENT AREAS USING ECOLOGICAL MODELING TO ADDRESS DIFFERENT ECOLOGICAL ISSUES

Numerous studies have utilized ecological models to tackle various issues in specific ecosystems, providing evidence of the widespread applications of ecological modeling worldwide. The following studies presented in this paper serve as evidence of ecological modeling applications worldwide.

Corrales *et al.* (2015) conducted a study in the northwestern Mediterranean Sea, focusing on the marine continental shelf and slope area from Toulon to Cape La Nao. Referred to as the Northwestern Mediterranean model (NWM), an ecological model was developed to examine the structure and functioning of this region, which encompassed previously studied areas like the Gulf of Lions and the Southern Catalan Sea. The study expanded the scope to cover an area of 45,547 km², ranging in depths from 0 to 1000 m. The selection of the study area took into account connectivity between regions, shared fish stocks, and fishing fleets. To construct the model, the researchers utilized input data from local scientific surveys, fishing statistics, published stomach content analyses, and empirical equations for consumption and production rate estimations. The model consisted of 54 functional groups, representing a range of organisms from primary producers to top predators. Both Spanish and French fishing fleets were included in the model. Ecological indicators were employed to analyze the data, and the results were compared with outputs from previous ecosystem models developed in the Mediterranean Sea and the Gulf of Cadiz. The findings of the study indicated that trophic flows were primarily associated with detritus, phytoplankton, zooplankton, and benthic invertebrates. Several keystone groups within the ecosystem were identified, including dolphins, benthopelagic cephalopods, large demersal fishes from the continental shelf, large pelagic fishes, and herbivorous salemma fish. The study also confirmed a significant and widespread fishing impact throughout the food web. The comparative analysis revealed shared structural and functional traits among ecosystems, such as the

important role of detritus, the dominance of the pelagic fraction in terms of flows, and the significance of benthic-pelagic coupling.

Ramírez *et al.* (2015) conducted a study focusing on the effects of a proposed Marine Protected Area (MPA) system on fisheries in a biodiversity conservation priority site in northern Chile. The authors employed a spatial dynamic modeling approach that integrated ecological, social, and economic criteria. They developed an Ecospace model specifically for the ecological benthic subsystems dominated by kelp beds off the Mejillones Peninsula, Chile. The study compared changes in fisheries indicators and the spatial distribution of fishing effort across five different scenarios. These scenarios included a no-MPA baseline scenario and four scenarios that incorporated proposed MPA core and buffer zones. The scenarios varied in terms of the dispersal rates, either high or low, for the species represented in the model. Overlay analysis was used to identify the zones and fishing grounds that would be impacted by the proposed MPA system, and the extent of this impact was assessed. The results revealed a significant overlap between the proposed MPA site and fishing grounds of high economic importance. This included a specific fishing ground where women are permitted to work. The study provided insights into the potential effects of the MPA system on fisheries and highlighted the spatial relationships between the proposed MPA and important fishing areas. This overlap raised concerns about potential displacement of women without alternative livelihood options, leading to possible social repercussions within the fishing community. Through the spatial food web model of the kelp forest, it was discovered that the accumulation of biomass in fished species was highly influenced by dispersal rates, especially in scenarios with smaller reserves. A noteworthy pattern emerged as fishing effort was redistributed at the boundaries of individual MPAs and open areas nearer to the port. Analysis of fisheries indicators revealed negative impacts in both MPA scenarios, including undesirable changes in catch and profits for rockfish and kelp exploitation. These findings raised concerns regarding the potential adverse consequences of implementing the proposed MPA system for the Mejillones Peninsula on the fishing community of Constitución Cove. To mitigate these potential negative effects on fisheries, the study suggested the integration of fisheries management objectives with biodiversity conservation in the planning process of the Mejillones Peninsula MPA system. By doing so, it may be possible to address the concerns of the fishing community and garner their support for future MPAs.

Halouani *et al.*, (2015) utilized the EcoTroph modeling approach to examine and characterize the food

webs of five Mediterranean marine ecosystems. Their objective was to investigate the ecosystems' responses to different simulated fishing scenarios. By conducting EcoTroph simulations, the authors assessed the sensitivity of each ecosystem to fishing. In the study, the effects of increasing or decreasing fishing mortality rates on both biomass and catch per trophic level were simulated across the five ecosystems. The results emphasized the substantial impact of high trophic level organism depletion in the Mediterranean Sea. Furthermore, the research revealed that the fisheries' influence, when analyzed at the trophic level scale, varied among ecosystems based on their trophic structure and exploitation patterns. Significantly, certain simulations demonstrated a top-down compensation effect. This effect occurred when a decrease in predator biomass resulting from fishing had an indirect positive effect on lower trophic levels. Through this comparative analysis, it became evident that ecosystems exhibiting noticeable top-down controls were less vulnerable to fluctuations in fishing mortality in terms of total ecosystem biomass. This finding suggested that the presence of top-down control can influence system stability.

In a study conducted by Gribble (2003), a trophic-based ecosystem model called the GBR-prawn was developed for the Great Barrier Reef. This model integrated a generalized template of a coral reef ecosystem with data collected from comprehensive surveys in the far northern region of the reef. The enhanced model included both trawl and line fisheries, with particular attention given to the effects of trawling on the penaeid prawn community in the lagoon and inter-reef habitat. The simulations using the GBR-prawn model revealed both positive and negative outcomes of prawn trawling and the associated 6:1 ratio of discarded by-catch on the Great Barrier Reef ecosystem. Certain species, such as endangered sea turtles, suffered negative impacts, while scavengers like seabirds experienced benefits. The study also highlighted that reducing trawling would come with ecological costs, in addition to the apparent advantages, due to the intricate nature of the Great Barrier Reef ecosystem and its trophic interactions. Another study by Bulman *et al.* (2014) concentrated on Australia, where EwE models have been widely utilized to assess the ecosystem effects of fishing. The study's key findings underscore the pivotal role of EwE models in informing sustainable fisheries management. These models, with their widespread application, have provided invaluable insights into the ecological consequences of fishing practices. They have shed light on how fishing activities impact marine ecosystems, including changes in species composition, trophic interactions, and ecosystem services. The study also highlighted that EwE models have been instrumental in supporting sustainable fisheries management

by informing decisions related to fishing quotas, conservation measures, and ecosystem-based management strategies. With some key findings on the effects of fishing practices on marine food webs, detrimental effects of bycatch and habitat degradation as well as overfishing of important species in higher trophic levels that could lead to ecosystem imbalance. the study suggests that EwE models have proven to be effective tools for assessing and managing the ecosystem effects of fishing in Australia. However, the study also notes that there are challenges, including uncertainties in model parameters and data limitations, which could affect the precision of predictions. Despite these challenges, the study underscores the importance of EwE models in promoting ecosystem-based fisheries management, and it calls for continued improvements in data collection, model calibration, and cross-disciplinary collaboration to enhance the reliability and applicability of these models in the future.

Bacalso and Wolff (2014) conducted a study in the Central Visayas, Philippines, aiming to create a trophic model of the shallow Danajon Bank. They employed a mass balance approach called Ecopath to depict the system's characteristics and its interactions with fisheries. The Ecopath model encompassed 37 functional groups and 17 fishing fleet types, representing the diverse catches and fishing activities in the Danajon Bank. The analysis indicated that the catch primarily consisted of fish and invertebrates from lower trophic levels, resulting in a relatively low mean trophic level for the fishery. The study revealed that the system dynamics were mainly influenced by top-down fishing pressure, evident from the low biomass and high exploitation levels observed in numerous upper trophic level groups, along with the absence of significant natural physical disturbances. Through the mixed trophic impacts (MTI) analysis, the study shed light on the impact of illegal and destructive fishing practices on the ecosystem's structure and dynamics. It was discovered that the collective annual harvest from illegal fisheries accounted for approximately 25% of the entire municipal fisheries catch in the area. This emphasized the importance of strengthening fisheries law enforcement by local government units to address these unlawful activities, as doing so could significantly enhance the potential benefits of legal fisheries. To construct a trophic system model of the Danajon Bank, the researchers utilized Ecopath with Ecosim (version 6.3, Christensen *et al.*, 2008). This model represents a balanced system where biomass flows are assumed to be in equilibrium within each ecological compartment or functional group over a specified time period.

In recent case study conducted by Reimer *et al.* (2022) which took into considerations of incorporating the uncertainty in parameter into models. The researchers treated

the parameters as random variables with distributions, rather than fixed quantities. They had introduced these methods with a motivating case study of sea ice algal blooms in heterogeneous environments comparing Monte Carlo methods with polynomial chaos techniques to help understand the dynamics of an algal bloom model with random parameters. Their results showed that modeling key parameters in the algal bloom model as random variables changes the timing, intensity and overall productivity of the modelled bloom. A promising avenue for the broader inclusion of parametric uncertainty in ecological models, leading to improved model predictions and synthesis between models and data, was provided by the computational efficiency of polynomial chaos methods.

4. CHALLENGES ENCOUNTERED IN ECOLOGICAL MODELING

Models of global climate have gained acceptance to the point where their predictions serve as a basis for multilateral government agreements with potentially huge economic implications (Pittroff and Pedersen, 2005). As the urgency to forecast ecosystem responses to global change grows, so do the number and complexity of predictive ecological models and the value of iterative prediction, both of which demand validation and cross-model comparisons. This challenges ecologists to provide predictive models that are reusable, interoperable, transparent and able to accommodate updates to both data and algorithms (Barros *et al.*, 2022). The ideal model for supporting environmental management decisions should be directly aligned with management objectives, provide unbiased predictions of the effects of alternative management approaches, offer sufficient precision, accurately estimate prediction uncertainty, be applicable across different locations and time periods, and be easily comprehensible. However, in reality, models often fall short of these ideals (Schuwirth *et al.*, 2019). Ecosystems are generally so complex that sparse data and knowledge make the development of models difficult (Pittroff and Pedersen, 2005). Evans (2012) mentioned that ecological forecasting models inevitably involve significant uncertainty in their predictions because there is often considerable uncertainty or inaccuracies in parameters in ecological models as cited by Reimer *et al.*, (2022). Such variance can propagate to downstream models. Overall, the uncertainty present in ecological forecasting models emerges from the imprecision of biological parameter estimates, the stochastic nature of ecological systems, and variations in physical predictions of the environment, affecting subsequent biological predictions (Evans, 2012).

Furthermore, several factors have been identified regarding the limitations and challenges associated with ecological modeling:

1. While ecological models are commonly formulated in research projects, their application in practical contexts is infrequent (Schuwirth *et al.*, 2019).
2. Effective communication of scientific findings to stakeholders is crucial. Model results should convey a clear and easily understandable message. Presenting model uncertainty in a comprehensible manner can be particularly challenging and requires appropriate visual presentation. It is essential to interpret model results in light of the specific questions the model was designed to address and the simplifications and assumptions made during its development. It should be acknowledged that no model can perfectly replicate the behavior of the system being modeled (Schuwirth *et al.*, 2019). One challenge for scientists, managers, and stakeholders is to appraise how well suited these models are to answer questions of scientific or societal relevance, that is, to perform, communicate, or access transparent evaluations of ecological models (Planque *et al.*, 2022).
3. The utilization of ecosystem modeling in fisheries management remains constrained due to two primary factors: the absence of explicit requests from managers for advice derived from ecosystem models, and the failure of modelers to effectively convey the significance and applicability of their work to management advisors (Coll *et al.*, 2015).
4. Despite the global acknowledgement of the significance of adopting an ecosystem-based approach to fisheries management, its implementation continues to be insufficient. The majority of fisheries regulations still adhere to the single-species approach, and only a handful of countries such as Europe, Latin America, The Mediterranean and North America have established formalized scientific advisory systems grounded in the ecosystem-based approach (Coll *et al.*, 2015).
5. Traditional fisheries management relies on population dynamics models that assume stable ecosystems with constant parameters. However, it is now widely recognized that such assumptions are seldom valid, as ecosystems are dynamic and continuously undergo changes in terms of their organization, resilience, vulnerability, and other characteristics (Link, 2011).
6. Environmental and ecological systems inherently entail significant uncertainties and exhibit nonlinear dynamics (Grêt-Regame *et al.*, 2013; Burkett *et al.*, 2005).
7. The stochastic nature of ecological models means that a single simulation represents only one random outcome among an infinite number of possible outcomes. Consequently, a single iteration of a stochastic model is inadequate to comprehensively characterize a model's prediction (Kennedy, 2019).
8. Biased input data has the potential to generate biased outcomes. Input variables that lack direct connections to the system can possess limited practical utility for environmental management and may produce false predictions based on coincidental correlations in the data (Schuwirth *et al.*, 2019).
9. Neglecting prior knowledge of crucial mechanisms can lead to overlooking the dynamic nature of the system and the vital feedback loops that exist between output variables (Robson, 2014).
10. Scaling, that is, changing from one scale to another, is not always straightforward, and sometimes can cause problems due to scale breaks, nonlinearities, feedbacks and heterogeneity in such pattern process relationships (Snell *et al.*, 2014). Additionally, scaling is sometimes not explicit, and confusion in terminology adds to scaling-related problems (Fritsch *et al.*, 2020). Scaling or process scaling is defined as translating information from one scale to the other. This review takes the perspective that scaling is inherent to modeling and elaborates how the scaling approaches that are available can be classified into pre-model, in-model and post-model scaling methods. This implies that scaling and the associated problems are probably more widespread than previously thought, since they cover so many different areas of modeling. Thus, we recommend that ecologists be aware of scaling problems especially where models do not explicitly aim at scaling (Fritsch *et al.*, 2020).

Modeling is widely used in ecology and its utility continues to increase as scientists, managers and policy-makers face pressure to effectively manage ecosystems and meet conservation goals with limited resources (Barros *et al.*, 2022). While numerous researchers around the world use a great variety of models to understand ecological dynamics and their responses to disturbances, only a small fraction of these models are ever used to inform ecosystem management (DeAngelis *et al.*, 2021). These statements

imply that ecological modeling faces various challenges, including limited practical application, effective communication of results, low uptake in fisheries management, inadequate implementation of the ecosystem-based approach, reliance on simplified assumptions, uncertainties and nonlinear dynamics, the need for multiple model runs, the importance of unbiased input data, and the consideration of prior knowledge and feedback mechanisms. Addressing these factors is crucial for enhancing the usefulness and effectiveness of ecological models in supporting environmental management decisions.

5. POSSIBLE SOLUTIONS TO ECOLOGICAL MODELING CHALLENGES

Given the urgency of better predictions of environmental change, the current slow progress of ecological modeling should be motivating and not deterring (Pittroff and Pedersen, 2005). Various approaches are being implemented to address the challenges associated with ecological modeling. Ensuring the quality of input data, output data, and results is of utmost importance in enhancing the confidence of researchers and managers in model outcomes and evaluations (Coll *et al.*, 2015). Effective management strategies should consider trophic interactions, environmental patterns, and ecosystem dynamics. Understanding how ecosystems evolve becomes essential in formulating adaptive strategies for sustainable management over time (Arreguín-Sánchez *et al.*, 2014). Additionally, socio-economic factors and impacts should be taken into account when developing empirical applications of Ecopath with Ecosim (EwE) to offer a comprehensive assessment to the industry, scientific community, and society at large (Coll *et al.*, 2015). By avoiding common pitfalls, such as implementing management strategies that are inappropriate for the area and lead to failure, as stated in the study by Toring-Farquerabao *et al.* (2021) involving the deployment of artificial reefs in Iloilo, Philippines, we can potentially make a significant positive impact. It is essential to be aware of the ten mistakes identified by Ainsworth and Walters (2015). Understanding these mistakes can help improve the effectiveness of management risks. Schuwirth *et al.* (2019) also outline six requirements to enhance the utility of ecological models for management support, particularly when justifying decisions to the public. These prerequisites encompass the need for a mechanistic comprehension of causality, aligning model input and output with management decisions, ensuring appropriate temporal spatial resolutions, quantifying uncertainties, attaining satisfactory predictive performance, and maintaining transparent communication. Planque *et al.* (2022) also presented a general protocol designed to guide the reporting

of model evaluation. The protocol is organised in three major parts: the objective(s) of the modeling application, the ecological patterns of relevance and the evaluation methodology proper, and is termed the OPE (objectives, patterns, evaluation) protocol. They have presented the 25 questions of the OPE protocol which address the many aspects of the evaluation process and then apply them to six case studies based on a diversity of ecological models. In addition to standardising and increasing the transparency of the model evaluation process, we find that going through the OPE protocol helps modellers to think more deeply about the evaluation of their models. From this last point, we suggest that it would be highly beneficial for modellers to consider the OPE early in the modeling process, in addition to using it as a reporting tool and as a reviewing tool. The OPE protocol is proposed as a tool to report the evaluation of ecological models.

For the development of a shared understanding and the facilitation of knowledge transfer between science and practice, collaboration between environmental decision-makers and ecological modelers is essential (Schuwirth *et al.*, 2019). Studies indicate the importance of engaging stakeholders, particularly decision-makers, in the early stages and throughout the process of ecosystem modeling. This ensures that the modeling efforts effectively address pertinent management objectives and gain the necessary support and investment from decision-makers (Coll *et al.*, 2015). Providing estimates of model uncertainty alongside expected outcomes is essential for environmental managers to accurately interpret results and make reliable conclusions. Transparency in communicating uncertainty enhances the credibility of scientists (Schuwirth *et al.*, 2019). Adhering to the Findability, Accessibility, Interoperability, and Reusability (FAIR) principles for data management enables models to be easily discovered and be used online. Enabling public access to the model's source code and documentation fosters verification and encourages discussions among peer scientists, facilitating ongoing development (Schuwirth *et al.*, 2019).

Ecological uncertainty can be represented into ecological models by treating parameters as random variables. It has provided a road map for analyzing such models, including introducing tools from modern uncertainty quantification such as PC expansions. Applying these methods in our case study provides a first step towards incorporating small scale heterogeneity in parameter values into regional models of ice algal blooms. Consideration of this heterogeneity results in changes in estimated bloom phenology and intensity, and should not be neglected if we are to understand this important component of polar ecology and biogeochemistry (Reimer *et al.*, 2022).

Finally, to enhance the plausibility of models, iterative testing of different management strategies, representing various input variables at several spatio-temporal scales and intensities, can improve the realism and performance of ecological models and their results. Thorough documentation and clear communication aid in the management of unrealistic expectations and build trust in the models (Schuwirth *et al.*, 2019). Barros *et al.* (2022) proposed a practical solution to this challenge based on the frequent Predictions and Evaluations of Reusable, Freely accessible, Interoperable models, built within Continuous workflows that are routinely Tested (PERFICT) principles, using a modular and integrated framework. We present its general implementation across seven common components of ecological model applications—(i) the modeling toolkit; (ii) data acquisition and treatment; (iii) model parameterisation and calibration; (iv) obtaining predictions; (v) model validation; (vi) analysing and presenting model outputs; and (vii) testing model code—and apply it to two approaches used to predict species distributions: (1) a static statistical model, and (2) a complex spatiotemporally dynamic model. By linking all stages of an ecological modeling exercise, it is possible to overcome common challenges faced by ecological modellers, such as changing study areas, choosing between different modeling approaches, and evaluating the appropriateness of the model. This ultimately creates a more equitable and robust playing field for both modellers and end users (e.g. managers), and contributes to position predictive ecology as a central contributor to global change forecasting. The authors demonstrated a practical solution to two pervasive problems in ecological simulation modeling that can encumber the use of large datasets and complex models, hinder scientific progress, decrease model transparency, and reduce the durability and reusability of ecological simulation models. By demonstrating how ecologists can develop applied ecological models using transparent and reusable integrated workflows and harnessing community contributions, we hope to contribute to moving predictive ecology forward in the field of global change research and forecasting. Furthermore, in the study of DeAngelis *et al.* (2021), they have searched, examined, and documented ‘success stories’ in ecological management using ecological modeling from the past. Researchers have found that there is not a unique way to conduct a research project that is useful in management decisions; however, research is more likely to have impact when conducted with many stakeholders involved and specific to a situation for which data are available. The study came up with the same conclusions that communication is key in the process: listening closely to stakeholders’ needs and

explaining in simple terms the scientific tools involved, their powers and their limitations.

6. FUTURE DIRECTIONS OF ECOLOGICAL MODELING

The key step in addressing the challenge of comprehending the ecological consequences of environmental change involves constructing realistic models of ecological systems. These models enable accurate predictions of the system's state under future changed conditions, facilitating a better understanding of the ecological consequences (Evans, 2012). The loss of ecosystem services due to climate change and coastal development is projected to have significant impacts on local economies and conservation of natural resources. Consequently, there has been an increase in coastal management activities such as living shorelines, oyster reef restoration, marsh restoration, beach and dune nourishment, and revegetation projects. Coastal management decisions are complex and include challenging trade-offs. Decision science offers a useful framework to address such complex problems (Martin *et al.* 2023). Martin *et al.* (2023) provided a synthesis about how decision science can help to integrate research from multiple disciplines (physical and life sciences) with management of coastal and marine systems. Authors have showed how decision science can be used as a framework to combine geomorphological and ecological modeling to help inform management decisions while considering uncertainty about system changes and risk tolerance. Coll *et al.* (2015) emphasized the importance of delivering practical management advice for various environmental management processes and adapting to global changes, such as climate change. To secure the long-term sustainability of the Ecopath with Ecosim (EwE) approach, active participation of the broader EwE community in initiatives initiated by the Ecopath International Research and Development Consortium is crucial (Coll *et al.*, 2015). Moreover, simple techniques such as Specific, Measurable, Achievable, Relevant, and Time-bound (SMART) tables combined with an expert elicitation can be done in a matter of days (Runge *et al.*, 2020). Using holistic and interdisciplinary approaches to management that integrate all components of the decision-making process can be beneficial to coastal management over the long term as the Dauphin study of Martin *et al.* (2023) have mentioned and also noted that complex models are not always necessary, and we want to avoid the misconception that decision analysis is always time consuming or necessarily involves complex models.

The scientific exploration of aquaculture is also gaining significance. A future challenge lies in connecting the

EwE approach with meticulous and refined aquaculture models. This integration would enhance the representation of the ecological impacts of aquaculture and support spatial planning for effective management (Coll *et al.*, 2015). Furthermore, an inclusive approach should consider socioeconomic dynamics and drivers. It is envisioned that future integrated approaches will incorporate socioeconomic models to better serve society's needs (Coll *et al.*, 2015). Nevertheless, the rapid advances in technology, geomorphological, and ecological modeling and optimization algorithms offer opportunities to integrate disciplines and monitoring programs to inform coastal management (Martin *et al.*, 2023). Coll *et al.* (2020) presented an updated version of EcoOcean (v2), a spatial-temporal ecosystem modeling complex of the global ocean that spans food-web dynamics from primary producers to top predators. Advancements include an enhanced ability to reproduce spatial-temporal ecosystem dynamics by linking species productivity, distributions, and trophic interactions to the impacts of climate change and worldwide fisheries. The updated modeling platform is used to simulate past and future scenarios of change, where we quantify the impacts of alternative configurations of the ecological model, responses to climate-change scenarios, and the additional impacts of fishing. EcoOcean v2 can contribute to the quantification of cumulative impact assessments of multiple stressors and of plausible ocean-based solutions to prevent, mitigate and adapt to global change.

7. CONCLUSION

In conclusion, this review underscores the importance of aligning ecological models with management objectives and ensuring that inputs accurately reflect environmental factors. Recognizing the trade-offs inherent in modeling complex ecological systems is crucial, considering the need to balance specific biological characteristics with generalizability. The discussion also highlights the growing importance of explicit spatial models in addressing ecological interactions and marine policy initiatives, though acknowledging the computational challenges they present. The caution against excessive focus on modeling intricacies in fisheries assessment emphasizes the need for a balanced approach, avoiding unnecessary complexity that may impede timely and practical analyses for effective fisheries policy design and ecosystem management. As researchers navigate the intricate networks of ecosystems, a judicious balance between model sophistication and practical utility is essential for informed decision-making and sustainable environmental management.

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