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Review Article

Lessons from seventy-five years of ecosystem modeling in the Northeastern US Shelf

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Abstract

As fisheries management agencies move toward an ecosystem-based management framework it has become common to develop large and complex models to investigate the dynamics of marine systems. We review the published literature using ecosystem models for the Northeastern US Shelf (NEUS) to identify trends in modeling practices, model complexification, model application, and model evaluation over the last seven decades. We reveal that NEUS ecosystem modeling efforts have focused primarily on the effects of commercial fisheries on individual stocks but rarely addressed questions related to climate change impacts. Additionally, we determined that only 14 of the 67 NEUS publications include model validation or evaluation, and we stress the importance of validation and evaluation for future NEUS ecosystem models. We compare modeling efforts in the NEUS to two other US large marine ecosystems, the California Current System and the Gulf of Mexico, to compare trends in model complexification and identify modeling techniques that could be applied in the NEUS. Finally, we draw on our synthesis of 75 years of NEUS ecosystem modeling to recommend modeling techniques and applications that have the potential to move NEUS fisheries management toward ecosystem-based management frameworks.

Keywords: ecosystem models; modeling practices; ecosystem-based management; Northeastern US Shelf; model complexity; model evaluation; recommendations

Introduction

Dynamics of marine ecosystems are characterized by major perturbations driven by environmental and biological variability. This variability results in shifts in species dynamics, productivity, and distribution. In the western Atlantic and globally, anthropogenic drivers of system perturbations are increasingly present, such as climate change (Perry et al. 2005, 2010, Pörtner and Peck 2010, Blanchard et al. 2012, Poloczanska et al. 2016, Free et al. 2019), commercial fisheries (Goñi 1998, Planque et al. 2010, Eriksson et al. 2011, Ortuño Crespo and Dunn 2017), ocean acidification (Denman et al. 2011, Doney et al. 2012, Haigh et al. 2015), and invasive species (Anton et al. 2019), among many others. Although managed species live in complex ecosystems, management practices tend to utilize single species approaches, which disregard environmental and ecosystem processes, and the combined effects of anthropogenic drivers and species interactions (Botsford et al. 1997, Moffitt et al. 2016).

It has long been recognized that interactions between the environment (temperature, salinity, and so on) and species are important drivers of population dynamics; however, a lack of data, models, and management frameworks have limited the incorporation of ecosystem responses to environmental changes into assessment models used for management (Eddy et al. 2023). Recent studies emphasized the need for a shift from a single species framework to an ecosystem framework due to its accountability of environmental and anthropogenic influences on the dynamics of systems (Walters 1986, Smith et al. 1999, Fulton et al. 2014, Dankel and Edwards 2016, Punt et al. 2016, Kaplan et al. 2021, Siple et al. 2021). Therefore, it is necessary to develop alternative methods that account for species interactions and environmental effects allowing for the management of individual stocks from an ecosystem-based perspective (Levin and Lubchenco 2008, Curtin and Prellezo 2010, Long et al. 2015).

Ecosystem-based management (EBM) shifts the management approach toward consideration of the entire ecosystem (i.e. commercial, recreational, and nonexploited species, species interactions, natural variability, and individual and combined effects of anthropogenic stressors) to inform future management policies (Fogarty 2014). EBM provides managers with detailed and often complex information, and it remains a challenge to effectively convey findings to inform policy. Thus, clear or consistent frameworks are yet to be defined for the application of EBM and *ad hoc* implementation can be difficult to integrate into actionable policy (Leslie and McLeod 2007, Ruckelshaus et al. 2008, Levin and Möllmann 2015).

One way to integrate an EBM approach is to use an integrated ecosystem assessment (IEA) approach as a framework (Levin et al. 2009). The authors defined IEA as "an incremental approach, in which integrated scientific understanding feeds into management choices and receives feedback from changing ecosystem objectives." (Levin et al. 2009). In other

words, IEA constantly includes new knowledge for management to assess the current state of the ecosystem and its recent dynamics. EBM and IEA frameworks rely on the use of end-to-end food web models, such as Ecopath with Ecosim (EwE; Pauly et al. 2000, Heymans et al. 2016), ATLANTIS (Fulton et al. 2011, Audzijonyte et al. 2019), OSMOSE (Travers-Trolet et al. 2014, Grüss et al. 2018), or other models that simulate time series for species ranging from primary producers to top-predators (Planque et al. 2022a, Sivel et al. 2023).

Historically, exploited stocks on the Northeastern Shelf of the USA (NEUS) display large shifts in abundance. Over the last three decades, management regulations have often not been successful at rebuilding commercial stocks such as Atlantic cod and winter flounder. These failures suggest that a new approach to understanding population dynamics is needed (Pershing et al. 2015, Frisk et al. 2018). The winter flounder stock was first declared overfished in 1983 and has never recovered (Frisk et al. 2018). Similarly, Atlantic cod experienced protracted periods of overharvest, suffered collapses during the 1970s and 1980s and has failed to recover (Shelton et al. 2006). The decline of these stocks is hypothesized to be due to overfishing, climate change, predation, or a combination thereof (Meng et al. 2016, Frisk et al. 2018, Han et al. 2021). Yet, these fisheries have only been managed through a single species approach. In the coming decades, further work on ecosystem models is required to lead fisheries management to a holistic understanding of a system's dynamics and productivity resulting in improved management of commercial fisheries.

In this paper, we address the following objectives for NEUS: (1) provide an overview of the modeling efforts that have been published in the primary literature; (2) explore the historical complexification of food web models; (3) review modeling focused on the assessment of anthropogenic drivers on ecosystems (climate change, fisheries, and other); (4) review the modeling aimed at assessing ecosystem structure and functioning (network analysis, trophic dynamics, and bioaccumulation); (5) review model validation and evaluation efforts; (6) compare NEUS ecosystem modeling efforts to two other USA large marine ecosystems, the California Current System (CCS) and the Gulf of Mexico; and (7) make research recommendations for future NEUS ecosystem modeling. The intent of this review (objectives 1–5) is not to critically evaluate each approach, but instead to provide brief introductions to section topics, highlight the historical focus and approaches used in previous research efforts, and to briefly critique approaches to identify potential avenues for future research. This is followed by brief summaries of ecosystem modelling in the two other regions (objective 6) and research recommendations derived from the review of the NEUS and comparison to other regions (objective 7).

Objective 1: modeling efforts for the NEUS area

Current state of the modeling efforts for the NEUS

This review aims to identify published literature that used end-to-end and food web models to address ecological and management questions in the NEUS area. We used *ISI Web of Science* and *Google scholar* to select published articles utilizing models of interest for the NEUS. The search was conducted using specific terms: "*food web model*," "*ecosystem model*," "*Ecopath with Ecosim*," "*ATLANTIS*," "*OSMOSE ecosystem model*," "*multispecies model*," and "*network analysis*." We included all publications, which matched one of the specific terms and one of the areas. In total, we found 67 studies developing or applying end-to-end and food web models to address ecological issues. These articles focused on the entire NEUS area and smaller ecosystems therein (Table 1, Fig. 1). Published studies were grouped according to the objectives of the model application and the topics addressed.

Among the 67 published applications, the literature search showed that the most applied food web model is the Ecopath framework (i.e. Ecopath, EwE, EMAX, or Rpath) with a total of 28 model applications for the NEUS and areas therein (Table 2). The next most applied modeling framework was the ATLANTIS mode or network analysis approaches (outside and/or prior to the development of Ecopath) to assess the effects of human drivers on the ecosystem structure (eight applications each). Finally, many published studies correspond to single applications of a model, such as the LeMANS model, a length–structure dynamics model for the Georges Bank system in one published paper by Rochet et al. (2011).

Focus of modeling efforts for the NEUS area

In the present review, we identified the individual topics addressed in the 67 publications to detect a possible trend in the development and application of food web models since the 1940s. In the studies included in our review, we found 46 topics that could be organized into four major themes (Fig. 2). The major themes included "*Management*," "*Model development*," "*Ecosystem structure and functioning*," and "*Food web characteristics*." Themes addressed in the publications show that prior to 2009 most papers published using food web models or network analysis focused on identifying *food web characteristics*.

Simultaneously, the number of papers addressing issues related to *management* rose in the late 2000s with an increase in occurrence of the term "management" in publications. However, the management of ecosystems in the NEUS area and smaller entities therein mostly focused on the effects of fisheries and the response of the ecosystem to given management strategies. Thirty-one studies out of 67 addressed the effects of species removal through harvesting on the global dynamics of the ecosystem (Table 1). Surprisingly, "climate change" did not occur often in the published literature as only three publications addressed issues linked to climate change over the entire time-period covered by our review. Although EBM frameworks call for the development of large ecosystem models accounting for multiple anthropogenic drivers, only a few applications include multipressure analysis and assessed the combined effects on food web dynamics.

Objective 2: complexification of food web models

A trend observed in the published literature using food web models for the NEUS area is model complexification over time (i.e. more species and more trophic interactions accounted for in the models, Fig. 3). Early published models defined functional groups by grouping multiple species based on similar morphological traits and behaviors; as seen in a Narragansett Bay model that accounts for only three major compartments of the ecosystem: phytoplankton, nutrients, and zooplank-

Table 1. List of studies applying food web models to the NEUS ecosystem and areas therein. The values in the "Temporal resolution" column correspond to: "-"—no temporal aspect, "Day"—daily resolution, "M"—monthly resolution, "S"—seasonal resolution, "Y"—yearly resolution, and "Dec"—decadal resolution. In the "Validation/Evaluation," "N/A" indicates that model evaluation was not performed or not reported.

#	Publication	Modelling approach	Area	Number of functional groups	Temporal resolution	Validation/ evaluation	Main objective
1	Clarke et al. (1946)	Production model	Georges Bank	11	M	N/A	Estimate the productivity of the Georges Bank ecosystem.
2	Kremer and Kremer (1982)	Narragansett Bay model	Narragansett Bay	3	M	N/A	Develop a modelling framework accounting for multiple processes including carnivorous behaviour in a multitrophic model.
3	Sissenwine (1984)	Energetic model	Georges Bank	4	Y	N/A	Describe the functioning of the Georges Bank ecosystem based on the energy budget.
4	Baird and Ulanowicz (1989)	Energy flow network model	Chesapeake Bay	36	S	N/A	Present a quantitative schematic of carbon exchanges in the Chesapeake Bay ecosystem to determine the seasonal magnitudes of carbon transfers and identify the trophic pathways in the food web and characterize the seasonal dynamics in the Chesapeake Bay ecosystem.
5	Ulanowicz and Tuttle (1992)	Quasi equilibrium model	Chesapeake Bay	13	–	N/A	Identify the response of functional groups of the Chesapeake Bay ecosystem to variations in the oyster population.
6	Iannuzzi et al. (1996)	Mass-balanced mechanistic food web model	Passaic River, New Jersey	4	–	Sensitivity analysis	Identify the influence of key exposure factors on distribution variations of the uptake of xenobiotic chemicals in estuarine organisms.
7	Monaco and Ulanowicz (1997)	Ecopath + network analysis	Delaware Bay/Narragansett Bay/Chesapeake Bay	37	–	N/A	Identify the variations of carbon exchanges across three spatially close estuaries characterized by different food web structure.
8	Abarca-Arenas and Ulanowicz (2002)	Chesapeake Bay Network model	Chesapeake Bay	50	–	N/A	Study the effect of trophic aggregation of information indices in the Chesapeake Bay food web.
9	Von Stackelberg et al. (2002)	Bioaccumulation model + spatial submodel + risk submodel	Coastal waters of New York and New Jersey	2	S	N/A	Present a framework for a spatially explicit risk assessment associated with contaminated sediments in aquatic environments.
10	Krause et al. (2003)	Social network model	Chesapeake Bay	45	–	N/A	Using a social network method to identify species complexes within food webs of the Chesapeake Bay.
11	Libralato et al. (2006)	EwE	Chesapeake Bay	33	Y	N/A	Develop a new method to estimate the keystoneness of one functional group based on their total impact in a mass-balanced model and discuss the ecological implications of identified keystone species.
12	Steele et al. (2007)	EMAX	Georges Bank	14	Y	N/A	Identify the nutrients and carbon flow budgets through the Georges Bank ecosystem.
13	Zhang and Chen (2007)	Ecopath	Gulf of Maine	24	–	N/A	Evaluate the changes in American lobster between 1980 and 1990.
14	Link et al. (2008)	EMAX	Georges Bank	31	–	N/A	Identify the implications of observed changes in ecosystem composition for fisheries production in the framework of earlier energy budgets for the Georges Bank ecosystem.

Table 1. Continued

#	Publication	Modelling approach	Area	Number of functional groups	Temporal resolution	Validation/ evaluation	Main objective
15	Tyrrell et al. (2008)	Multispecies virtual population analysis	NEUS	23	Y	N/A	Elucidate the importance of predation on local prey populations in the scenario of lower groundfish and higher pelagic fish and elasmobranch abundances.
16	Christensen et al. (2009)	EwE	Chesapeake Bay	45	Y	N/A	Describe a novel tool that can be used to define management policies on fisheries in the future.
17	Collie et al. (2009)	End-to-end budget model	Georges Bank	17	Y	N/A	Identify the effects of variation in ecological processes on the yields of haddock and Atlantic cod on the Georges Bank ecosystem.
18	Gaichas et al. (2009)	Ecopath	Georges Bank	17	–	N/A	Identify the differences in energy budget between the Gulf of Maine, Georges Bank, the Norwegian Sea, the Barents Sea, the Eastern Bering Sea, and the Gulf of Alaska.
19	Gamble and Link (2009)	MS-PROD model	NEUS	24	–	N/A	Investigate the trade-offs between ecological and fisheries effects on ecological communities.
20	Johnson et al. (2009)	Network analysis	Chesapeake Bay	36	S	N/A	Investigate the seasonal dynamics of the Chesapeake Bay food web.
21	Kartascheff et al. (2009)	Network analysis	NEUS	Not specified	–	N/A	Study the conditions for a positive complexity–stability relationship in the niche, cascade, nested hierarchy, and random models based on the fraction of surviving species.
22	Link et al. (2009)	EMAX	Gulf of Maine	33	–	N/A	Identify the response of two major ecosystem networks to large-scale perturbations in model input parameters.
23	Overholtz and Link (2009)	Energy budget model	Gulf of Maine	16	Y	N/A	Identify the effects of single perturbations on the Gulf of Maine ecosystem dynamics.
24	Garrison et al. (2010)	Multispecies virtual population analysis extended	Georges Bank	4	Y	Sensitivity analysis	Proof of concept using the new MSVPA-X model on Atlantic menhaden in the Western North Atlantic.
25	Link et al. (2010)	ATLANTIS	NEUS	45	Y	Visual comparison with observations	Identify the performance of the Atlantis model for the NEUS area for management purposes.
26	Ma et al. (2010)	EwE + Chesapeake water quality model	Chesapeake Bay	45	Y	N/A	Study the effect of increased submerged aquatic vegetation on trophic interactions of blue crab young-of-the-year and adults.
27	North et al. (2010)	Oyster restoration optimization + nitrogen–phytoplankton–zooplankton–detritus (NPZD)	Chesapeake Bay	4	–	N/A	Link ecosystem prediction and human use to present important restoration trade-offs.
28	Runge et al. (2010)	Nitrogen–phytoplankton–zooplankton–detritus (NPZD)	Gulf of Maine	4	S	N/A	Explore the feasibility of using coupled physical–biological models as an integrative tool for understanding climate forcing of Atlantic cod and other fish populations, using the Atlantic cod stock in the Gulf of Maine as an example.

Table 1. Continued

#	Publication	Modelling approach	Area	Number of functional groups	Temporal resolution	Validation/ evaluation	Main objective
29	Steele and Gifford (2010)	Trophic centered model and species centered model	Georges Bank	17	Y	N/A	Study the difference between the trophic-centered and the species-centered modelling approach.
30	Byron et al. (2011a)	Ecopath	Narragansett Bay	15	–	PREBAL	Model the carrying capacity of farmed oysters in the Narragansett Bay.
31	Byron et al. (2011b)	Ecopath	Narragansett Bay	16	–	PREBAL	Calculate the shellfish carrying capacity in the Narragansett Bay.
32	Frisk et al. (2011)	EwE	Delaware Bay	47	Y	N/A	Identify the effect of marsh habitats restoration on Delaware Bay productivity.
33	Nuttall et al. (2011)	Ecopath	Great South Bay	42	Dec	PREBAL	Study the trend of maturity in Great South Bay over the last 120 years.
34	Rochet et al. (2011)	LeMANS model	Georges Bank	21	–	N/A	Compare the communities of Georges Bank and the North Sea.
35	Salas and Borrett (2011)	Network analysis	NEUS	Not specified	–	Sensitivity/ Uncer- tainty analysis	Meta-analysis of the role and implications of indirect effects on food web properties across multiple ecosystems within the NEUS area.
36	Gamble and Link (2012)	AGG-PROD model	NEUS	3	Y	N/A	Exploring the effects of harvesting, competition, predation, and climate on the individual functional groups of the NEUS ecosystem.
37	Jin et al. (2012)	End-to-end trophic network model + computable general equilibrium model	Georges Bank	17	–	N/A	Identify the welfare effects of changes in alternative combinations of yields from fielding guilds and alternations of biological productivity.
38	Niquil et al. (2012)	Network analysis	Narragansett Bay	14	–	N/A	Study the effects of variations in environmental and estuary shapes on the morphological classification of benthic and pelagic estuaries.
39	Zhang et al. (2012)	EwE	Gulf of Maine	24	Y	N/A	Study the interactions between lobster, cod, and other functional groups in the Gulf of Maine ecosystem.
40	Ji et al. (2013)	Nitrogen–phytoplankton–zooplankton–detritus (NPZD)	Gulf of Maine/Georges Bank	4	S	N/A	Assess the relative importance of bottom-up and top-down controls of different copepod species in different areas of the Gulf of Maine—Georges Bank regions.
41	Nye et al. (2013)	ATLANTIS	NEUS	49	Y	N/A	Identify the effects of warming and top predator removal in temperate marine ecosystems.
42	Ruzicka et al. (2013)	ECOTRAN e2e	Georges Bank	22	–	Sensitivity analysis	Study the uncertainties in prey–predator functional responses and identify potential compensatory changes to community structure and ecosystem-level energy transfer efficiencies over time.
43	Townsend (2014)	Chesapeake fisheries ecosystem model (CB-FEM)	Chesapeake Bay	45	Y	N/A	Explore how management decisions in one section affects all the other components of the ecosystem.

Table 1. Continued

#	Publication	Modelling approach	Area	Number of functional groups	Temporal resolution	Validation/ evaluation	Main objective
44	Xiao and Friedrichs (2014)	Nitrogen–phytoplankton–zooplankton–detritus (NPZD)	Mid-Atlantic Bight	Not specified	Day	Cross-validation	Study the effect of increased species resolution at lower trophic levels on the levels of chlorophyll and particulate organic carbon in food web models.
45	Byron et al. (2015)	Ecopath + economic input–output model	Narragansett Bay	15	–	PREBAL	Study the socioeconomical and ecological impacts of aquaculture development in the Narragansett Bay area.
46	Morgan and Sulikowski (2015)	Ecopath	Gulf of Maine	30	–	PREBAL	Identify the ecosystem effects of the spiny dogfish recovery since 2004.
47	Byron and Morgan (2016)	Ecopath	Gulf of Maine	29	–	PREBAL	Study the trophic role of spiny dogfish in combination with harbor seals and white sharks in the Gulf of Maine area.
48	Olsen et al. (2016)	ATLANTIS	NEUS	45	Y	Skill performance metrics	Evaluate the skills of the ATLANTIS model to make forecasts and test management strategies.
49	Smith et al. (2016)	Ecopath	Gulf of Maine	20	–	PREBAL and sensitivity analyses	Study the interaction between diadromous fishes that occupy lower trophic levels as forage and nondiadromous fish species that uses estuaries as nursery grounds.
50	Van Der Zee et al. (2016)	Network analysis	Narragansett Bay	Not specified	–	N/A	Compare the sensitivity of food web properties in the areas of the Narragansett Bay salt marshes and the Banc d'Arguin seagrass meadows to the effect of habitat modifying species.
51	Fay et al. (2017)	ATLANTIS	NEUS	45	Y	N/A	Identify the effects of ocean acidification on species biomass and fisheries yields.
52	Olsen et al. (2018)	ATLANTIS	NEUS	45	Y	N/A	Present the contribution of end-to-end ecosystem models to EBM with a specific focus on ocean acidification.
53	Ruzicka et al. (2018)	ECOTRAN e2e	Georges Bank	30	Y	N/A	Study the role of food web structure and physical context in defining ecosystem dynamics.
54	Wildermuth et al. (2018)	Quantitative loop analysis	Georges Bank	Not specified	–	N/A	Investigate the use of qualitative models to study the dynamics of socio-economical systems, identify possible trade-offs between management objectives, and study the effect of the uncertainty in the system structure on model outcomes and associated management implications.
55	Dias et al. (2019)	EwE	NEUS	59	Dec	N/A	Study the consequences of increasing forage fish abundance on their predators, on the environmental health, on ecosystem services, and human well-being.
56	Fay et al. (2019)	ATLANTIS	NEUS	45	Y	N/A	Identify the consequences of management strategies on socio-economical components, such as regional sales, wages, and employment.
57	Chagaris et al. (2020a)	EwE + MICE models	NEUS	17	Y	N/A	Present the EwE and MICE model framework used to derive ecological reference points for management.

Table 1. Continued

#	Publication	Modelling approach	Area	Number of functional groups	Temporal resolution	Validation/ evaluation	Main objective
58	Chapman et al. (2020)	Ecopath	Gulf of Maine	20	–	PREBAL	Identify the response of bivalves carrying capacity to climate change and decrease aquaculture development in coastal Maine.
59	Innes-Gold et al. (2020)	EwE	Narragansett Bay	15	Y	PREBAL and Monte Carlo simulations	Identify recent changes in ecosystem dynamics and test the performance of the EwE model for management purposes using the Narragansett Bay ecosystem as a case study.
60	Sun et al. (2020)	Network analysis	NEUS	31	–	N/A	Compare the resistance of biodiversity between motif-based centrality and random sequence food webs.
61	Han et al. (2021)	EwE	Gulf of Maine	25	Y	N/A	Identify the recent changes in the Gulf of Maine ecosystem dynamics, compare them to past changes, and test if fisheries can explain the observed changes.
62	Innes-Gold et al. (2021)	EwE + agent-based model for fishers behavior	Narragansett Bay	15	Y	N/A	What are the combined effects of commercial and recreational fisheries on the Narragansett Bay ecosystem while accounting for recreational fishers behaviour.
63	Lucey et al. (2021)	Rpath	Georges Bank	29	Y	N/A	Present the newly developed Rpath tool.
64	Caracappa et al. (2022)	ATLANTIS	NEUS	89	S	N/A	Test the performance of the ATLANTIS model to catch expected spatial and seasonal patterns and test the performance of the ATLANTIS model zooplankton functional group to respond to primary producer forcing.
65	Dias et al. (2022)	EMAX	Gulf of Maine	45	Y	PREBAL	Identify the response of the alosine group to reduced fisheries and increased river to ocean habitat connectivity.
66	Heinichen et al. (2022)	EwE	Narragansett Bay	15	Y	N/A	Present a framework to account for the temperature-dependent bioenergetics to simulate food web dynamics.
67	Mason et al. (2023)	Bioaccumulation model	Gulf of Maine	8	–	N/A	Identify the factors that control the bioaccumulation and trophic transfer of MeHg in estuarine food webs.

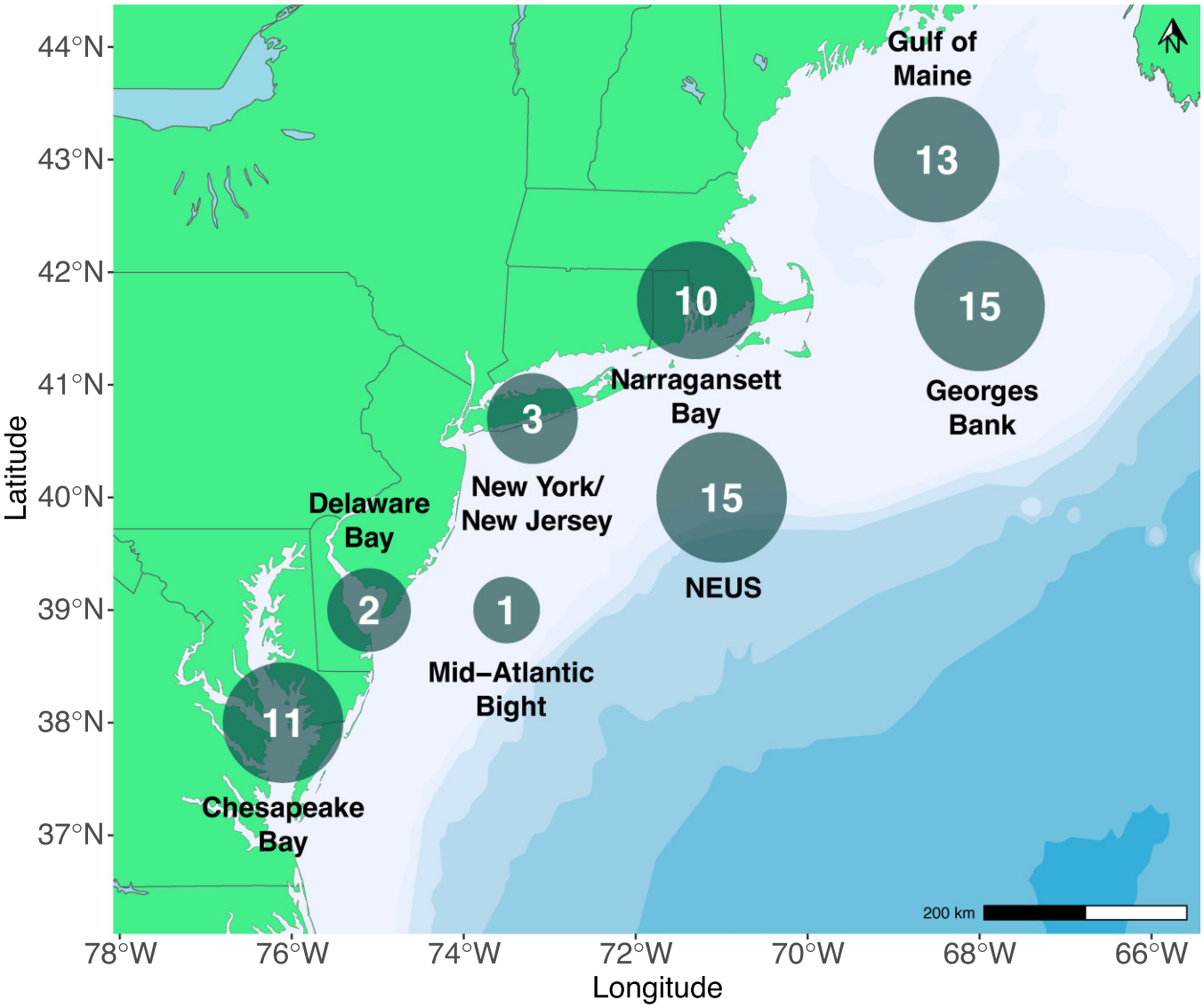

Figure 1. Heterogeneous modeling efforts in the NEUS region and areas therein. The size of the circles is proportional to the number of model applications for the area. The number in the circle corresponds to the number of models developed and applied for the given area. The total number of model sums up to 70 models given that Monaco and Ulanowicz (1997) applies three different models within the NEUS area and Ji et al. (2013) applies a model to two different areas.

ton (Kremer and Nixon 1978). Later, more general questions about dynamics of natural systems and the species composing them became the focus of modelers, which led to the development of more complex models by coupling existing models. The complexity of ecosystem models increased along multiple axes: the number of species and/or functional groups incorporated (Fig. 3), and the number of modules (i.e. submodels included in the larger ecosystem model) representing multiple facets of ecosystems (e.g. bioaccumulation of pollutants).

The number of species/functional groups incorporated into ecosystem models increased with the development of the first mass-balanced models for the Georges Bank ecosystem, which accounted for 11 (Clarke et al. 1946) and 10 functional groups (Sissenwine 1984). More recent models increased in complexity with the development of end-to-end models, such as EwE, modeling frameworks that include the effects of fisheries on systems' trophic dynamics. The number of functional groups in these models are highly variable between and within individual subareas. For example, EwE models focusing on the Gulf of Maine ecosystems range from 20 (Chapman et al. 2020) to 30 functional groups (Morgan and Sulikowski 2015) (Table 1). The increase in model structure complexity is largely due to finer partitioning of functional groups, the use of individual species (e.g. Christensen et al. 2009), or the addition of multiple ontogenetic stages for species (e.g. Dias et al. 2019).

The spatial extent of ecosystem models has increased to reflect the distribution of commercial stocks more accurately. Among published models for the whole NEUS area, the Energy Modeling Analysis Exercise (EMAX) used the EwE modeling framework to study ecosystem dynamics and their response to important anthropogenic drivers (Steele et al. 2007, Link et al. 2008, 2009, Dias et al. 2019, 2022). Similarly, ATLANTIS models for the whole NEUS area explore the dynamics of large marine ecosystems while accounting for biogeochemical processes (Link et al. 2010, Nye et al. 2013, Olsen

Table 2. Number of applications per model type in the NEUS area

Model type applied	Number of applications
Production model	1
Narragansett Bay model	1
Energetic model	1
Energy flow network model	2
Quasi-equilibrium model	1
Mass-balanced model	1
Ecopath/EwE/EMAX	28
Network analysis	8
Chesapeake Network model	1
Bioaccumulation model	1
Social Network model	1
MSVPA/MSVPA-extended	2
End-to-end budget model	3
MS-PROD/AGG-PROD	2
ATLANTIS	8
NPZD	4
LeMANS	1
Quantitative loop analysis	1

et al. 2016, 2018, Fay et al. 2017, Ruzicka et al. 2018, Caracappa et al. 2022).

Lastly, models have increased in complexity by coupling trophic models with biogeochemical models. Ma et al. (2010) coupled an EwE model with the Chesapeake Bay Water Quality Model to assess the effects of increased submerged aquatic vegetation on blue crab trophic dynamics while accounting for water quality. Important questions, such as how bioaccumulation of pollutants effects species dynamics (Von Stackelberg et al. 2002), how fisheries economics effects management strategies (Jin et al. 2012, Byron et al. 2015), and how the behavior of individuals species affects system dynamics and resulting yields (Innes-Gold et al. 2021) were also investigated using coupled models. The ability of contemporary models to handle complex species interactions, environmental variables, migration, stock structure, spatial dynamics, and many other drivers; raises the question at what level of complexity is the model output no longer useful?

Collie et al. (2016) suggested the existence of a "sweet spot" corresponding to a model representation of the ecosystem of intermediate complexity, where the uncertainty in management indicators is the lowest. Extreme complexity is not always necessary to model complex dynamics and inform management policies (Maxwell et al. 2015). Higher complexity implies a higher need for data to simulate accurate ecosystem dynamics (Fulton et al. 2003, Geary et al. 2020). However, the required data is not always available for all species in the ecosystem resulting in large uncertainties and inaccurate predictions of future ecosystem dynamics (Collie et al. 2016). In their study, Xiao and Friedrichs (2014) demonstrated that too much complexity can reduce model performance by reproducing observed chlorophyll-a and particulate organic carbon patterns using five models characterized by differing levels of complexity. They found the most complex model did not perform the best, but rather the 1P1Z model (one phytoplankton and one zooplankton group) was most accurate in reproducing the observed patterns (Xiao and Friedrichs 2014). Models of intermediate complexity for ecosystem assessment (MICE; Plagányi et al. 2014) represent an alternative to more complex models and may be characterized by lower uncertainties due to lower complexity and fewer data requirements. In the NEUS area, a MICE was developed based on the EMAX model and applied to derive ecological reference points (ERPs) for Menhaden in the Northwest Atlantic Continental Shelf (Chagaris et al. 2020a). Nevertheless, management requires input from both complex and simpler models to provide useful and appropriate advice to stakeholders (Steele and Gifford 2010).

Objective 3: assessment of anthropogenic drivers in ecosystems

Climate change

Surprisingly, only a few model applications accounted for climate change or temperature variations in the 67 papers included in this study. Among these few papers, three approaches to incorporate temperature effects in ecosystems models were described: (1) altering energy transfers between trophic levels in response to changes in ocean temperature (Chapman et al. 2020), (2) using the Q_{10} temperature coefficient (Rao and Bullock 1954, Mundim et al. 2020) to model the effects of climate change by modifying the organismal metabolic rate parameters (Nye et al. 2013, Heinichen et al. 2022), and (3) coupling ecological models to biophysical models to force nutrient inputs (Runge et al. 2010). Where Chapman et al. (2020) changed the biomass ratios between secondary/tertiary producers and primary producers to alter the energy transfer between trophic levels, Nye et al. (2013) and Heinichen et al. (2022) included parameter value variations based on modeled metabolic rate response to temperature changes in their simulations. Coupling ecosystem models with biophysical models has the potential to be a powerful approach to model climate change effects on ecosystem dynamics as it accounts for temporal and spatial dynamics.

General studies published on increased temperature effects on fish suggest that higher temperatures result in changes in physiology, behaviour (Pörtner and Peck 2010), and limit the capacity to cope with additional stressors (Alfonso et al. 2021). Pörtner and Peck (2010) also highlight the potential effects of altered physiology on fish populations and their consequences at an ecosystem level. In EBM frameworks, using ecosystem models that integrate the effects of climate change can help to reveal the temperature-dependent fish population dynamics, identify how the combination of temperature variations and additional stressors affect ecosystem structure and functioning, and highlight the role of climate in ecosystem dynamics. Historically, neither climate change nor temperature variations have been the focus of published ecosystem models in the NEUS, except for three publications we included in this review.

Fisheries

Fisheries impact marine ecosystems via the overall removal of biomass and the selective removal of targeted fish species, sizes, and trophic levels. Complex ecosystem models can provide important information for fisheries management, such as ERPs (Tyrrell et al. 2011, Smith et al. 2015, Chagaris et al. 2020a, Drew et al. 2021) or species carrying capacity (Byron et al. 2011a, b). However, it is important to note that ERPs are not independent of environmental perturbations and interspecific interactions (e.g. predation and resource competition; Gamble and Link 2009, Garrison et al. 2010). Additional information for fisheries management can be derived from ecosystem models evaluating the impact of restoration

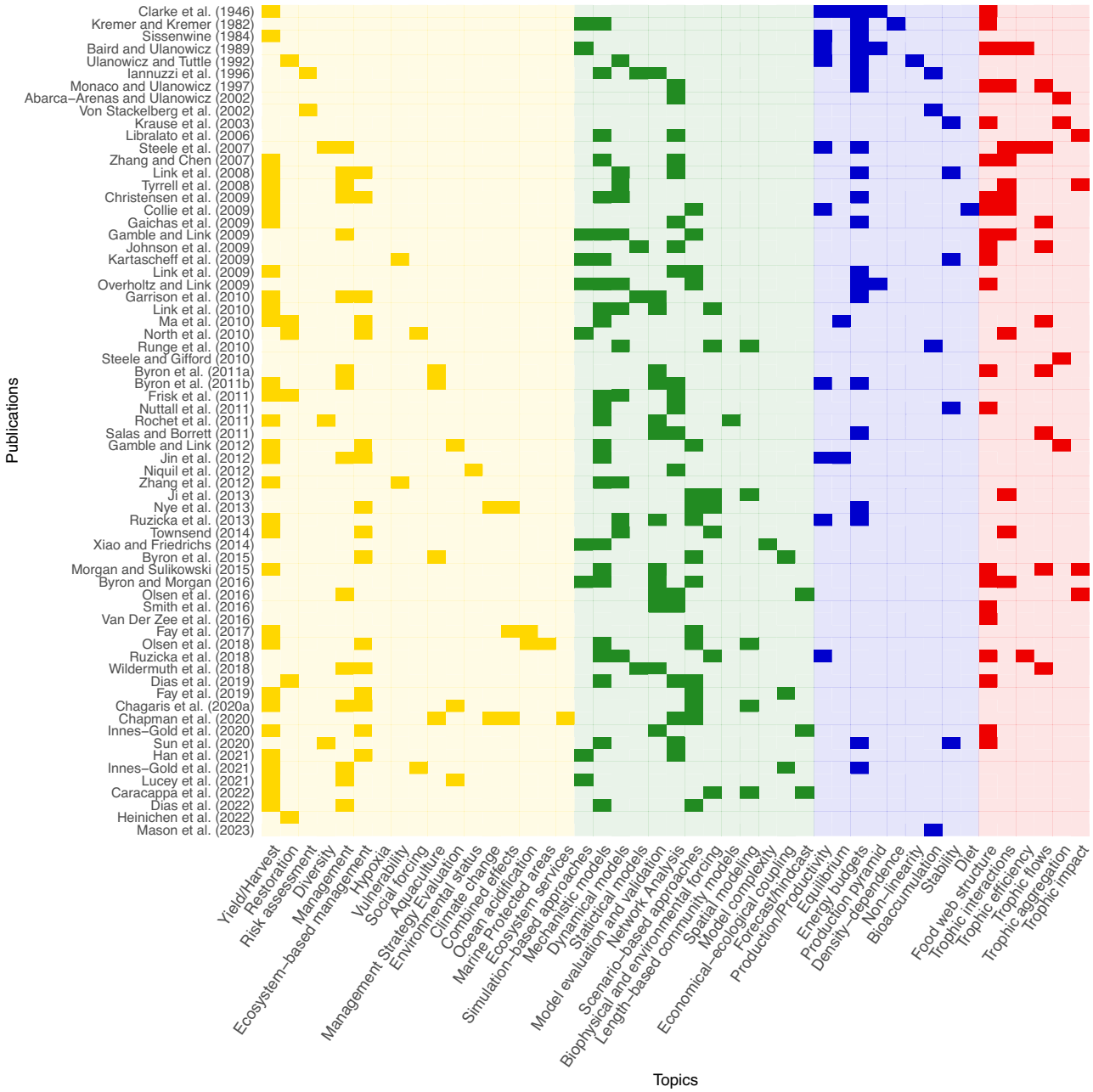

Figure 2. Evolution of modeling objectives in model applications for the NEUS area and regions therein. Colored cells indicate topics addressed in each publication. Colors stand for overarching topics addressed in modeling studies (yellow: "*Management,*" green: "*Model development,*" blue: "*Ecosystem structure and functioning,*" and red: "*Food web characteristics.*"

efforts while incorporating the effects of environmental perturbations and interspecific interactions (Ulanowicz and Tuttle 1992, Frisk et al. 2011, Chagaris et al. 2020a). Yet, most published model applications aiming at providing information for management focus on individual species. For example, Byron et al. (2011a) uses an EwE model to derive the carrying capacity of cultured oysters in the Narragansett Bay without reporting the state of other commercial species. Only a few studies highlight changes at an ecosystem level due to human intervention (e.g. Frisk et al. 2011).

Beyond management-oriented results, ecosystem models have also been used to assess the effects of fisheries on ecosystem structure and functioning. In the Gulf of Maine, higher fishing rates were found to potentially alter the functioning and the structure of the whole ecosystem (Overholtz and Link 2009, Innes-Gold et al. 2020, Han et al. 2021). Recently, sociological and economic aspects of fisheries have been incorporated into existing ecosystem models. These developments have allowed for the investigation of the effects of changes in fishing intensity on the fishers' income (Fay et al. 2019) and the effects of individual fisher behavior on species dynamics (Innes-Gold et al. 2021).

Other anthropogenic activities

Other than fisheries and climate change, many additional anthropogenic and environmental stressors affect marine ecosystems. In the NEUS, the ATLANTIS model was used to (1) in-

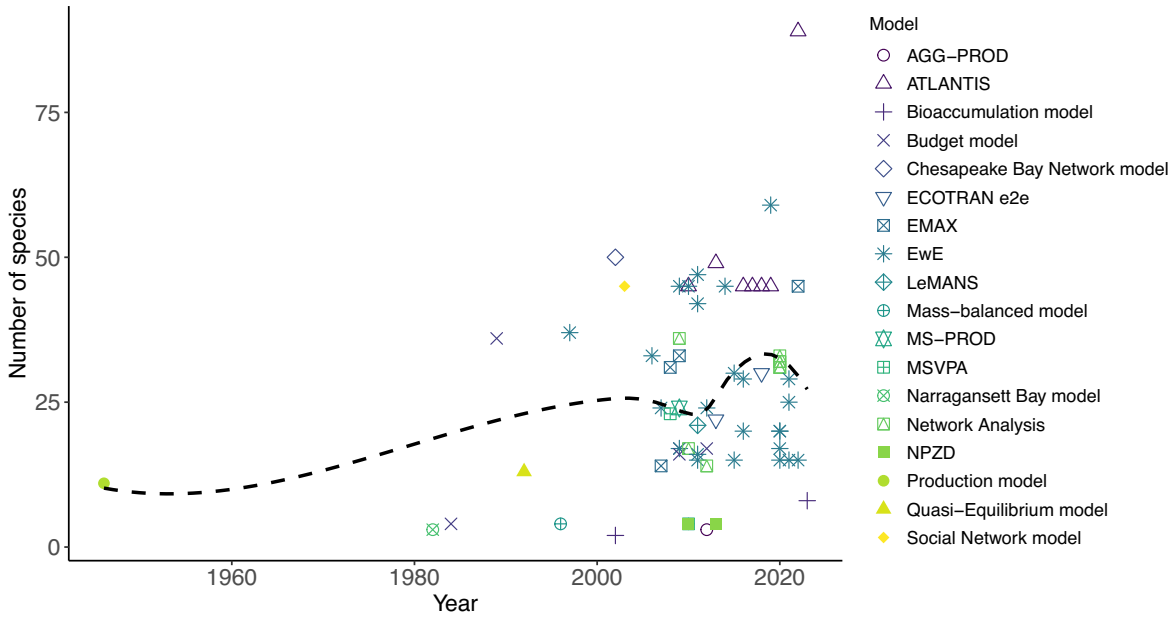

Figure 3. Complexification of ecosystem models in the NEUS area and regions therein. Each point corresponds to a model published for a given year and the associated number of species/functional groups. The shape and color of each point corresponds to a given modeling framework.

vestigate the effects of ocean acidification on ecosystem structure, functioning, and dynamics (Fay et al. 2017), and (2) explore the tradeoffs between species, management actions, and societal choices when the ecosystem is challenged by changing ocean acidification, spatial management, and fishing pressure in eight different marine systems (California Current, Guam, Northern Gulf of California, Chesapeake Bay, Nordic and Barents Sea, Gulf of Mexico, Northeast USA, and Southeast Australia; Olsen et al. 2018). Besides the NEUS ATLANTIS model, a multispecies length-based model (LeMANS) was used to evaluate how different levels of fishing selectivity affects biodiversity within the Georges Bank and North Sea systems (Rochet et al. 2011).

An important element highlighted in this review in the NEUS is that only a few models investigated the combined effects of anthropogenic drivers (Table 1). This trend is common to most coastal and marine ecosystems (Simeoni et al. 2023) although cumulative impacts represent a significant threat to ecosystem health (Beusen et al. 2022). In their systematic review of cumulative impacts of climate change and human stressors, Gissi et al. (2021) highlighted the response of marine ecosystem dynamics to combined drivers is often variable. However, the authors emphasize the need to identify interactions between multiple drivers to develop appropriate management actions to mitigate the effects of stressors.

Objective 4: exploring ecosystem structure and functioning

Ecological network analysis

Ecological network analysis (ENA) uses metrics to describe the structure and the functioning of food webs and can be based on model outputs or on direct observations (Wulff et al. 1989). Based on information theory and the assumption that an ecosystem can be summarized to a set of flows between nodes, Lindeman (1942) and MacArthur (1955) derived the first metric of ENA quantifying the number of possible paths for energy to flow through the ecosystem (i.e. the Shannon–Weaver index). This metric was utilized as a measure of stability of the ecosystem in classic ecological literature (Odum 1953). Published works for the NEUS and areas therein used ENA to investigate food web properties, such as stability and related concepts (e.g. complexity, connectivity, ascendency, and maturity; Table 3) based on food web model outputs (Abarca-Arenas and Ulanowicz 2002, Kartascheff et al. 2009, Frisk et al. 2011, Nuttall et al. 2011, Van Der Zee et al. 2016, Sun et al. 2020). These applications highlighted the positive correlation between ascendancy, connectance, and stability of the ecosystem (Abarca-Arenas and Ulanowicz 2002, Johnson et al. 2009).

ENA tools have been incorporated into more complex modeling frameworks, such as EwE (Christensen and Pauly 1992). A common practice in the literature is to compare the ENA indices from Ecopath models corresponding to two different time periods (Zhang and Chen 2007, Frisk et al. 2011, Nuttall et al. 2011) or different systems (Libralato et al. 2006, Niquil et al. 2012). The comparison of ENA between two time periods allows users to evaluate the effects of stressors or management actions on the ecosystem structure and functioning. More complicated models, such as ATLANTIS, allow for an in-depth investigation of how abiotic and biotic variables impact ecosystem stability but have not been utilized in the NEUS. Using ENA with complex model outputs enables the investigation of the consequences of complex ecological perturbations on ecosystem structure and functioning (Ruzicka et al. 2018)

Trophic dynamics

Historically, food web models were developed to explore and describe the carbon, energy, or nutrient exchanges between compartments of the food web (Clarke et al. 1946, Kremer and Kremer 1982). "Energy budgets" and the theory that energy transfer efficiency between trophic levels can be used to describe ecosystem functioning was the base to investigate car-

Table 3. List of definitions for concepts associated to Ecological Network Analysis (ENA). Note: some of the terms meaning/interpretations have been debated since originally defined and we do not enter that discussion in this review.

Term	Definition	References
Stability	Overarching term describing the response of an ecosystem to return to its equilibrium. Can be defined in four components: 1. An ecosystem is considered stable if the entire set of parameters return to equilibrium after a perturbation. 2. Resilience measures the speed at which the ecosystem returns toward equilibrium. 3. Resistance measures the time an ecosystem parameter remains unchanged following a perturbation. 4. Variability measures the variance of population over time.	Pimm (1984)
Complexity	Overarching term describing the structure of an ecosystem: 1. Species richness corresponds to the number of species/functional groups. 2. Connectance is the ratio between the number of interspecific links and the number of possible links.	Pimm (1984)
Maturity	Overarching concept describing the stage of succession at which an ecosystem is in. The concept relies on the idea that every ecosystem tends toward a mature and stable final stage	Odum (1969)
Ascendency	Indicator of ecological maturity measuring the ecosystem activity given its organization. It is often associated to the concept of "capacity" (i.e. the maximum activity of the ecosystem given its structure) and "overhead" (i.e. activity needed for the ecosystem to reach capacity)	Allesina et al. (2009)
Total System Throughput (TST)	Sum of all flows (transfer + import + export) in the food web	Finn (1976)
Finn Cycling Index (FCI)	Measure of the contribution of TST due to energy/biomass cycling	Finn (1976)
Average Path Length (APL)	Average number of food web compartments through which the energy/biomass is flowing from trophic level 1 to the highest trophic level	Finn (1976)

bon and energy budgets for different temporal and spatial scales (Sissenwine 1984, Baird and Ulanowicz 1989, Monaco and Ulanowicz 1997). More recently, complex models estimating energy budgets were developed (EMAX; Steele et al. 2007, Link et al. 2008). These more complex models enabled testing of the effectiveness of management strategies by simulating ecosystem trophic dynamics under specific management scenarios (e.g. Link et al. 2009, Dias et al. 2022).

Food web dynamics can be affected by trophic dynamics through nontrophic interactions (Gamble and Link 2009, Van Der Zee et al. 2016, Ruzicka et al. 2018). Some studies emphasized the importance of including nontrophic interactions in ecosystem models to simulate realistic trophic dynamics of natural systems. Including nontrophic interactions allows for the evaluation of external drivers, such as fisheries on species having indirect interactions with harvested species (Gamble and Link 2009) that impact trophic dynamics.

Accounting for trophic interactions in ecosystem models allows users to investigate the role of specific functional group types in the structure and functioning of marine ecosystems, especially small pelagic fish or forage fish (Link et al. 2009, Overholtz and Link 2009, Smith et al. 2016, Dias et al. 2019, 2022). Ecosystem models were also used to explore the mechanisms defining the trophic dynamics of food webs, such as trophic control (Overholtz and Link 2009, Ji et al. 2013). Trophic control is a widely studied characteristic of food webs because it allows for an overview of the major mechanism of the response of the food web to environmental and anthropogenic drivers. Bottom-up control often stands for climate-controlled dynamics while top-down indicates predation- or fisheries-driven dynamics. However, it is not always clear if systems are driven by environmental drivers, predation/harvesting, or both (Overholtz and Link 2009, Ji et al. 2013). Intensive human activity, resulting in the alteration of the physical environment, increasing temperature, overharvesting, and habitat loss, can lead in the occurrence of regime shifts or seasonal variability in ecosystem structure and functioning. These changes can be highlighted by investigating the dominance regimes, or network indices, such as the average trophic level or ecosystem maturity (Zhang and Chen 2007, Johnson et al. 2009, Nuttall et al. 2011, Han et al. 2021). Globally, the published literature for the NEUS highlights the importance of species interactions in individual species dynamics and calls for managing natural resources from an ecosystem context.

Bioaccumulation

Bioaccumulation is defined as "the intake of a chemical and its concentration in the organism by all possible means, including contact, respiration and ingestion" (Alexander 1999). Bioaccumulation can potentially become problematic through the process of biomagnification (i.e. transmission of chemicals to higher trophic levels via predation and their accumulation in higher trophic level tissues) and needs to be better understood given increasing pollutant concentrations (Ivar do Sul and Costa 2014). With models that can explore and reproduce the mechanism for bioaccumulation, it is possible to investigate the potential effects of pollutant contamination on human health. Furthermore, available studies have shown that pollution and climate change can have additive effects on coastal ecosystems (Cabral et al. 2019). Thus, it is necessary to develop food web modeling techniques that allow incorporation of bioaccumulation of pollutants. In the NEUS, we found only three examples of biological models coupled to bioaccumulation models (Iannuzzi et al. 1996, Von Stackelberg et al. 2002, Mason et al. 2023). Identifying factors that facilitate the

transfer and the accumulation of chemical pollutants across marine food webs would help to define appropriate management policies and prevent major public health issues in the future.

Objective 5: ecosystem model validation and evaluation

Validation and evaluation of numerical models are essential to the model development process (Schuwirth et al. 2019). The concepts of validation and evaluation are long standing principles in ecological modeling. However, no general consensus exists on the exact definitions of validation and evaluation (Augusiak et al. 2014, Eker et al. 2019). For example, Rykiel (1996) defines validation as the process after which "*a model is acceptable for its intended use because it meets specified performance requirements*," whereas Oreskes (1998) assigns the term "evaluation" to a similar definition. Recent work on the terminology suggests that "model evaluation" should test if the model is "*fit for purpose*" (Jakeman et al. 2006, Parker 2020). Model evaluation is an essential step of the model application, during which the model's performance to address the initial goal is assessed by comparing model outputs to independent data. Here, we consider model evaluation as the process to assess goodness of fit between model outputs and observation data, and methods assessing how uncertainty can affect users' conclusions. We consider model validation as the process of testing the realism in the model outputs (i.e. the model produces realistic outputs or model outputs reflect the combination of processes included in the model).

In the NEUS, only 14 publications out of the 67 included in this study mention using model validation or evaluation (Table 1 and Fig. 2). We also observed that only one study conducted model validation and performed a sensitivity analysis to test the robustness of model outputs to the uncertainties in the model parametrization (Byron and Morgan 2016). Not surprisingly, most EwE frameworks applied the recommended model prebalancing diagnostics (i.e. PREBAL; Link 2010), which corresponds to a set of metrics providing insight on model structures following assumptions of mass-balanced systems conducted on the model output. For instance, the PREBAL protocol checks that input biomasses follow the assumption of a 90% biomass loss between two trophic levels. It allows users to identify incompatibilities between the model structure and biological theory before accepting a balanced model given initial inputs. However, there is no certainty that a system at any moment is in equilibrium (i.e. migration and immigration) and does not necessarily follow the PREBAL assumptions.

In the NEUS literature, model evaluation was performed using two different approaches. The most common approach involved running a sensitivity analysis to identify changes in model output over a specified range of input parameter values (Iannuzzi et al. 1996, Garrison et al. 2010, Byron and Morgan 2016, Wildermuth et al. 2018). For example, Ruzicka et al. (2013) conducted a sensitivity analysis to assess the response of higher trophic levels to variations in the biomass of lower trophic levels. The second most common approach to evaluate model performance involved comparing model outputs to historical observations. For instance, Link et al. (2010) evaluated the skills of the ATLANTIS model for the NEUS by assessing the spatial overlap between the simulated chlorophyll-a distribution and satellite derived estimates of chlorophyll-a.

Objective 6: comparison with the California Current and the Gulf of Mexico systems

The CCS

In the CCS, the complexification (i.e. the increasing number of functional groups and model components) trend over the last 40 years was not as visible as for the food web models in the NEUS because, CCS are on average more complex compared to the NEUS models (141 functional groups versus 59 functional groups; Gaichas et al. 2010, Dias et al. 2019), although the applied modeling frameworks to the CCS were similar to the NEUS models (i.e. EwE, ATLANTIS, and so on).

The CCS models were used to assess multistressor impacts on ecosystem dynamics (Kaplan et al. 2010, 2017, Marshall et al. 2017), identify the effects of significant shifts in key species on the ecosystem (Radovich 1982, Zwolinski and Demer 2012, Kaplan et al. 2017), investigate the implications of key species dynamics shifts for future management strategies (Kaplan and Levin 2009, Marshall et al. 2014, Hodgson et al. 2018), explore the uncertainties related to ecosystem processes included in large models (Gaichas et al. 2012), quantify and predict the consequences of pollutant dispersion in the environment (Alava and Gobas 2016, Alava et al. 2016), and to explore the potential combined effects of pollution and climate change on food webs (Alava et al. 2018).

This brief overview of CCS model applications shows that available NEUS model applications could be expanded to investigate multistressor impacts on ecosystems. However, the methods used for the CCS will potentially not be directly transposable to the NEUS given that the CCS is an upwelling system, and its physical dynamics differs from the NEUS. The comparison of CCS and NEUS model applications also reflects a notable difference in the major modeling objectives between the two areas, represented in the published primary literature. Where a significant effort to develop EBM is visible for the CCS published literature, NEUS model applications aim at assessing the effects of single stressors on commercial stocks.

The Gulf of Mexico

In the Gulf of Mexico, the complexification trend over the last 30 years was similar to the complexification of food web models in the NEUS with a gradual increase in model complexity between the earlier models and the most recent ones. The average model complexity was similar between the Gulf of Mexico and the NEUS (40 functional groups versus 59 functional groups) (Ainsworth et al. 2015, Robinson et al. 2015, Masi et al. 2017, Sagarese et al. 2017, Chagaris et al. 2020b, Morzaria-Luna et al. 2022, Berenshtein et al. 2023). Yet, published models for the Gulf of Mexico include additional modeling frameworks, such as the OSMOSE model, which incorporates a size structure to estimate fishing effects on ecosystem dynamics (Grüss et al. 2016a).

Similar to the NEUS, researchers used ENA to summarize ecosystem model simulation outputs for the Gulf of Mexico. With this method, they investigated the structure and functioning of the Gulf of Mexico ecosystem (Arreguín-Sánchez and Manickchand-Heileman 1998, Cruz-Escalona et al. 2007, Robinson et al. 2015, Geers et al. 2016, Sagarese et al. 2017, Lewis et al. 2022). Specifically, Gulf of Mexico model appli-

cations focused on ecosystem dynamics, trophic interactions, or food web structures (Sagarese et al. 2017, Woodstock et al. 2021). They were also applied in a management context to deriving ERPs (Chagaris et al. 2020b, Berenshtein et al. 2023), total allowable catches (Grüss et al. 2016b), as well as testing management strategies (Arreguin-Sanchez et al. 2008). These model application objectives for the Gulf of Mexico are similar to model application objectives for the NEUS area.

Additionally, Gulf of Mexico ecosystem models were adapted to evaluate important local stressors, such as hypoxia (de Mutsert et al. 2016) and oil spills (Ainsworth et al. 2018, Dornberger et al. 2020, Rohal et al. 2020, Chagaris et al. 2020b).

Objective 7: recommendations for future model developments in the NEUS

This review of 75 years of ecosystem modeling in the NEUS has highlighted several principal areas for future research and ecosystem model application. Here, we offer recommendations for *Research Applications* and *Model Use and Development*.

Research applications

Climate change: temperature along the US east coast has increased at a rate of 0.36°C per decade from 1959 to 2021 (du Pontavice et al. 2023). Patterns of ecosystem restructuring in response to climate change can be summarized in three hypotheses: (1) species composition will turnover and warm water species will outcompete endemic species, (2) new species assemblages will result from new distribution ranges, and (3) biodiversity will decline and generalist species will dominate (Staudinger et al. 2021). Our review suggests that despite the large suite of modeling techniques available, the effects of climate change on the NEUS ecosystem have not been a significant focus for ecosystem modelers except for a few applications studying temperature variations on commercially valuable species.

This review has revealed several ecosystem modeling techniques that could be implemented in the NEUS system to assess the effects of climate-driven temperature shifts. Climate-driven temperature changes could be incorporated into EwE models via the Arrhenius equation, which integrates the temperature dependence of organismal metabolic reactions (Heinichen et al. 2022). Coupled ecological and biophysical models could be used to force primary production under different temperature scenarios (Aydin et al. 2005, Kearney et al. 2012). Specifically, the North Pacific Ecosystem Model for Understanding Regional Oceanography, an NPZD model (Kishi et al. 2007), has been employed to simulate the dynamics of planktonic communities, and the outputs from this model have been used to parametrize an EwE model for the pelagic Eastern Pacific Subarctic Gyre ecosystem. A similar technique could be employed for the NEUS to simulate climate-driven planktonic community shifts and parameterize a NEUS EwE model to evaluate ecosystem restructuring in response to climate change. *We recommend future modeling efforts consider biophysical and coupled ecological–physical models to represent an ecosystem under climatic forcing to explore the consequences of temperature change*.

Migration and subpopulation structure: migration is a key mechanism by which animals maximize fitness in heterogeneous environments (Roff 2002) with migration behaviors supporting either panmictic or structured subpopulations (Frisk et al. 2014). Many species also display migratory contingents, where individuals of the same genetic population become migratory or resident during early life history (Secor 1999). This complex life history makes it difficult to predict how a species will respond to changing environmental conditions (i.e. climate change), especially those species with subpopulation structure that may not be as amendable to range shifts when compared to panmictic species.

The response of migratory species with local subpopulation structure and/or natal homing will likely differ compared to a species with a panmictic population structure (Frisk et al. 2014). For example, in the NEUS, winter flounder has a local subpopulation structure, suggesting low exchange between natal estuaries and the existence of migratory contingents (Sagarese and Frisk 2011, O'Leary et al. 2013, Siskey et al. 2020). Thus, the population not only displays local subpopulation structure (Dolan et al. 2024), but these subpopulations have resident and ocean migratory contingents (Siskey et al. 2020). In this case, the species ability to adapt to a warming environment would be achieved on a subpopulation basis possibly showing changes to local stock productivity; however, its migration cycle limits its ability to shift its range as is common response to warming oceans. In contrast, winter skate has a broad spatial range and exhibited a large migration pulse in the 1980s between geographic regions that mimicked a regime shift on Georges Bank when community analyses assumed a closed system and did not consider migration behavior of winter skate (Frisk et al. 2014). What was initially thought of as a regime shift driven by internal system dynamics was instead a migratory event likely driven by regional environmental conditions and movement between open systems (Frisk et al. 2008, 2010, 2014, 2019). In this case, an understanding of subpopulation structure and migration dynamics would have better informed the dynamics of both the species and the species interactions that form the ecosystem.

Over the last several decades, the understanding of migration dynamics, stock and population structure, and resulting impacts on population productivity have greatly expanded, highlighting the need to incorporate such realistic behavior into ecosystem models. *We recommend that modelers consider species-specific subpopulation and behavioral traits (contingents, partial migration) in future ecosystem models to better understand system dynamics and responses to biotic and abiotic influences, such as climate change*.

Modeling multiple anthropogenic drivers: in the NEUS, large marine ecosystem models have been developed for decades (e.g. EMAX and ATLANTIS), yet we reviewed only three studies looking at the combined effects of multiple drivers. The available literature suggests that interacting drivers can emphasize the impact of individual drivers (i.e. synergistic effects) or compensate them (i.e. antagonistic). For example, a recent study for the Barents Sea showed that increased temperature resulted in lower biomass across the entire food web and higher fishing mortality on commercial groups triggered by compensatory dynamics (Sivel et al. 2023). The authors also showed that fishing had a "structuring" effect on the response of the species biomass to increased temperature. *We recommend that future modeling efforts focus on disentangling the cumulative effects of multiple anthropogenic drivers instead of concentrating our efforts on individual pressures, especially fisheries*.

Management strategy evaluation (MSE): managing fish stocks can be challenging due to trade-offs at the ecosystem level and uncertainty in the ecological knowledge and models' structure. Thus, a tool integrating the uncertainties and simplifying communication with stakeholders is necessary. MSE addresses these two objectives by adopting a scenario-based simulation approach based on operating models that enable assessment of the performance of a management strategy based on the trade-offs (Smith 1994, Punt et al. 2016). In the NEUS, there are many MSE frameworks developed for individual species, such as Atlantic Surf clams in both the Mid-Atlantic Bight (Kuykendall et al. 2017, 2019) and in the entire NEUS area (Hofmann et al. 2018), Atlantic cod in the Gulf of Maine (Sun et al. 2019), red knot and horseshoe crab in the Delaware Bay (Smith et al. 2013), American lobster in the Gulf of Maine (Vasquez Caballero et al. 2023), and Summer flounder in the mid-Atlantic (Mid-Atlantic Fishery Management Council 2022). In their 2020–2024 strategic plan, the Mid-Atlantic Fishery Management Council set as an objective (Objective 11.1) to "*expand the use of Management Strategy Evaluation (MSE) to determine/evaluate the impacts of management decision on fishing communities and other resource users*" (Mid-Atlantic Fishery Management Council 2019).

The calls for EBM go back decades (Link 2002, Pikitch et al. 2004) and while many studies have evaluated management on a system scale, few examples exist of formally adopting EBM into policy. However, ecosystem-level MSEs have been developed using ecosystem models (Fulton et al. 2014, Weijerman et al. 2016, Kaplan et al. 2021). Link et al. (2011) justified the development of an ATLANTIS model for the NEUS by its capacity to simulate whole MSE cycles. In our review, we did not find applications of ecosystem models in a MSE framework. We recommend that managers and modelers take advantage of the existing modeling frameworks, such as EwE or ATLANTIS, others, to set up ecosystem-level MSE frameworks for the NEUS to explore their use in setting policy for a variety of management needs including commercial species management and projecting climate impacts.

Model use and development

Complexification: creating taxonomically complex models and incorporating system realism has a trade-off with model parsimony. Large models require extensive datasets for parametrization, which are often unavailable for groups or species resulting in many output uncertainties (Geary et al. 2020). These uncertainties must be addressed to provide useful information to managers during the decision-making process (Link et al. 2012). Besides increasing the amount of data through sampling, an alternative option is to develop MICE models. Although MICE models reduce the taxonomic resolution of food webs, they allow users to focus on species of interest and resolve their dynamics (Punt and Butterworth 1995, Plagányi et al. 2014). In the NEUS, some model applications focus on individual species, such as American lobster (Zhang and Chen 2007, Zhang et al. 2012), Atlantic cod (Collie et al. 2009, Runge et al. 2010), Atlantic menhaden (Garrison et al. 2010), or spiny dogfish (Morgan and Sulikowski 2015). Utilization of a MICE model to focus on a single species, from an ecosystem perspective, would require less time and computational investment. *We recommend that studies focusing on individual species consider developing and using MICE models that may better represent the model focus and reduce the number of parameters.*

Model evaluation: in 1976, George Box stated that "*all models are wrong, but some are useful*." The statistician emphasized that models are a simplified representation of natural systems and never reflect the "truth". However, he also specified that it is important to define "*how wrong a model has to be to not be useful*" (Box and Draper 1987). In other words, it is essential to evaluate the performance of our models to determine how useful they are for management. Our review highlighted that ecosystem models developed for the NEUS are not systematically evaluated nor validated. First, we would like to promote and encourage modelers to evaluate the performance of their models in relation to their initial objectives. Does the model provide realistic patterns of variability? Does the model reproduce observed patterns from natural systems? How certain are model outputs considering the initial modeling assumptions? What are the possible sources of uncertainty in the model (i.e. model structure uncertainties and input parameters uncertainties)? How sensitive are the model outputs to the individual sources of uncertainty? One needs to address these questions to ensure that the model provides the best possible advice for management. Complex ecosystem models are often developed to address many questions, and the parametrization can vary greatly from one application to the other depending on the scientific question (Parker 2020, Saltelli et al. 2020). Consequently, each model application should be linked to an evaluation of the *fit for purpose* of the model to a specific application (Planque et al. 2022b). Planque et al. (2022b) presented a protocol for reporting the evaluation of ecological models to create transparency and standardization. In our review, although the authors who performed a model evaluation mentioned it in their methods sections, the conclusions of their sensitivity analysis or other used methods are not always reported. *We recognize that model evaluation is not a one-size-fits-all situation, but we recommend that modelers define appropriate model evaluation criteria specific to their study and follow published evaluation protocols as appropriate, such as PREBAL and those recommended by Planque et al. (2022b).*

Conclusion

This review revealed that even with many of the elements needed to achieve the promise EBM offered decades ago in place; several challenges remain, and new obstacles emerge as both expectations and demands on model structure and data evolve over time.

The rarity of ecosystem models driving management in the NEUS, and globally, raises important questions about whether the EBM is the tool that will successfully address the great need to manage human impacts on ecosystem dynamics in a rapidly changing world. Can modern complex data-hungry models reliably inform system and individual species dynamics to successfully set policy? Although the models listed in this review vary in complexity and their primary objectives, they generally match the required criteria for EBM presented by Pikitch et al. (2004) 20 years ago. Still, the applications of models to support EBM management remain rare in our review even with the current and pending threat of climate change; a topic seemingly well fit for ecosystem models to handle. However, the implementation of MSE frameworks remains a challenge because of the large uncertainties in the formulation of key ecological processes driving the dynam-

ics of individual stocks (Sánchez et al. 2019). The challenge remains whether researchers and management agencies can integrate current knowledge of the environment, species ecology, and system dynamics in a timeframe needed for effective policy in a period of rapid environmental change. In the coming decades ecosystem models that incorporate environmental drivers, ecological and biological realism have the potential to unravel the competing impacts on species productivity (i.e. fishing, predation, competition, and environmental change), if utilized in the management process (Townsend et al. 2019) and supported by appropriate data.

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Author contributions

Elliot Sivel (Conceptualization [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Visualization [equal], Writing – original draft [equal], Writing – review & editing [equal]), Tatum Eigenberger (Writing – original draft [equal]), Allegra Ervin (Investigation [equal], Writing – original draft [equal]), Farrah Leone (Investigation [equal], Writing – original draft [equal]), Maria Manz (Investigation [equal], Writing – original draft [equal]), Madison Muehl (Investigation [equal], Writing – original draft [equal], Writing – review & editing [equal]), Ashley Nicoll (Investigation [equal], Writing – original draft [equal]), Amanda Stigliano (Investigation [equal], Writing – original draft [equal]), and Michael G. Frisk (Conceptualization [equal], Funding acquisition [equal], Methodology [equal], Project administration [equal], Supervision [equal], Writing – original draft [equal], Writing – review & editing [equal])

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Data availability

All data are incorporated into the article and its online supplementary material.

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