Advancing Ecosystem-Based Fisheries Management on the Grand Banks of Newfoundland

Raquel Ruiz Díaz

A thesis submitted to the School of Graduate Studies
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy

in

Fisheries Science

Memorial University

Abstract

Traditional fisheries management has long operated within a single-species lens. Yet, the persistent degradation of marine ecosystems, loss of biodiversity, and the consequential decline in ecosystem services highlight the imperative to embrace new approaches to resource management. This thesis explores various methods to advance ecosystem-based fisheries management (EBFM) on the Grand Banks of Newfoundland (3LNO NAFO divisions), filling knowledge gaps on the impacts of climate change on snow crab, yellowtail flounder and Atlantic cod biomass and distribution, and the role of forage species and top predators on the stability of the Grand Banks community. By using spatio-temporal models, which capture spatial and temporal correlations in data and account for species habitat preferences, I detected a northern shift in the average location of biomass for Atlantic cod, suggesting either a northward movement of the 3NO southern stock or a rapid recovery of the 2J3KL northern stock. In contrast, the centre of gravity of snow crab and yellowtail flounder have remained relatively stable over time. I also developed new spring biomass indices for these species in the 3LNO divisions. I used species distribution models to forecast changes in focal species distribution and biomass by the end of the century. These models use bottom temperature data from three climate models (GFDL-ESM4, IPSL-CM6A-LR, and ACM) and three emissions scenarios (SSP1-2.6 and SSP3-7.0/SSP4-6.0) to force the projections. The findings suggest that warming is expected to reduce the biomass of snow crab and yellowtail flounder, while increasing the biomass of Atlantic cod, especially in the 3NO stock. Furthermore, I developed a size spectrum model to evaluate bottom-up versus top-down controls. My findings indicate that Atlantic cod may play a more important role than forage fish in the stability of the Grand Banks community. Overall, this thesis provides critical insights into the application of EBFM on the Grand Banks. It emphasizes the necessity for adaptive management strategies in response to climate-driven changes and highlights the importance of advanced modelling approaches to understanding complex ecological interactions.

General summary

Traditional fisheries management has focused on one species at a time. But as our oceans face serious threats like habitat loss and declining biodiversity, we need new ways to protect marine life. This research explores different modelling approaches to advance ecosystem-based fisheries management (EBFM) on the Grand Banks of Newfoundland. EBFM aims to maintain ecosystem structure and function. Using advanced computer models, I tracked historical changes in the locations of snow crab, yellowtail flounder and Atlantic cod on the Grand Banks. I found that the centre of gravity of Atlantic cod biomass is moving north, which may be indicating a northern shift in the 3NO southern stock or an increase in 2J3KL northern stock biomass , while snow crab and yellowtail flounder have remained in their usual areas. I also calculated new biomass indices that can be used in future species assessments. To understand future changes in species distributions, I developed a species distribution model that uses temperature outputs from different climate change models and scenarios. The results suggest that warming waters could lead to fewer snow crab and yellowtail flounder but more Atlantic cod in the Grand Banks. This patterns suggests a need to develop adaptation plans to help fisheries overcome the negative impact of climate change. Furthermore, by developing a model that integrates individual size, I simulated the Grand Banks food web to better understand the roles of forage fish (capelin and sand lance) and top predators (Atlantic cod) in the ecosystem. I found a strong top-down control on the Grand Banks. Overall, this research underscores the importance of incorporating ecosystem considerations into fisheries management. By understanding species interactions and the impacts of climate change, we can work to prevent or mitigate harm to marine species and fisheries.

Acknowledgements

I would like to express my deepest gratitude to my supervisor, Tyler Eddy, for his support and guidance throughout this journey. I appreciate his flexibility in allowing me to pursue the areas of research that interested me the most. I am also grateful to my Ph.D. committee members, Mariano Koen-Alonso, Jonathan Fisher, and Sherrylynn Rowe, for their insightful feedback, constructive suggestions, and stimulating discussions. Their collective wisdom and expertise have enriched my work and broadened my perspectives. I also want to thank Andrew Cuff, Andrew Roberts and Darrel Mullowney, who provided the databases and/or help with their interpretation, and to the DFO technicians and scientists involved in collecting the samples. The research presented in this thesis was supported by Fisheries and Oceans Canada, the Atlantic Fisheries Fund, an NSERC Discovery Grant, and the School of Graduate Studies of Memorial University.

I want to thank my family for their unconditional love, unwavering belief in me, and constant encouragement to pursue my dreams, even when it meant being far from them. Their support has been the cornerstone of my journey, and I am forever grateful. [*También quiero agradecer a mi familia por su amor incondicional, su fe inquebrantable en mí y por animarme constante a perseguir mis sueños, incluso cuando eso significaba estar lejos de ellos. Su apoyo ha sido la piedra angular de mi viaje, y estaré eternamente agradecida*]. I also want to thank my partner, Juan, for being my anchor during the highs and lows of this journey and for being my LaTeX guru.

A special thanks to Team Zissou for their camaraderie, kindness, and humour, which made the Ph.D. challenges more manageable and the milestones more memorable.

Lastly, to all the friends I have made along this path, thank you for making Newfoundland feel like home, for turning challenges into adventures, and for filling my life with laughter and cherished memories.

"Caminante, son tus huellas
el camino y nada más;
Caminante, no hay camino,
se hace camino al andar.
Al andar se hace el camino,
y al volver la vista atrás
se ve la senda que nunca
se ha de volver a pisar.
Caminante, no hay camino
sino estelas en la mar"

—Antonio Machado (Spanish poet)

Co-Authorship Statement

The research presented in this dissertation was conducted by Raquel Ruiz Díaz under the supervision of Dr. Tyler Eddy and the guidance of the committee members Mariano Koen-Alonso, Jonathan Fisher and Sherrylynn Rowe. It contains material from four manuscripts that have either been published, are under review, or are in preparation for publication. Some of the manuscripts included the collaboration of external researchers such as Maria Grazia Pennino (Spanish Institute of Oceanography), Frederic Cyr (Fisheries and Oceans Canada), Katja Fennel and Lina Garcia-Suarez (both affiliated to Dalhousie University) and Jonathan Reum (Alaska Fisheries Science Center, NOAA).

Manuscripts published in peer-review journals:

- **Chapter 2** is published as Ruiz-Diaz, R. 2023. Using an EBFM lens to guide the management of marine biological resources under changing conditions. *Fish and Fisheries*, 24, 199–211.

  Ruiz-Diaz was the author responsible for conceptualizing, screening and reviewing the literature, preparing the original draft, writing and editing, visualization, and supervising the manuscript.

- **Chapter 3** is published as Ruiz-Diaz, R., Pennino, M.G., Fisher, J.A. and Eddy, T.D., 2024. Decadal changes in biomass and distribution of key fisheries species on Newfoundland's Grand Banks. *PLOS One*, 19(4), p.e0300311.

Ruiz-Diaz, Pennino, Fisher and Eddy conceptualized this paper. Ruiz-Diaz was responsible for the methodology, data manipulation, formal analysis, visualization and original draft. Ruiz-Diaz, Pennino, Fisher and Eddy collaborated on writing, reviewing and editing; Eddy facilitated funding acquisition.

Manuscript under review in peer-journals:

- **Chapter 4** is under review as Ruiz-Diaz, R., Koen-Alonso, M., Cyr, F., Fisher, J.A.D., Rowe, S., Fennel, K., Garcia-Suarez, L. and Eddy, T.D. 2024. Climate models drive variation in projections of species distribution on the Grand Banks of Newfoundland. *PLOS Climate*, Under Review.

  Ruiz-Diaz, Eddy, Koen-Alonso, Fisher, and Rowe were responsible for the conceptualization; Ruiz-Diaz was responsible for the methodology, data manipulation, formal analysis, visualization and original draft; Cyr was also involved in data manipulation; Garcia-Suarez and Fennel provided ACM model output; Ruiz-Diaz, Koen-Alonso, Cyr, Fisher, Rowe, Fennel, and Eddy collaborated on writing, reviewing and editing; Eddy facilitated funding acquisition.

Manuscript getting ready for submission:

- **Chapter 5** is in preparation for submission as Ruiz-Diaz, R., Reum, J. and Eddy, T.D. 2024. Top-down ecosystem control of the Grand Banks of Newfoundland. *In prep.*

  Ruiz-Diaz, Reum and Eddy conceptualized this paper. Ruiz-Diaz was responsible of the methodology, data manipulation, formal analysis, visualization and original draft. Reum helped with the calibration of the model. Ruiz-Diaz, Reum and Eddy collaborated on writing, reviewing and editing; Eddy facilitated funding acquisition.

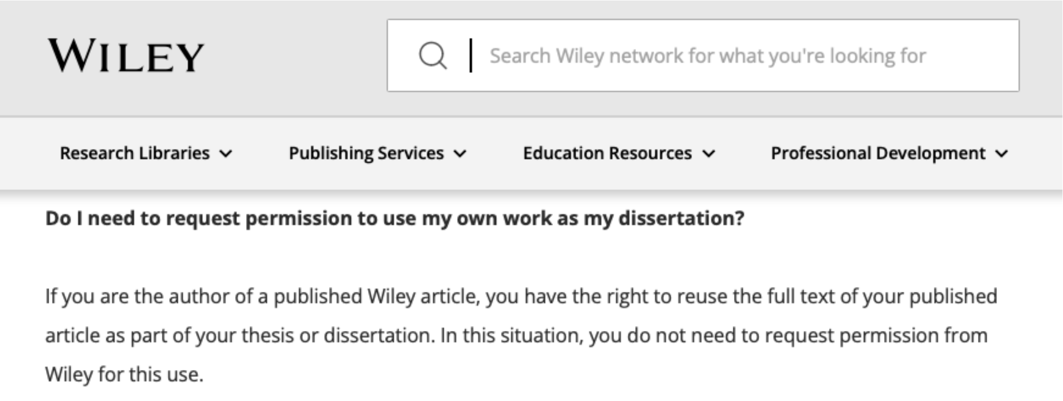
Other publications

Journal Articles and reports

- Duplisea, D.E., Eddy, T., Robertson, M.D., **Ruiz-Diaz, R.**, Solberg, C.A., and Zhang, F. 2024. "The ghosts of overfishing past that haunt the effectiveness of present day fisheries management and potential solutions". *In Prep.*
- Eddy, T. D., Duplisea, D., Robertson, M. D., **Ruiz-Diaz, R.**, Solberg, C. A., and Zhang, F., 2023. "Barriers to implementation of dynamic reference points in fisheries management". *Facets, 8, 1-10.*
- **Ruiz-Diaz, R.**, Dominguez-Petit, R., and Saborido-Rey, F., 2022. "Atlantic Cod Growth History in Flemish Cap Between 1981 and 2016: The Impact of Fishing and Climate on Growth Performance". *Frontiers in Marine Science, 9, p.876488.*
- Zhang, F., Eddy, T., Duplisea, D., Robertson, M., **Ruiz-Diaz, R.**, and Solberg, C., 2021. "Report on Ocean Frontier Institute (OFI) Workshop on Fisheries Management Reference Points in Highly Dynamic Ecosystems". *EcoEvoRXiv*

Publication Permissions

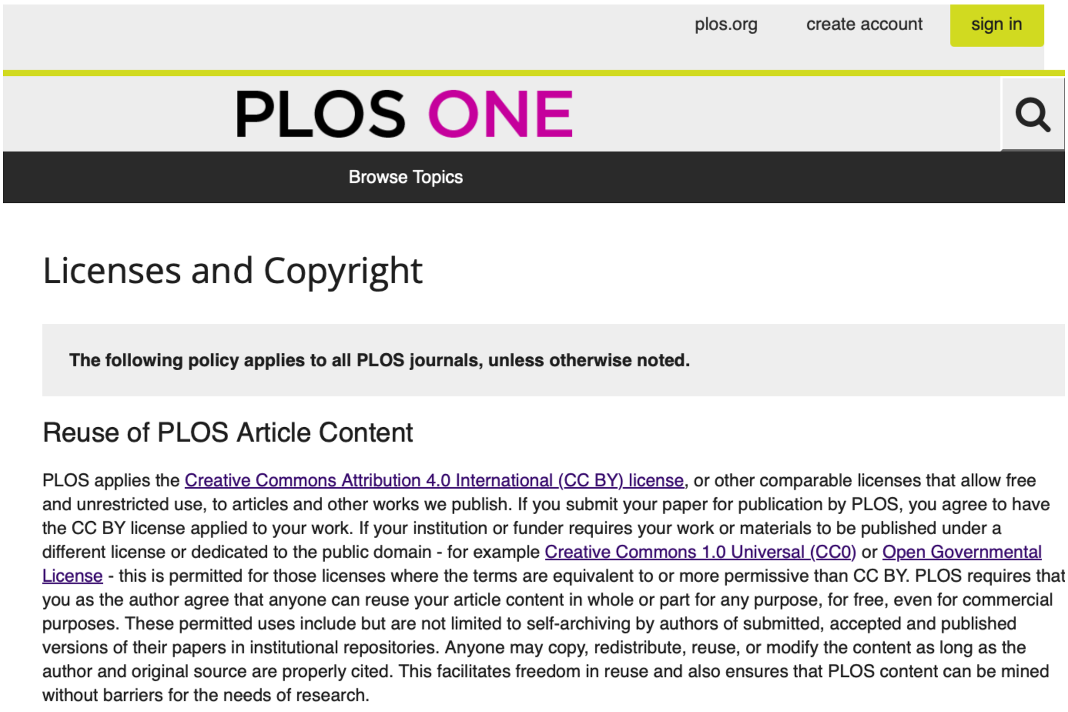
Chapter 2



Do I need to request permission to use my own work as my dissertation?

If you are the author of a published Wiley article, you have the right to reuse the full text of your published article as part of your thesis or dissertation. In this situation, you do not need to request permission from Wiley for this use.

Chapter 3



Licenses and Copyright

The following policy applies to all PLOS journals, unless otherwise noted.

Reuse of PLOS Article Content

PLOS applies the Creative Commons Attribution 4.0 International (CC BY) license, or other comparable licenses that allow free and unrestricted use, to articles and other works we publish. If you submit your paper for publication by PLOS, you agree to have the CC BY license applied to your work. If your institution or funder requires your work or materials to be published under a different license or dedicated to the public domain - for example Creative Commons 1.0 Universal (CC0) or Open Governmental License - this is permitted for those licenses where the terms are equivalent to or more permissive than CC BY. PLOS requires that you as the author agree that anyone can reuse your article content in whole or part for any purpose, for free, even for commercial purposes. These permitted uses include but are not limited to self-archiving by authors of submitted, accepted and published versions of their papers in institutional repositories. Anyone may copy, redistribute, reuse, or modify the content as long as the author and original source are properly cited. This facilitates freedom in reuse and also ensures that PLOS content can be mined without barriers for the needs of research.

Chapter 4

Licenses and Copyright

The following policy applies to all PLOS journals, unless otherwise noted.

Reuse of PLOS Article Content

PLOS applies the Creative Commons Attribution 4.0 International (CC BY) license, or other comparable licenses that allow free and unrestricted use, to articles and other works we publish. If you submit your paper for publication by PLOS, you agree to have the CC BY license applied to your work. If your institution or funder requires your work or materials to be published under a different license or dedicated to the public domain - for example Creative Commons 1.0 Universal (CC0) or Open Governmental License - this is permitted for those licenses where the terms are equivalent to or more permissive than CC BY. PLOS requires that you as the author agree that anyone can reuse your article content in whole or part for any purpose, for free, even for commercial purposes. These permitted uses include but are not limited to self-archiving by authors of submitted, accepted and published versions of their papers in institutional repositories. Anyone may copy, redistribute, reuse, or modify the content as long as the author and original source are properly cited. This facilitates freedom in reuse and also ensures that PLOS content can be mined without barriers for the needs of research.

Contents

List of Figures

List of Tables

CHAPTER 1

Introduction

1.1 The Grand Banks of Newfoundland

The Grand Banks of Newfoundland are located to the south and east of the island of Newfoundland. They include the Grand Bank, Whale Bank, Green Bank, and St. Pierre Bank, which are all submerged banks found at average depths of 200 meters (DFO, 2007b). In this thesis, I defined the Grand Banks as the NAFO divisions 3LNO (Figure 1.1).

The Grand Banks are influenced by the colder and nutrient-rich Labrador Current and the warmer and nutrient-poor North Atlantic Current (the northern branch of the Gulf Stream), ice formation/melting, and variations in the heat flux and surface winds (Han et al., 2008). This is a very dynamic system with a marked seasonal variation in primary production resulting from variations in light availability and thermocline stratification (Cyr et al., 2024). The thermocline is shallower and stronger in summer and deeper and weaker in winter. This results in pronounced winter mixing and nutrient-rich waters (Zhao et al., 2013). However, light limitations reduce winter productivity. In spring, increased light and nutrients lead to a productivity bloom. By late summer, nutrient depletion and reduced mixing lower productivity, while autumn brings cooler temperatures and storms that reintroduce nutrients to the surface, allowing for a brief autumn bloom before declining light limits productivity again. Winter storms replenish nutrients for the next spring bloom (Kaiser et al., 2011).

From late spring to fall, the Grand Bank's vertical temperature structure is dominated by a layer of cold water (0 °C) trapped between the seasonally heated top layer and the warmer slope water due to stratification caused by temperature differences. This layer, called the cold Intermediate Layer (CIL), can reach 170 m depth (Cyr and Galbraith, 2021; Cyr et al., 2022). The area occupied by the CIL varies from one year to the next and is related to the North Atlantic Oscillation (Cyr and Galbraith, 2021). These features create spatial variability in bottom temperature on the Grand Banks, with the south (3NO divisions) being warmer than the north (3L division).

In recent years, a warming trend has been observed in the Northwest Atlantic (Gonçalves Neto et al., 2021; Saba et al., 2016), including the Grand Banks (Cyr and Galbraith, 2021) (Figure 1.2). This warming may be influenced not only by warmer air temperatures, which increase heat transfer to the upper ocean layers, but also by a slowing of the shelf-break jet. The slower jet reduces the supply of fresh, cold, and nutrient-rich waters from the Labrador Current to the Grand Banks (Jutras et al., 2020; Garcia-Suarez et al., 2023). This phenomenon is connected to the hypothesis of a weakening Atlantic Meridional Overturning Circulation (Gonçalves Neto et al., 2021).

The Grand Banks is considered an independent ecosystem production unit within the Newfoundland and Labrador shelf ecosystem due to its distinct high productivity and well-defined marine community (Pepin et al., 2014; Koen-Alonso and Cuff, 2018). As my research aims to inform ecosystem-based fisheries management, I will use the Grand Banks as the spatial scale of analysis, despite some stocks being managed at different units (e.g., Atlantic cod 2J3KL and 3NO stocks).

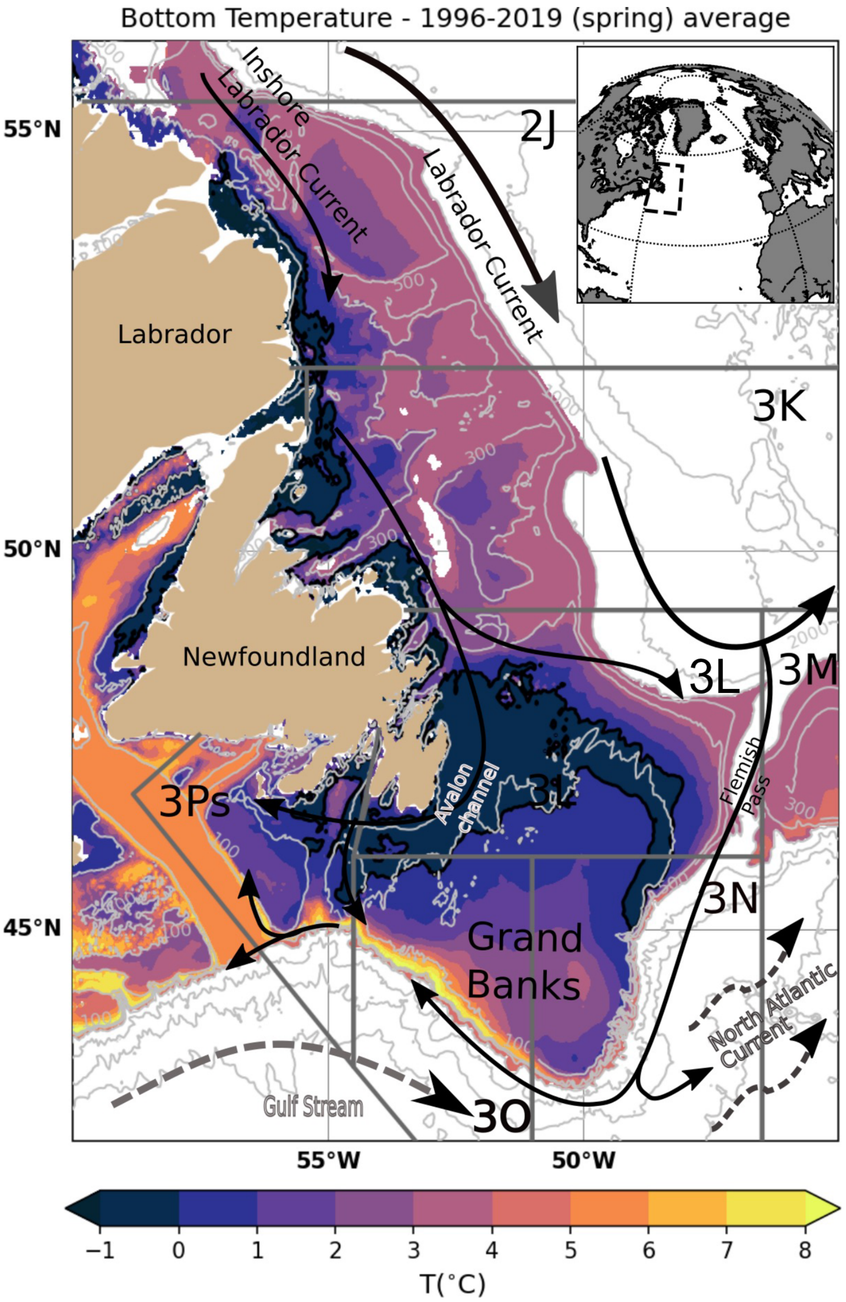
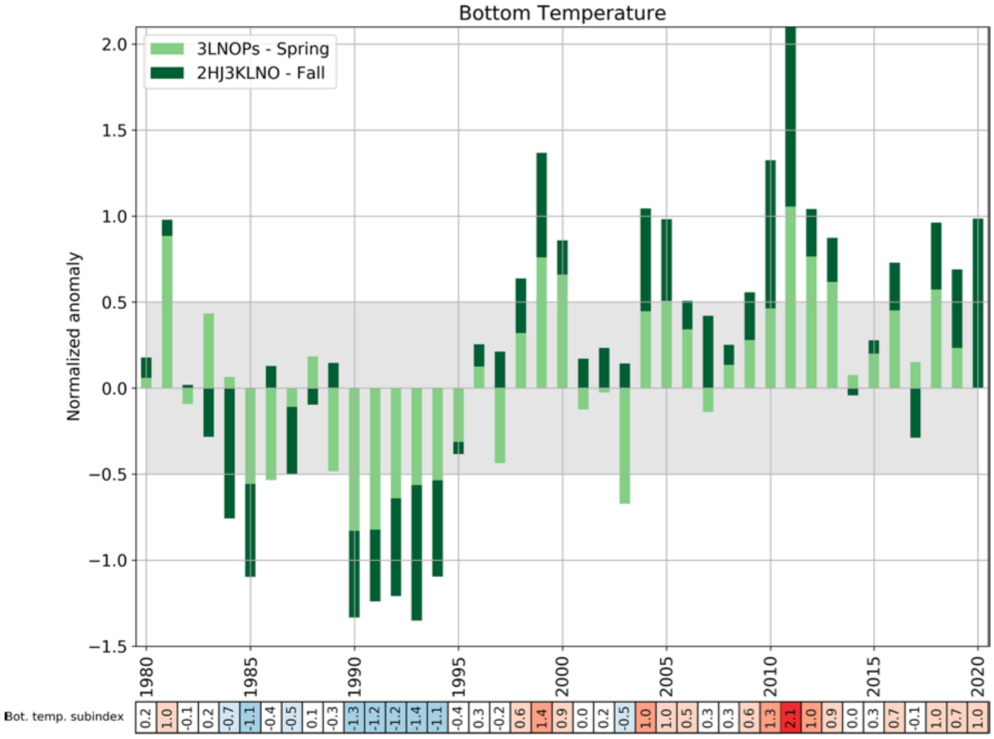


FIGURE 1.1: Map of the average spring bottom temperature during the historical period (1996-2019) interpolated over the Grand Banks. Isobaths are indicated in light grey; Northwest Atlantic Fisheries Organization NAFO divisions boundaries are indicated with grey rectangles. Black arrows show the main currents of the region.



1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
0.2	1.0	-0.1	0.2	-0.7	-1.1	-0.4	-0.5	0.1	-0.3	-1.3	-1.2	-1.2	-1.4	-1.1	-0.4	0.3	-0.2	0.6	1.4	0.9

2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
0.0	0.2	-0.5	1.0	1.0	0.5	0.3	0.3	0.6	1.3	2.1	1.0	0.9	0.0	0.3	0.7	-0.1	1.0	0.7	1.0

Figure 1.2: Normalized anomalies of bottom temperature in NAFO Divisions 3LNOPs (spring) and 2HJ3KLNO (fall). This time series corresponds to the average of the two seasons, in which each contribution is represented. The shaded area corresponds to the 1981-2010 average ±0.5 SD. The numerical values of this time series are reported in a colour-coded scorecard at the bottom of the figure. This time series is one component of the NL climate index. Source (Cyr and Galbraith, 2021)

1.2 Evolution of the Grand Banks' fisheries

For approximately 500 years, national and international fishing fleets travelled to the Grand Banks to catch high-value species such as cod, haddock, and flatfish species. However, the species began to exhibit signs of overfishing in the 1970s, which led to the establishment of fishing regulations (mesh size and catch quotas) and Canada's decision in 1977 to extend its exclusive economic zone (EEZ) to 200 nautical miles (DFO, 2007a). Since the Grand Banks stretches from national (within EEZ) to international waters, fisheries are administered by two different institutions, Fisheries and Oceans Canada (DFO) and the Northwest Atlantic Fisheries Organization (NAFO), respectively, advising fisheries in national and international waters. Despite government efforts to prevent groundfish depletion, most stocks on the Newfoundland Shelf and Grand Banks collapsed in the early 1990s (Pedersen et al., 2017). As a result, fishing moratoria were established for many groundfish species (DFO, 2019). The collapse has been attributed to both overfishing and extremely cold environmental conditions, though there is ongoing debate about their relative contributions. While overfishing is widely regarded as the primary driver, particularly for top predators like Atlantic cod, some studies highlight the role of environmental variability—such as colder temperatures—affecting recruitment and growth rates. Current research suggests that these factors acted synergistically, with overfishing weakening the population's resilience to environmental stressors, contributing to the ecosystem regime shift toward a crustacean-dominated community (Dempsey et al., 2017; Pedersen et al., 2017).

Since the collapse, the status of numerous fisheries on the Grand Banks has varied: some species and stocks have recovered, others have remained at low levels, and shellfish have become more prominent. The American plaice (*Hippoglossoides platessoides*) 3LNO stock has been under moratorium since 1995, often caught as bycatch in otter trawl fisheries targeting yellowtail flounder, skate, and redfish

(Wheeland et al., 2021). Similarly, the Atlantic cod (*Gadus morhua*) 3NO stock has been under a moratorium since 1994 and is also bycatch in the same fisheries as American plaice (Cadigan et al., 2022a). The northern stock of Atlantic cod, 2J3KL, was under a moratorium, with limited stewardship and recreational inshore fisheries allowed (DFO, 2022b) from 1992 until this year (2024) in which a direct commercial fishery was opened with a TAC of 18,000 t. The redfish (*Sebastes mentella*) 3LN stock is currently open for fishing, having been under a moratorium from 1998 to 2009 (Rogers et al., 2022) while the 3O stock remains open without closure in the past (Wheeland et al., 2022). The turbot (*Reinhardtius hippoglossoides*) 3KLMNO stock (Regular, 2023) and the yellowtail flounder (*Limanda ferruginea*) stock 3LNO (Parsons et al., 2023) are also open to fisheries, with a moratorium on the latter from 1995 to 1997. The witch flounder (*Glyptocephalus cynoglossus*) fishery stock 3NO is open, following a moratorium from 1995 to 2014, and is often bycatch in yellowtail, redfish, skate, and turbot fisheries (Parsons et al., 2020). The capelin (*Mallotus villosus*) stock 2J3KL offshore fishery has been closed since 1990, though the inshore fishery remains open (DFO, 2022a), whereas the 3NO stock has been under a moratorium since 1992 (NAFO, 2021a). The snow crab (*Chionoecetes opilio*) fishery in the 2HJ3KLNOP4R divisions remains open (DFO, 2023a). In contrast, Northern shrimp (*Pandalus borealis*) in 3LNO divisions have had no direct fishery since 2015, with a complete fishing halt from 2015 to 2021 (NAFO, 2021b). Lastly, the thorny skate (*Raja radiata*) stock 3LNO is open for fishing, with this species predominating (95%) among the mixed skate catches (Sosebee et al., 2022).

1.3 Ecosystem-based fisheries management

The Fisheries Act is Canada's primary legislation for protecting fish and their habitats (Fisheries Act, 1985). In 2019, the Act was modernized through Bill C-68 to highlight sustainable management, best practices, and the adoption of precautionary and ecosystem-based approaches. Single-species fisheries management often fails to consider species interactions, bycatch, and environmental variability, including the impacts of climate change (Hilborn, 2011). Hence, transitioning from single-species management to ecosystem-based fisheries management (EBFM) is crucial for implementing the updated Act. Globally, only 2% of assessed stocks include environmental or ecosystem information (Skern-Mauritzen et al., 2016), though this percentage is now higher in the US (24%) (Marshall et al., 2019) and Canada (46%) (Pepin et al., 2022).

EBFM recognizes that fish populations are influenced by interactions with other species (Pikitch et al., 2012), habitat change (Armstrong et al., 2021), climate change (Hollowed et al., 2013; Bell et al., 2022), and human activities (Hilborn et al., 2020). These changes increase the uncertainty in the scientific basis for decision-making in single-species fisheries management approaches. Ecosystem-based fisheries management (EBFM) addresses these challenges by integrating ecosystem considerations into the decision-making process, aiming to preserve ecosystem integrity (structure and function) while meeting societal and human needs (Pikitch et al., 2004). Advancing EBFM requires the use of multiple approaches and models, as no single model can fully capture the complexity of marine ecosystems (Geary et al., 2020). Employing different models offers complementary insights, addresses various aspects of ecosystem dynamics, and validates results through cross-model comparisons. Integrating EBFM into routine management practices is crucial for effectively addressing ecosystem uncertainty, especially in highly dynamic regions like Newfoundland and Labrador.

1.4 Research objectives

This thesis explores various methods to advance EBFM on the Grand Banks of Newfoundland, focusing on changes in habitat, climate and predator-prey interactions (Figure 1.3). In particular, it aims to fill knowledge gaps about species habitat preferences, the impacts of climate change on snow crab, yellowtail flounder and Atlantic cod biomass and distribution, and the role of forage species (capelin and northern sand lance), and top predators on the stability of the Grand Banks community.

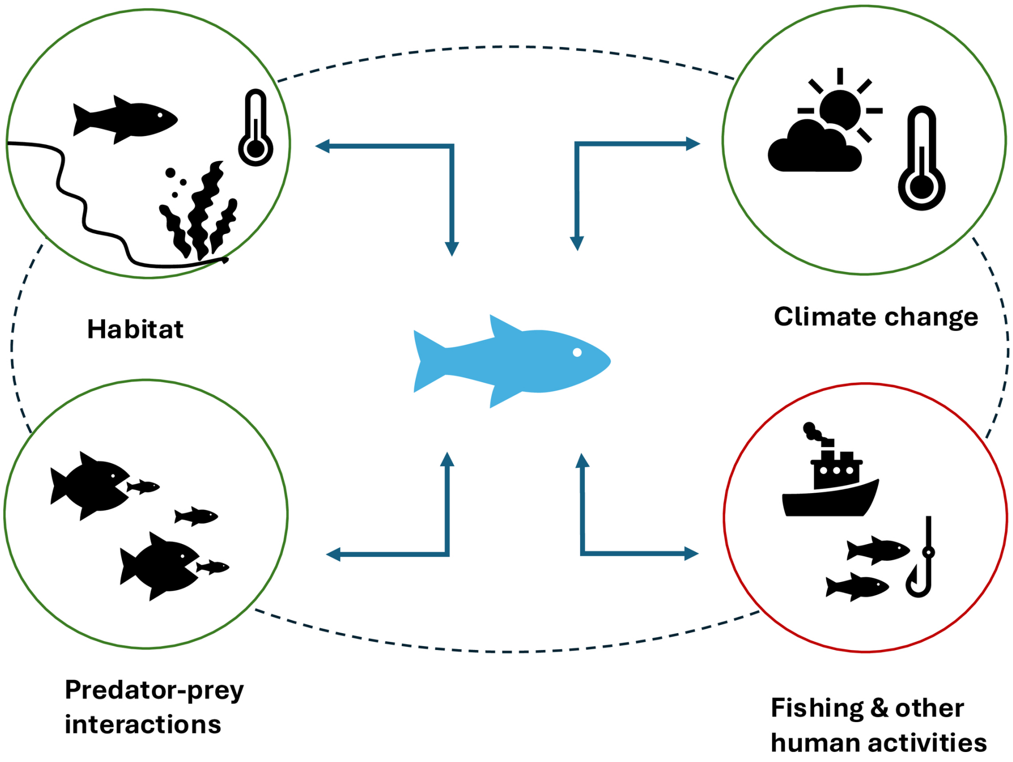


FIGURE 1.3: Overview of factors explored in advancing ecosystem-based fisheries management (EBFM) on the Grand Banks. Components related to habitat changes, climate effects, and predator-prey interactions are shown in green; fishing impacts and other anthropogenic activities are marked in red, indicating they are not directly assessed in this dissertation.

I focused on the post-collapse period (1996-2019) to avoid issues related to the change of fishing gear in the bottom trawl multi-species survey (i.e., very low catchability for shellfish and forage species). I also focused on the spring data because the fall surveys, particularly in 2004–2006, were affected by the absence of deep sets, reduced coverage, and extended timelines due to vessel breakdowns and unplanned changes (Brodie et al., 2007). The thesis is divided into six chapters (including introduction (Chapter 1) and general conclusions (Chapter 6). Chapter 2 establishes the groundwork by reviewing the existing literature on ecosystem-based fisheries management (EBFM). It compiles information on the tools and models available for implementing EBFM and explores how to integrate ecosystem information into current management processes. By identifying methods and research directions, this chapter lays the foundation for the subsequent chapters. Chapter 3 examines historical changes in species biomass and distribution using spatio-temporal models whereas Chapter 4 explores projections of species distribution to the end of the century under three climate models and low and high emissions scenarios. Both chapters 3 and 4 focus on snow crab (*Chionoecetes opilio*), yellowtail flounder (*Limanda ferruginea*), and Atlantic cod (*Gadus morhua*). These species were selected due to their varying recovery trajectories following the groundfish collapses in the early 1990s and their significance to Newfoundland and Labrador's fishing sector. Chapter 5 focuses on developing a multispecies size spectrum model to evaluate bottom-up controls (driven by forage fish) versus top-down controls (driven by Atlantic cod) in the Grand Banks. This model incorporates the size distribution and interactions of eleven key species that constitute the major community of the Grand Banks. It captures the dynamics of growth, species interactions, and changes in trophic niches throughout their life stages. Through simulations, I assessed the direct and indirect ecological consequences of changing biomass on the target species- capelin, sand lance, and Atlantic cod- and evaluated their importance for the stability of the Grand Banks' community. Understanding the role of these species within the ecosystem enables us to anticipate how changes in one part of the food web might cascade throughout the entire community. Finally, Chapter 6 synthesizes the findings from the previous chapters and highlights the major contribution of this research towards advancing EBFM implementation on the Grand Banks of Newfoundland.

CHAPTER 2

Managing resources under changing conditions

2.1 Abstract

The management of natural resources is currently more challenging than ever before. Climate change and human population growth pose a threat to marine ecosystems as we know them. In order to preserve ecosystems, biodiversity, and ecosystem services, management of biological resources must adopt a holistic strategy. Ecosystem-Based Fisheries Management (EBFM) enables these objectives by managing natural resource use at the ecosystem level. However, EBFM objectives and implementation can sometimes be unclear, particularly when framed in the context of shifting conditions. This research reviews the strategies available for managing marine biological resources within the EBFM framework and in a changing environment. The purpose of this publication is to guide the decision on whether and how to change current management strategies in order to achieve policy goals. The manuscript starts with a review of ecosystem indicators and ecosystem models used to detect and describe changes in ecosystem dynamics and stocks productivity under present and future conditions. Then, I summarize the different frameworks and methods available for integrating this information into the decision-making process. Currently, some of the options available to integrate ecosystem realism into the fisheries advice include using ecosystem models in the Management Strategy Evaluation (MSE) process, adjusting single species reference points with ecosystem information, and implementing risk-equivalent empirical approaches. However, barriers that impede the adoption of these techniques exist,

and I conclude the study by identifying them and providing literature-based solutions to overcome them from an interdisciplinary perspective.

2.2 Introduction

Management of natural biological resources has historically used a one-species framework. However, the continual loss of ecosystems, biodiversity, and the resulting loss of ecosystem services in both terrestrial and marine systems (Leclère et al., 2020; Nicholson et al., 2021; Worm et al., 2006) demonstrates the necessity of adopting new techniques for managing natural resources. Many of the ecosystem services we acquire from the ocean, such as provisioning (e.g. food security), climate regulation and maintenance (e.g. protection against coastal erosion), and cultural functions (e.g. recreation and traditions) are supported by marine biodiversity; Therefore, its removal has detrimental local and global effects. The decline of marine biodiversity may be attributable to overfishing (FAO, 2020), climate change (Worm and Lotze, 2021), and other anthropogenic stressors such as habitat degradation and pollution (Sala and Knowlton, 2006). Increasing human population exerts further stress on marine ecosystems and their capacity to deliver benefits for humans, resulting in complicated dynamics with numerous competing objectives that society must address (e.g. sustainability and food security) (Karnauskas et al., 2021).

Current fisheries management is mostly centred on constructing single-species models to assess population dynamics of the target stock and its response to alternative management scenarios (Hilborn and Walters, 2013; Skern-Mauritzen et al., 2016). However, this strategy has some limitations. On one hand, traditional single-species fisheries management often does not account for species interactions, bycatch, and habitat destruction, which conflicts with conservation strategies designed to protect and conserve marine wildlife (such as “The Endangered Species

Act" and "The Marine Mammal Protection Acts" in the United States and "The Species At Risk Act" in Canada) (Hilborn, 2011). Another limitation of single-species stock evaluations is their reliance on models that make strong assumptions on population processes such as reproductive success, mortality, and growth, often assuming these processes remain constant (stationarity) over time (Britten et al., 2017; Vert-Pre et al., 2013). Environmental variability and climate change could disrupt some of these processes, rendering this strategy ineffective (O'Leary et al., 2020). Climate change alters ocean conditions, such as currents, coastal upwellings, and water temperature, hence affecting primary productivity and species distributions and abundance on local and global scales (ICES, 2021). These ongoing changes in marine ecosystems increase the uncertainty surrounding decisions regarding fisheries management. These changes are especially true for small forage fish species since they are extremely susceptible to environmental fluctuation (Bakun et al., 2010). These findings highlight the necessity of adopting a holistic strategy, such as ecosystem-based fisheries management (EBFM), rather than keep focusing on a single species frame.

Ecosystem-Based Fisheries Management seeks to conserve the integrity (structure and function) and diversity of ecosystems, as well as satisfy societal and human demands for food and socioeconomic advantages, without degrading ecosystems (Pikitch et al., 2004; Zhou et al., 2010). Implementing EBFM is a challenging task that has suffered some reluctance from regulatory institutions due to concerns related to the lack of clarity on EBFM objectives and implementation process (Lidström and Johnson, 2020; Trochta et al., 2018). However, efforts have been made to overcome these concerns and currently, implementing EBFM is totally feasible (Murawski, 2007; Patrick and Link, 2015). A global review of fish stock assessments indicated that only 2% of them incorporate information regarding external drivers of productivity (Skern-Mauritzen et al., 2016). Nonetheless, the implementation of EBFM moves in a spectrum of incremental complexity and, when looking at EBFM in a broader context, Marshall et al. (2019) found that ecosystem information is integrated in 24% of 206 fish stocks assessed in the US, although its inclusion is more often qualitative than quantitative. Similar results have been found in Canada, with 21of the 178 stocks assessed including environmental factors quantitatively (Pepin et al., 2022). Even though the full implementation of EBFM still needs some work, an improvement in the status of marine species populations has been observed, probably due to combined progress in EBFM implementation and single species models (Link and Marshak, 2021).

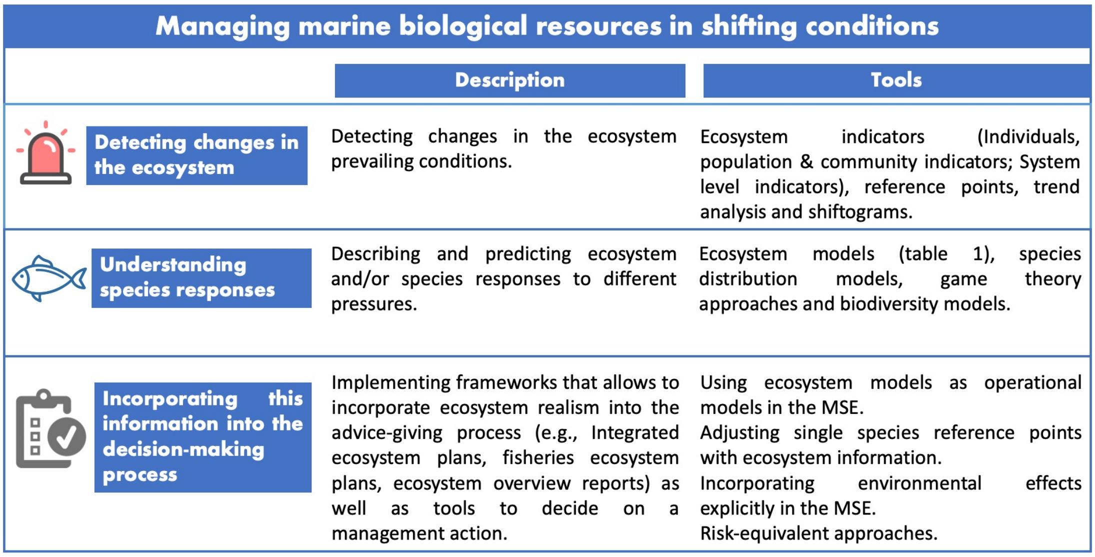
Numerous authors, such as Essington and Punt (2011), have argued that the transition from SSFM to EBFM should be gradual, building on conventional methods rather than replacing them entirely. In contrast, Berkes (2012) emphasized the need to move beyond traditional techniques and adopt interdisciplinary approaches to avoid repeating past mistakes. In any case, fostering the adoption of EBFM as well as promoting ecosystem restoration and conservation are required to achieve global conservation targets (such as UN Sustainable Development Goals-SDGs14 Life below water and Global Post-2020 Biodiversity targets), safeguarding wildlife, and preserving national economies and wellbeing (Razzaque et al., 2019; Ward et al., 2022). Due to the cumulative long-term effects of human activities on marine ecosystems and biodiversity, which have caused a shift in ecosystem baselines (Pauly et al., 1995; Rodrigues et al., 2019), the management of marine resource use is likely more difficult now than ever. This paper provides a guideline for managing marine biological resources in a changing environment and within the EBFM approach. In particular, I focus on the use of ecosystem indicators and ecosystem models to detect and describe changes in ecosystem dynamics and stock productivity under present and future scenarios. Then, frameworks and tools for incorporating this information into the current existing management process are presented.

2.3 Managing marine biological resources in a changing environment

Marine biological resource management often entails monitoring the productivity of the target species over time and activating a management response when predefined values or reference points are attained (Hall and Mainprize, 2004). However, significant changes are being observed in aquatic systems driven by climate change (e.g. temperature increment, water column stratification, ocean acidification, changes in ocean circulation, among others), which may alter the productivity and distribution of marine species (Barange et al., 2018; ICES, 2021). In general, marine species are moving poleward at an average of 72 km/decade and deeper in the water column (Poloczanska et al., 2013). Severe decreases in species biomass have already been attributed to alterations in ecological conditions driven by climate change (Litzow et al., 2019; Lotze et al., 2019). As a result, reference points could become ineffective if they remain based on historical productivity levels, failing to account for shifts in ecosystem productivity. This puts species at risk of overfishing, as current fishing pressure may be unsustainable under changing environmental conditions, even before noticeable biomass declines occur (Britten et al., 2017). Detecting changes in the prevailing conditions of an ecosystem is, therefore, the first step in determining whether to implement new management measures, at least for those species that are likely to be impacted by those changes. This section summarizes steps for managing marine biological resources under shifting conditions (Figure 2.1).

2.3.1 Detecting changes in ecosystem prevailing conditions

Indicators enable evaluation of an ecosystem's status and identification of changes in the prevailing conditions, serving as the foundation for deciding on new management actions. A good indicator must have a theoretical foundation, be sensitive to



Managing marine biological resources in shifting conditions

	Description	Tools
Detecting changes in the ecosystem	Detecting changes in the ecosystem prevailing conditions.	Ecosystem indicators (Individuals, population & community indicators; System level indicators), reference points, trend analysis and shiftograms.
Understanding species responses	Describing and predicting ecosystem and/or species responses to different pressures.	Ecosystem models (table 1), species distribution models, game theory approaches and biodiversity models.
Incorporating this information into the decision-making process	Implementing frameworks that allows to incorporate ecosystem realism into the advice-giving process (e.g., Integrated ecosystem plans, fisheries ecosystem plans, ecosystem overview reports) as well as tools to decide on a management action.	Using ecosystem models as operational models in the MSE. Adjusting single species reference points with ecosystem information. Incorporating environmental effects explicitly in the MSE. Risk-equivalent approaches.

Figure 2.1: Guideline for managing marine biological resources in shifting conditions.

a perturbation, be easily quantifiable, cost-effective, and straightforward to comprehend (Rice and Rochet, 2005; Rochet and Rice, 2005). No single indicator can capture all the changes that may be occurring in an environment; therefore, a combination of indications is required (Fulton et al., 2005). To save time and resources, the number of indicators should be maintained as low as feasible while still meeting management requirements (Rice and Rochet, 2005). Two groups of indicators can be identified in the literature: (i) indicators derived from individuals, populations, and communities such as size-based (e.g. fish size and size spectra slope), trophic-based (e.g., mean trophic level of the community), life-history-based (e.g., life span), and species-based indicators (e.g., species richness) (Coll et al., 2016; Tam et al., 2017). They can be defined using data from surveys, captures, and ecological models (Briton et al., 2019) and provide pertinent information on the ecosystem's integrity, stability, and resilience. (ii) Ecosystem-level indicators that give information on the ecosystem's production limits. They allow the assessment of whether an ecosystem has been overfished or perturbed (Fogarty et al., 2016;

Libralato et al., 2019; Link and Watson, 2019). Indicators that can exhibit a warning signal before a regime shift occurs in the ecosystem are crucial for developing management strategies that prevent unintended ecosystem changes. In this sense, ecosystem-level indicators are a good starting point for detecting changes in the ecosystem since they track few ecosystem components and hence, they are relatively quick to calculate. For instance, the Fogarty index evaluates the ratio of total catches to total primary productivity in the ecosystem, detecting early signs of ecosystem overfishing (Link and Watson, 2019). Ecosystem regime shift could also be detected by using trend analysis (e.g. sequential t-test analysis of regime shift -STAR; (Punt et al., 2014)) and shiftograms (Lindegren et al., 2012).

2.3.2 Understanding ecosystem and species response to different pressures

Changes in species biomass and distribution can be predicted using species distribution models that link the distribution of the target species with abiotic variables (Leach et al., 2016), joint species distribution models that allow linking the distribution of the target species to abiotic and biotic variables (Sadykova et al., 2017) and community joint species distribution models (Tikhonov et al., 2020). To model the future impact of climate change on the ecosystem level, ecosystem models could be developed and forced with climate change scenarios to forecast the medium and long-term impact of climate change on species productivity (Holsman et al., 2020). Ecosystem models (EMs) are essential tools for ecosystem-level work, and have been implemented in a variety of disciplines, including natural resource management (Grüss et al., 2017), wildlife conservation (Rendall et al., 2021), agriculture Balbi et al. (2015), and environmental health (Topping and Lagisz, 2012). Ecosystems, in a nutshell, consist of biological components, the abiotic environment (non-living components), the processes and interactions within them, and the physical area where they function (Geary et al., 2020). Ecosystem models can describe those interactions and hence, be used to enhance understanding of a system and predict its response to different pressures (Fulton et al., 2014). For modelling marine ecosystems, qualitative (e.g. conceptual models) and quantitative approaches could be used to describe the ecological and socioeconomic facet of the fishery, and the relationships between them (Kasperski et al., 2021; Plagányi, 2007). In the present study, the classification of O'Farrell et al. (2017); Plagányi (2007) were combined to provide a complete description of marine ecosystem models approaches based on their structures. Specific model examples were also included to complement this description Table 2.1. Ecosystem models can be used to inform strategic and tactical management advice. Strategic advice focuses on broad policy issues like achieving biodiversity goals, maintaining ecosystem services, and accounting for socioeconomic considerations; providing long-term directions. Tactical advice, on the contrary, operates on a finer scale and provides short-term advice; it requires the specification of harvest control rules to meet the policy goals (Collie et al., 2016; Howell et al., 2021). Developing an ecosystem model to inform fisheries management entails finding a compromise between model complexity (and related uncertainties) and model performance to answer the management question (the "sweet spot"; Collie et al. (2016)). Therefore, before constructing an ecosystem model, a good practice would be defining the objectives (whether they are describing, forecasting, or deciding on management actions), considering the spatial scale and temporal dynamics, and thinking on the focus of our model in terms of ecosystem components (individual species, aggregated groups, or whole-ecosystem) and ecosystem processes that regulate ecosystem dynamics (trophic dynamics, dispersal, perturbations that impact individual components, and perturbations that affect the whole ecosystem) (Geary et al., 2020).

There are other approaches that could be useful for assessing the future impact of climate change on marine ecosystems. For instance, game theory approaches could

Table 2.1: Literature-based summary of ecosystem model approaches with examples of specific models (adapted from O'Farrell et al., 2017 and Plagányi, 2007)

Model categories	**Description**	**Examples of specific models**	**Abbrev.**	**Reference**
Conceptual and qualitative models	Schematic model that outline relevant components, processes and interactions of the ecosystem. These models allow us to create a shared understanding of the systema and to verify that all essential processes are identified. They are especially relevant in data-poor situations as the knowledge of users and experts are combined and integrated in the model.	Qualitative Network model	QNMs	Reum et al., 2021
		Bayesian Belief Networks	BBNs	McCann et al., 2006
		Fuzzy cognitive maps	FCMs	Baker et al., 2018
Extensions of single-species models	In these models, additional factors like environmental parameters are added to single-species models to assess their effects on stocks productivity and life-history traits.	Extended single-species assessment models	ESAMSs	Hollowed et al., 2000
		Extension of single-species individual-based models	ESIBMS	Clack et al., 2001
Dynamic multi-species models	These models represent the key components of the ecosystem that interacts with the target species. They typically require information on diet and species overlap. In this category we can find the model of intermediate complexity recommended by Collie et al. (2016) to provide tactical advice.	Globally applicable Area Disaggregated General Ecosystem Toolbox	GADGET	Pérez-Rodríguez et al., 2019
		Models of Intermediate Complexity	MICE	Plagányi et al., 2014
		spatio-temporal models of intermediate complexity	MICE-in-space	Thorson et al., 2019
		Climate-enhanced multi-species assessment	CEATTLE	Holsman et el., 2020
		Multi-species virtual population analysis	MSVPA	Kinzey and Punt., 2009
Agent/ **Individual-based models** **(IBMs)**	Individual/ agent-based models follow individuals and their properties to understand their effects on populations and community dynamics. A peculiarity of this model is that the individual/agent represented could be an individual or a composite unit (like fishing fleets).	InVitro	InVitro	McDonald et al., 2006
		Object-oriented Simulator of Marine ecosystems Exploration	OSMOSE	Shin and Cury 2004
whole of ecosystem models	The energy flows (from primary producers to higher tropic levels) are tracked in these models. They include several species or aggregated groups (taxonomic or functional). Predation and fishing mortality can be simultaneously regarded.	Comprehensive Aquatic System Models	CASM	Bartell et al. 1999
		Ecopath with Ecosim	EwE	Christensen and Walters 2004
Biogeochemical-based end-to-end models (E2E):	End-to-end models account for bottom-up interactions by representing the biogeochemical cycle, linking it with plankton up to the top predators. They also account for top-down interactions.	Atlantis	Atlantis	Fulton et al., 2004
		North Pacific Ecosystem Model for Understanding Regional Oceanography	NEMURO	Kishi et al., 2011
		Forage Euphausiids abundance in space and time	FEAST	Ortiz et al., 2016
Customized models.	These models are a combination of different model platforms. They represent top-down and bottom-up interactions and are especially useful to assess the impact of climate change on marine ecosystems.	Alaska Climate Integrated Modeling.	ACLIM	Hollowed et al., 2020
Trait-based model	Trait-based models describe the structure and functioning of ecological communities from the organisms' properties. Size-based models are included in this category.	Multi-species size spectrum model	MIZER	Scott et al., 2014; Reum et al., 2020

aid in comprehending the shift in migration pathways of highly migratory species. Mariani et al. (2016) developed a migration game model for tunas that focuses on migrating dynamics leading to the "ideal free distribution strategy", which is the evolutionary strategy of habitat selection in which species distribute across multiple patches to minimize competition and maximize fitness. This type of model is not only useful for researching highly migratory species but also the distributional changes of transboundary and straddling populations since it provides the foundation for a discussion on how changes in species distribution affects international agreements (Palacios-Abrantes et al., 2022; Pinsky et al., 2018). Another example includes using trait-based models, which describe the structure and functioning of ecological communities from the organisms' properties (Barnett et al., 2019).

The trait-based method relies on the Darwinian principle of natural selection, which holds that individuals within a species optimize their fitness and performance by adapting to their environment (Kiørboe et al., 2018). Monitoring trait variations (e.g. morphology, physiology and phenology measurements) within an ecosystem is useful for capturing system-level responses to climate change and enables improved management advice (Barnett et al., 2019). Size spectrum models are one example of the trait-based models gaining prominence for estimating the impact of climate change on stock productivity (Forestier et al., 2020; Fulton and Gorton, 2014). These methodologies are getting special attention because they can lead to the creation of climate-adaptive strategies that could enhance the resilience of the fishing sector (Bryndum-Buchholz et al., 2021).

Moreover, ecosystem models could benefit from the integration of new methodologies such as biodiversity models (i.e., models that project the current state of or the effect of environmental change on the biological components of ecosystems, such as genes, species, functional groups, and communities; (Weiskopf et al., 2022)) for understanding the ecosystem response to a perturbation or management intervention and so evaluate different goals. Loss of biodiversity impacts species and genetic diversity from local to global biodiversity pools (Harvey et al., 2017) and reduces an ecosystem's ability to recover after a disturbance (Sala and Knowlton, 2006). Biodiversity models can replicate environmental impacts on biodiversity by explicitly or indirectly incorporating biological processes. In particular, macroecological models stand out for their ability to capture ecological processes relevant to species and ecosystem-level (Pollock et al., 2020). For instance, macroecological models that represent β-diversity (compositional dissimilarity among species between locations) can be used to address the effects of habitat alteration on biodiversity (Hoskins et al., 2020).

2.3.3 Deciding on a management action

To achieve global conservation objectives, we must create and implement frameworks that permit the incorporation of ecosystem realism into management recommendations. In fisheries management, this include the Integrated Ecosystem Assessments (Levin et al., 2018), the NAFO roadmap (Koen-Alonso et al., 2019) and the Marine Strategy Framework Directive (EU, 2008). The implementation of such frameworks result in the creation of plans and reports that can inform managers (e.g. integrated ecosystem plans (Denit, 2016), fisheries ecosystem plans (Levin et al., 2018), and ecosystem overview reports (ICES, 2021; Stephenson et al., 2019). Although decision-making can still occur using qualitative assessments or expert judgment, a quantitative evaluation of the performance of the different management actions is recommended, commonly referred to as Management Strategy Evaluation (MSE); Ecosystem models could be utilized as part of the MSE process to determine the most appropriate management action that will allow us to reach our goal (Kaplan et al., 2019; Lucey et al., 2021). The MSE process fundamentally depends on defining objectives and performance measurements, addressing uncertainties, identifying potentially feasible management alternatives, simulating management option applications, presenting results, and selecting a management strategy (Punt et al., 2016a). It comprises two key components, the operational model and the management strategy (including the assessment process, which ideally is not simply a variant of the operational model). The feedback loop between the two is a crucial component of MSE since it allows for the identification of both the management action to be implemented and the ecosystem response to that action (Perryman et al., 2021). Simulating MSE with ecosystem models has been done for a number of management objectives, including defining harvest control rules that take into account the important role of forage species in the ecosystem (Punt et al., 2016b), defining spatial closures (Dichmont et al., 2013), considering risk equivalency and tiered harvest strategies (Dichmont et al., 2017), and evaluating how combinations of management levers can meet multispecies fishery and EBFM objectives (Fulton et al., 2019; Fulton and Gorton, 2014).

Furthermore, ecosystem and environmental information could be used to adjust single-species reference points and so incorporate more realism into the decision-making process (Townsend et al., 2019; Bentley et al., 2021). For example, target fishing mortality calculated by single-species models can be re-scaled using ecosystem model's outputs (Howell et al., 2021). The previous example used adjusted fishing mortality F_{ECO} to set the fishing quota in the previous example. This approach has been applied in the Irish Sea to identify environmental drivers influencing the productivity of the target stock and in the United States to account for the effect of a forage fish species as a driver of the striped bass population (as the species' primary source of food) (Howell et al., 2021).

In the case of the unavailability of multispecies and/or ecosystem models, a way to include ecosystem realism in the advice is by explicitly considering environmental factors in the single-species MSE process. For example, Punt et al. (2022) developed a framework to integrate the effect of temperature and pH on growth and survival of king and snow crab, and decide on harvest control rules. In another example, Pacific sardine management includes the use of an environmental buffer (called E_{MSY}) to account for the impact of temperature on the productivity of the stock. E_{MSY} is based on a three-year average of the California current sea surface temperature and is incorporated directly into the harvest control rule and allowable catch (Hill et al., 2017). Finally, risk-equivalent approaches could quantify the risk of a status quo management strategy under different climate change scenarios and define the fishing exploitation rates required to reach the policy goal (Duplisea et al., 2021).

2.4 Discussion: barriers and solutions

The sluggish adoption of EBFM can be attributed in part to the complexity that develops while operating at the ecosystem level and the structural inertia of the management systems, particularly the need to conform to current administrative frameworks (Howell et al., 2021; Marshak et al., 2017)). In this context, path dependency (i.e. earlier decisions barring specific future options) has been identified as a factor preventing decision-makers from adopting alternative management strategies and causing institutions to stagnate in sub-optimal phases (Méndez et al., 2019). Because adopting a new strategy needs funds for getting information -data, investment in training, and time for learning and executing the models, resource restrictions often result in path dependence (Fulton, 2021). This, together with the short-term goals focus of fisheries management (Kirk et al., 2007), limits the adoption of the strategies described in this manuscript. Moreover, the methodologies presented here account for more components (ecological, social, and economic) than those applied in single-species fisheries management; Thus, scientists need to work with managers and decision-makers to fill knowledge gaps. Finally, including stakeholders and local community members in the process could contribute to minimizing the trade-off between achieving policy goals (e.g. conservation goals) and socioeconomic issues (e.g. maintaining economic revenue or food provisioning) (Christie et al., 2017). Identifying users' needs is crucial for the success of the policy goal and requires the inclusion of stakeholders in the decision-making process. This inclusion involves building relationships, considering cultural protocols, and organizing regular meetings and workshops (Iwamoto et al., 2019). Knowledge co-production is a popular method for enhancing knowledge transfer. The process for producing high-quality co-production knowledge should be context-oriented (situated within a particular social, economic, and ecological context), pluralistic (recognize the different experiences and knowledge of the actors involved in the process), goal-focused (goals clearly specified and agreed among actors), and interactive (participatory method with continual interaction among actors) (Norström et al., 2020). In their evaluation of how EMs have been used to inform managers in the United States, Townsend et al. (2019) determined that regular communication and collaboration among stakeholders, modellers, and managers were essential to the success of the process. Participation of diverse actors in the decision-making process improves comprehension of the research's obstacles and limitations, as well as the establishment of a sense of ownership that fosters broad communication and, eventually, boosts awareness among other members (Cvitanovic et al., 2015). Other approaches to enhance knowledge exchange include hiring scientists in decision-making agencies (e.g. NOAA, DFO or CSIRO) or directly integrating them in the decision-making process (e.g. as members of scientific advisory or participatory assessment groups), utilizing knowledge brokers (individuals who are embedded within the research team or institution and act as intermediaries to facilitate knowledge exchange), and boundary organizations (similar to knowledge brokers but not ingrained within the research team or institution) (Cvitanovic et al., 2015). These strategies may assist in overcoming obstacles to adopting novel methods such those presented in this study. A further reluctance to include these methods into the decision-making process is the uncertainty associated with them (e.g. uncertainty relates to observation and estimation, model, implementation, and communication; (Link et al., 2010)). However, several options have been proposed to quantify and express model uncertainties, such as model ensembles, fitting models to observations and data, performing risk analysis, sensitivity analysis on the input parameters and model, outputs visualization, and implementing a MSE approach (Geary et al., 2020; Link et al., 2010; Peterman, 2019). Model ensembles consist of multiple ecosystem models applied to the same system, which are used to evaluate any ecosystem response with uncertainty quantified by comparing model outputs. Due to the features incorporated in each model, unique dynamics and structures can be captured by distinct models. Hence, similar outcomes across models imply the consistency of such outcomes (Lewis et al., 2021). Using numerous models also decreases the uncertainty amplification caused by model predictor reliance (Dahood et al., 2020). There are two sorts of model comparison: the development of alternative models using the same inputs, calibration and validation methodologies, and the construction of models separately (Kaplan et al., 2019; Kasperski et al., 2021). Additionally, conceptual and qualitative models could be combined with stakeholder-mapping exercises to find information gaps and highlight uncertainty in a participative process (Rounsevell et al., 2021). Finally, visualization tools, serious gaming, and gamification could be utilized to stimulate learning, motivate and inspire collaboration, so facilitating the attainment of desired results (Fulton, 2021). Last but not least, fully implementing EBFM requires understanding ocean exploitation as a socioecological system in which resources, users, and government entities are fundamentally interconnected (Ostrom, 2009). EBFM could benefit from the use of ecological models (Table 2.1) to simultaneously address the ecological and human dimensions (henceforth referred to as coupled socioecological system models) (Kasperski et al., 2021). A lot of work still remains in this field as, until now, most indicators used to account for the human dimension mostly relate to economic objectives associated with fisheries (e.g. revenue, fishing effort, and market price). Fewer indicators have been employed to evaluate community health, food security, compliance, and oversight (Hornborg et al., 2019). Coupled socioecological system models typically have greater uncertainty than ecosystem models, as they incorporate sociological and political aspects (Fulton et al., 2014). Using coupled socioecological system models within a MSE framework could elucidate pertinent trade-offs resulting from competing EBFM's ecological, economic, and social objectives (e.g. conservation objectives versus economic rewards) and co-benefits derived from a particular management action (Fulton et al., 2014; Kaplan et al., 2021).

2.5 Conclusions

Ecosystem-Based Fisheries Management requires reforming the governance and institutional framework by incorporating scientists and stakeholders into the decision-making process, resulting in a decentralized management system with shared decision-making power among actors. Implementing EBFM differs based on data availability and management objectives, requiring identification of EBFM objectives in a collaborative manner from the outset. This collaboration should continue throughout the entire process to allow the co-production of knowledge. In addition, eliminating path dependency requires offering the necessary resources and training, and employing an approach that fits the management action timeline. EBFM should seek satisfactory solutions (agreed upon among stakeholders) rather than an ideal one given the conflicting objectives between different groups and the interactions in the ecosystem (Fogarty, 2014). Typically, this search for satisfactory solutions requires comparing several management approaches to a predetermined set of objectives throughout the management strategy evaluation process.

The complete adoption of EBFM requires first developing indicators that account for the ecological and human dimensions of the fisheries. These indicators can be used to establish thresholds for management objectives. Thereby, ecological indicators could be used to alert us to the need to change current management strategies by detecting changes in the ecosystem prevailing conditions (Libralato et al., 2019; Link and Watson, 2019).

Ecosystem-Based Fisheries Management objectives can be evaluated within the MSE framework with ecosystem models as operational models (ideally, coupled socioecological system models that allow for the assessment of trade-offs between the ecological, social, and economic aspects of the fishery) (Fulton et al., 2014; Kasperski et al., 2021). Ecosystem models can predict the response of the ecosystem and/or target species to different pressures (Section 2.3) and so inform suitable management decision (Fulton et al., 2014). However, for an ecosystem model to aid in decision-making, it must be adapted to the pertinent policy question. In addition, the components and spatio-temporal scales of the ecosystem model should fit the management purpose and model capability, and it should focus on the ecosystem components directly affected by the management action (Geary et al., 2020). Finally, less data-demanding approaches which also allow the incorporation of ecosystem realism into the management advice exist, such as adjusting single species reference points with ecosystem information (Howell et al., 2021), implementing risk-equivalent empirical approaches (Duplisea et al., 2021) and explicitly including environmental effects in the single species MSE process (Hill et al., 2017; Punt et al., 2022).

The most comprehensive strategy for offering long-term strategic guidance for achieving policy goals in a changing environment would be to couple these models with climate change projection scenarios to establish climate-smart adaptation plans that strengthen the fishing industry's resilience in the medium and long term (Bryndum-Buchholz et al., 2021). In this sense, trait-based models, biodiversity models, species distribution models, and game theory are powerful methods to assess future changes in marine ecosystems, especially related to climate change and habitat modification (Barnett et al., 2019; Forestier et al., 2020; Pollock et al., 2020). Therefore, the implementation of such a strategy is needed to advance decisions regarding suitable policies and actions for accomplishing local and global conservation and biodiversity goals.

CHAPTER 3

Decadal changes in species biomass and distribution

3.1 Abstract

Canadian fisheries management has embraced the precautionary approach and the incorporation of ecosystem information in scientific assessments, though its application in policy decisions remains more limited. Accurate estimation of fish stock biomass is crucial for ensuring sustainable exploitation of marine resources. Spatio-temporal models can provide improved indices of biomass because they capture spatial and temporal correlations in data and can account for environmental factors influencing biomass distributions. In this study, I developed a spatio-temporal generalized additive model (st- GAM) to investigate the relationships between bottom temperature, depth, and the biomass of three key fished species on the Grand Banks from 1996 to 2019: snow crab (*Chionoecetes opilio*), yellowtail flounder (*Limanda ferruginea*), and Atlantic cod (*Gadus morhua*). My findings revealed changes in the centre of gravity of Atlantic cod that could be related to a northern shift of the southern 3NO stock within the Grand Banks or to a faster recovery of the northern 2J3KL stock in last 5 years. Atlantic cod also displayed hyperaggregation behaviour, with the species showing a continuous distribution over the Grand Banks when biomass is high. These findings suggest a joint stock assessment between the 2J3KL and 3NO stocks would be advisable. However, barriers such as differing management priorities and regulatory frameworks may need to be addressed to achieve collaboration between the two distinct regulatory bodies

(i.e., DFO and NAFO) in charge of managing the stocks. Snow crab and yellowtail flounder centres of gravity have remained relatively constant over time. I also estimated novel indices of biomass, informed by environmental factors (temperature and depth) that were compared to the traditional strata-based biomass indices used in the stock assessments. My study represents a step towards ecosystem-based fisheries management for the highly dynamic Grand Banks.

3.2 Introduction

Stock assessments aim to evaluate the status of a population by evaluating biomass and fishing mortality relative to reference points to define catch limits (Punt, 2023). Time series of biomass indices are often used to calibrate stock assessment models, primarily derived from fisheries-independent data collected from scientific surveys. These surveys commonly employ a stratified-random sampling design to generate estimates of absolute biomass by using area-swept information (Martell, 2008; Smith, 1990). This approach involves dividing the study area into different strata based on specific characteristics, such as depth or habitat type. Within each stratum, random samples are collected. Random stratified sampling increases the precision of the estimates when the population is homogenously distributed among strata. However, variability in habitat preference may exist within strata, compromising the robustness of this approach (Morin, 2011). This approach also requires sampling all strata at each sampling event, which is not always possible due to inclement weather, and ship repairs, among others.

Spatial correlation is a common feature of fisheries data. It occurs when observations collected at different locations are not independent of each other, as nearby observations tend to be more similar than distant observations (Tobler, 1970). If unaccounted for, spatial correlation can lead to biased estimates of biomass and abundance (McGilliard et al., 2015). This issue also applies to the correlation of objects through time (i.e., temporal correlation) (Cressie and Wikle, 2015). Spatio-temporal generalized mixed effect models (GLMMs) and generalized additive models (GAMs) can account for spatial correlation that characterize fisheries survey data (Thorson et al., 2015). The latter are more flexible because they are fit using smoothing spline terms, making them especially useful for addressing non-linear relationships (Martínez-Minaya et al., 2018). These models explicitly account for both spatial and temporal correlations in a dataset (Redding et al., 2017), and can incorporate information about environmental variables that may be driving species biomass and distribution (Lloret-Lloret et al., 2021). Another advantage of these methods is that they employ spatial interpolation throughout the region of interest, helping to address incomplete sampling issues (Martínez-Minaya et al., 2018). Spatio-temporal models can improve predictions for areas and years with little or no data and can be more precise than with design-based methods (i.e., strata-based index) and conventional GLMMs and GAMs (i.e., without spatio-temporal effects) (Shelton et al., 2014; Grüss and Thorson, 2019).

My study focuses on the practical application of spatio-temporal Generalized Additive Models (st-GAMs) (Thorson et al., 2016) to understand the biomass dynamics and distributional changes of snow crab (*Chionoecetes opilio*), yellowtail flounder (*Limanda ferruginea*), and Atlantic cod (*Gadus morhua*) on the Grand Banks of Newfoundland from 1996 to 2019. The Grand Banks is a highly productive region where two distinct water masses, the Labrador Current and the Gulf Stream, converge. The Labrador Current brings fresh and nutrient-rich waters, while the Gulf Stream carries warmer and saltier waters. This combination of conditions makes the Grand Banks a productive but also dynamic and highly variable ecosystem (Han et al., 2008, 2011). The Grand Banks experienced a regime shift in the early 1990s characterized by the collapse of Atlantic cod, yellowtail flounder and other groundfish species. However, species such as snow crab and northern shrimp proliferated during that time (Koen-Alonso and Cuff, 2018). The shift was attributed to a combination of factors, including overfishing and changes in environmental conditions (Dempsey et al., 2017). In the last 5 years, the species in my study have exhibited different dynamics, with snow crab experiencing a significant decline, Atlantic cod remaining persistently low and yellowtail flounder recovering to pre-collapse levels. Currently, the yellowtail flounder fishery is operating as a Marine Stewardship Council (MSC) certified fishery (Knapman et al., 2020).

The Grand Banks constitute an independent ecosystem production unit within the Newfoundland and Labrador Shelf, characterized by high ecosystem productivity and a well-defined marine community (Koen-Alonso and Cuff, 2018; Pepin et al., 2014). I used this ecosystem production unit as the spatial scale of focus and examined how it relates to the management units of the study species. My study contributes to the evolving landscape of ecosystem-based fisheries management by applying advanced modelling techniques to uncover spatio-temporal patterns in snow crab, yellowtail flounder and Atlantic cod dynamics. These species were selected based on their variable responses post-collapse, their cultural and economic fisheries importance, and their distinct movement behaviours. Gadoids are streamlined swimmers; flatfish are bottom- dwellers that perform undulatory movements, and snow crabs have legs that allow for lateral movement. These adaptations are shaped by the specific ecological niches and lifestyles of each species. By incorporating environmental variables into the analysis (bottom temperature and depth) and considering spatial correlation , I explored species-habitat associations and calculated environmental-informed biomass indices that can be used in stock assessment models. Finally, I assessed the effect of fishing on the environmental-informed biomass indices.

3.3 Material and Methods

3.3.1 Data sources

Multi-species survey

Fisheries and Oceans Canada (DFO) has conducted annual stratified-random multispecies bottom trawl surveys on the Grand Banks, located in the Northwest Atlantic since 1971 (Rideout et al., 2021) (Figure 3.1). The survey is conducted in spring and fall and has changed sampling gear and coverage over time. Fall surveys range from September to December [mean observations of 275 per year], although in 2014 the survey took place in January and only 140 samples where taken. Fall surveys have had issues with an absence of deep sets, reduced coverage, and timing extensions due to vessel breakdowns and unplanned changes, particularly in 2004–2006 (Brodie and Stansbury, 2007). In contrast, the spring survey (April-June) has had more consistent coverage [mean observations of 282.5 per year], although the 2006 and 2017 surveys had lower coverage [194 and 191 observations, respectively]. To limit variability introduced by changes in the surveys, I utilized data from surveys conducted in spring (6,780 observations in total). Since 1996, spring surveys have been conducted with the CCGS Alfred Needler and Campelen 1800 shrimp trawl gear, sampling up to 732 meters in depth. The trawl survey collects data on the abundance, size, and biomass of numerous groundfish and shellfish species, in addition to other biological information (i.e., size, maturation status, body condition, stomach contents) (Rideout and Ings, 2019).

Biomass data were used to create two response variables for each species: presence/absence and conditional-to-presence-biomass (i.e., biomass > 0). Abiotic explanatory variables were bathymetry (here called depth) and bottom temperature, also obtained from the DFO bottom trawl survey (Table 3.1). These covariates

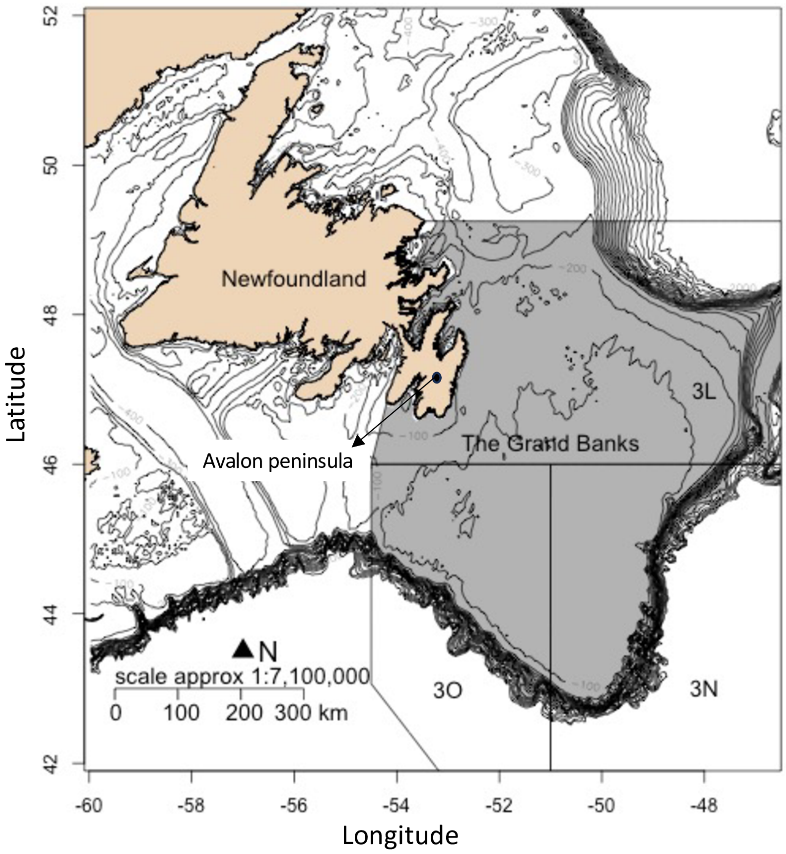


FIGURE 3.1: The Grand Banks of Newfoundland (grey). Solid lines indicate the management unit boundaries of the North Atlantic Fisheries Organization (NAFO) divisions (3L, 3N and 3O).

were selected based on their well-known relationship with the distribution and productivity of the study species (Windle et al., 2012; Colbourne and Walsh, 2006; Drinkwater, 2005). The relationship between the study species and salinity is less understood in this region and was not considered here. Finally, I assumed that expected fish biomass is proportional to the area surveyed (referred to as the swept area); thus, I included the swept area (log-transformed) as offset in all the models to account for the variation in effort.

Prediction grid

I created a 5x5 km grid for the Grand Banks with 274,461 grid points. I used gridded bathymetry data with spatial resolution of 15 arc seconds ($\approx 0.004°$) obtained

TABLE 3.1: List of response and explanatory variables included in the st-GAM

	Name	Description	Units
Explanatory variable	Depth	Bathymetry at sampling location	metres
	Temperature	Bottom Temperature at sampling location	ºC
Response variable	Occurrence & conditional-to-presence biomass	Presence/absence and biomass of snow crab (*Chionoecetes opilio*)	Kg.tow^{-1} (live weight)
	Occurrence & conditional-to-presence biomass	Presence/absence and biomass of Atlantic cod (*Gadus morhua*)	Kg.tow^{-1} (live weight)
	Occurrence & conditional-to-presence biomass	Presence/absence and biomass of yellowtail flounder (*Limanda ferruginea*)	Kg.tow^{-1} (live weight)

from the General Bathymetric Chart of the Oceans (GEBCO) project and manipulated it with the R package marmap (Pante and Simon-Bouhet, 2013) to extract depth values at the center of each grid point. Rasters of bottom temperature data for the same period (1996-2019) were provided by DFO. These rasters were created using data from different sources (DFO multispecies survey, Atlantic Zone Monitoring Program (AZMP) hydrographic campaigns, International Oceanographic Campaigns (IOC), ARGO program, etc) (Cyr et al., 2022). All data were vertically averaged in 5 m bins, and a linear interpolation was applied to fill the missing bins. I selected the data corresponding to the spring season (April- June), for which data were averaged on a regular 0.1° × 0.1° grid. Horizontal linear interpolation was applied to address missing data on grid cells (full description in (Cyr et al., 2022)). I tested the correlation between these databases (i.e., GEBCO and DFO temperature interpolation) with trawl station observations to assess accuracy (Figure A.2 and Figure A.3).

Fishing and strata-based biomass indices data

Finally, fishing data aggregated at the division level were obtained from the NAFO STLATLANT database. Strata-based indices of snow crab (DFO, 2023a), yellowtail flounder (Parsons et al., 2021) and Atlantic cod (Rideout et al., 2021) were collected from the stock assessments of the species over the same time period (1996-2019) and compared to the new environmental-informed indices.

3.3.2 Spatio-temporal modelling

An exploratory analysis highlighted that species biomass data have two main features, namely strong spatial and temporal dependence and a large proportion of observed zeros (i.e., zero-inflated data). To address this reality, I developed a delta-gamma generalized additive model (GAM) using the R-package sdmTMB (Anderson et al., 2022). This model separately analyzes species occurrence (biomass information is transformed to 0 and 1 according to species absence and presence, respectively) and conditional-to-presence biomass (observations with positive biomass values) and combines both predictions in a final biomass estimate (Thorson et al., 2015). To model the non-linear relationship between explanatory and response factors, covariates were included in the model as random factors with a smoothing term (p-splines) (Anderson et al., 2022). Depth was log-transformed for better model convergence. Delta gamma models are commonly used in the literature to perform analyses similar to this one (Paradinas et al., 2020; Pennino et al., 2022). I considered $Z(s,t)$ to be the spatiotemporally distributed occurrence and $W(s,t)$ the conditional-to-presence biomass at location s and time t. The final model formulation is:

$$Z(s,t) \sim \text{Bernoulli}(\pi(s,t)) \tag{3.1a}$$

$$W(s,t) \sim \text{Gamma}(\mu(s,t),\phi) \tag{3.1b}$$

$$\text{logit}(\pi(s,t)) = \beta_Z + Y_i + \sum_{i=1}^{I} f_i(X_i(s,t)) + V_Z(s,t) \tag{3.1c}$$

$$\log(\mu(s,t)) = \beta_W + Y_i + \sum_{i=1}^{I} f_i(X_i(s,t)) + V_W(s,t) \tag{3.1d}$$

where $\pi(s,t)$ represents the probability of occurrence at location s and time t; and $\mu(s,t)$ and ϕ are the mean and variance of the conditional-to-presence biomass, respectively. The linear predictors, which represent the intercept of each variable associated with the parameter $\pi(s,t)$ and $\mu(s,t)$, are represented by β_Z and β_W, respectively. The survey year was added as a fixed effect in the model (Y_i). f_i represents any function applied to the covariates X_i, which in the present study were smoothing terms (p-splines). $V_Z(s,t)$ and $V_W(s,t)$ refer to the spatio-temporal structure of the occurrence and conditional-to-biomass model, respectively.

sdmTMB relies on the integrated nested Laplace approximation (INLA) to discretize the space by defining a Delaunay triangulation mesh, which in turn creates an artificial set of neighbours over the study area, and Gaussian Markov random fields (GMRF) to model spatial dependencies between observations (Anderson et al., 2022; Lindgren and Rue, 2015). My approach involved constructing a Delaunay triangulation mesh with a defined minimum distance of 20 km, resulting in a mesh comprising 467 vertices (Figure A.1). I tested different mesh configurations, accounting for the spatial distribution of sampling locations and evaluated model performance to avoid overfitting. The mesh scale was selected based on a balance between spatial resolution and computational efficiency, ensuring it was fine enough to capture meaningful spatial patterns without introducing excessive complexity. Cross-validation techniques were used to verify that the results were consistent across different configurations. To test which model performs better, I evaluated the spatial effect by running a model with and without the spatial component. The spatio-temporal component was modelled as the Kronecker product of the spatial effect and the temporal effect, which was tested using three approaches: 1) a first-order autoregressive effect (AR1), with a parameter ρ regulating the degree of autocorrelation between random field deviations from one year to the next;

2) a random walk (RW); and 3) an independent and identically distributed (iid) process, where the random fields are independent across time steps. These were tested to determine which performed better.

3.3.3 Model selection and validation

I calculated Pearson's rank correlation index and the variance inflation factor (VIF) of the covariates before the model ran. This step helped avoid correlation and collinearity among explanatory variables (Zuur et al., 2010). I did not find any substantial correlation among the covariates ($R < 0.6$ and $VIF < 3$), allowing us to proceed with including depth and bottom temperature in the st-GAM.

To assess the importance of bottom temperature, depth, and the spatial component on species spatial distribution, Akaike differences were used instead of stepwise variable selection because they account for model selection uncertainty (Akaike, 1981; Burnham and Anderson, 2004). To test model predictability, I carried out a k-fold cross-validation in which data were randomly split in $k = 4$ folds of equal size. In each iteration, one of the folds is held to test the data, while the other 3 are used to train the model. Then, I used the expected log pointwise predictive density ($ELPD$) to evaluate the model's predictive accuracy (Anderson et al., 2022; Vehtari et al., 2017). To validate models, residuals were visually inspected to ensure that spatial patterns were not detected and that residuals were normally distributed for snow crab (Figure A.9, Figure A.10 and Figure A.11); yellowtail flounder (Figure A.12, Figure A.13 and Figure A.14); and Atlantic cod (Figure A.15, Figure A.16 and Figure A.17).

3.3.4 Biomass index and centre of gravity calculation

I summed up the estimated biomass from the predictions and multiplied them by cell area to calculate the biomass index. In the case of snow crab, species catchability in the bottom trawl survey was lower than 1 (Dawe et al., 2010). To account for this issue, a conversion factor was calculated using a Delury depletion regression analysis on fishery catch rate data from logbooks from 2000 to 2016 (Mullowney et al., 2017) and biomass estimates were adjusted (divided) by a factor of 0.126. Agreements between the new biomass indices (spatially-aggregated biomass) and strata-based indices (strata-aggregated biomass) reported in the stock assessment of snow crab (DFO, 2023a), yellowtail flounder (Parsons et al., 2021) and Atlantic cod (Rideout et al., 2021) were assessed by using the coefficient of determination, R^2. For snow crab, the strata-based indices were estimated using fall survey data, whereas my environmental-informed indices were estimated using spring data. The models used in the assessment of all stocks except 3NO Atlantic cod require biomass indices as input (snow crab assessment uses biomass trends, yellowtail flounder a Schaefer surplus production model and 2J3KL Atlantic cod a state-space model). Therefore, the new biomass indices developed in the present study are comparable and could be used in the assessment of the species. Finally, we estimated the centre of gravity of the populations with the following formula:

$$CG_y = \frac{\sum\limits_{i=1}^{n} x_i w_i}{\sum\limits_{i=1}^{n} w_i} \tag{3.2}$$

where CG_y is the centre of gravity at a given year, x_i is the location (x or y-coordinates) of the grid cell, w_i is the species biomass estimated at each grid cell i, and n is the total number of grid points in the study area ($n = 274,461$) (Hollowed, 1992). I also calculated the species centre of gravity directly from the data using mean weight.

3.3.5 Fishing impact

I was unable to account for the impact of fishing due to a lack of spatially resolved fishing effort data that could be integrated into the model. Despite this limitation, I endeavoured to explore the fishing effect on species biomass using a linear regression model with species biomass at the divisional level (3L, 3N, and 3O) as the response variable and fishing catch data aggregated at the same level (NAFO STLATLANT database) as the explanatory variable. I only investigated yellowtail flounder and snow crab because the commercial Atlantic cod fishery on the Grand Banks has remained closed since 1992 due to the slow recovery after its collapse, with individuals being captured as bycatch and in recreational (known as the food fishery) and small vessel, inshore commercial fisheries (DFO, 2019).

3.4 Results

For all species, models that included spatial effects produced better fit. Similarly, models that included bottom temperature and depth effects as covariates performed better (Table 3.2). My results showed that the spatial effect explained most of the variability in the biomass data, followed by depth and temperature, respectively (Table 3.2-ΔAIC values). I also tested different spatio-temporal configurations (AR1, RW and iid) and found that the autoregressive spatiotemporal structure (AR1) had higher predictive accuracy for snow crab and yellowtail flounder, while independent and identically distribution (iid) performed better for Atlantic cod (Table 3.2-ΔELPD values). AR1 has a ρ parameter that indicates the degree of correlation from one year to the next. I found that yellowtail flounder biomass had $\rho = 0.73$ and snow crab biomass had $\rho = 0.71$.

Table 3.2: Models used to identify the best configuration based on Akaike Information criteria differences (ΔAIC) and expected log pointwise predictive density weights (ΔELPD). The model structure indicates the different configurations tested in the model. Note that bottom temperature (temp) and depth were added as smoothing terms (p-spline). df indicates the degree of freedom, AIC is the Akaike information criteria, and ΔAIC indicates differences among AICs. ELPD is the expected log pointwise predictive density, and differences among ELPDs are indicated by ΔELPD. The best model configuration is in bold.

Model structure		df	AIC	ΔAIC	ELPD	ΔELPD
snow crab						
biomass	**year + temp + depth + spatial + AR**	65	16165.08	0.00	0.066	0.000
biomass	year + temp + depth + spatial + RW	63	16227.41	-62.33	0.017	-0.048
biomass	year + temp + depth + spatial + iid	63	16380.88	-215.80	0.017	-0.049
biomass	year + depth + spatial + iid	59	16421.67	-256.59	-0.010	-0.077
biomass	year + spatial + iid	55	16719.23	-554.15	-0.057	-0.123
biomass	year + spatial	53	17429.39	-1264.31	-0.379	-0.446
biomass	year	49	22066.03	-5900.95	-1.123	-1.190
yellowtail flounder						
biomass	**year + temp + depth + spatial + AR**	65	25270.75	0.00	-2.601	0.000
biomass	year + temp + depth + spatial + RW	63	25320.52	-49.77	-2.632	-0.031
biomass	year + temp + depth + spatial + iid	63	25406.76	-136.01	-2.614	-0.013
biomass	year + depth + spatial + iid	59	25416.07	-145.32	-2.646	-0.044
biomass	year + spatial + iid	55	25624.18	-353.43	-2.652	-0.050
biomass	year + spatial	53	25998.47	-727.72	-2.882	-0.281
biomass	year	49	33741.03	-8470.28	-4.392	-1.791
Atlantic cod						
biomass	year + temp + depth + spatial + AR	65	26026.72	0.00	-1.121	-0.007
biomass	year + temp + depth + spatial + RW	63	26241.75	-215.03	-1.220	-0.106
biomass	**year + temp + depth + spatial + iid**	63	26126.11	-99.39	-1.113	0.000
biomass	year + depth + spatial + iid	59	26315.88	-289.16	-1.119	-0.006
biomass	year + spatial + iid	55	26990.33	-963.61	-1.194	-0.081
biomass	year + spatial	53	28139.83	-2113.11	-1.500	-0.387
biomass	year	49	31308.14	-5281.42	-2.195	-1.082

3.4.1 Spatial and covariate effects

The spatial random field represents consistent deviations in space through time that are not accounted for by depth and bottom temperature covariates. Higher spatial deviations were found in the north of the Grand Banks for snow crab occurrence, while they were higher near the nose and tail of the Banks for snow crab biomass (Figure 3.2 a&b). Higher spatial deviations of yellowtail flounder probability of occurrence and biomass were both found in the southern part of the Grand Banks (Figure 3.2 h&i). Higher spatial deviations of Atlantic cod occurrence were found in the western part of the Banks and in the 3O division, while spatial deviations were higher in the south (3NO division) and around the Grand Banks' periphery for Atlantic cod biomass (Figure 3.2 o&p). Higher probability of snow crab occurrence and biomass was associated with colder temperatures, below 0 °C (Figure 3.2 c&d), and at depths of about 100 m for occurrence and 450 m for biomass (Figure 3.2 e&f). For yellowtail flounder, both higher probability of occurrence and higher biomass were predicted for temperatures close to 3 °C and shallower depths around 80 m (Figure 3.2 j&m). Atlantic cod probability of occurrence was predicted to be highest at temperatures close to 3 °C and depths of 300 m (Figure 3.2 q&r). Highest biomass of Atlantic cod was predicted to occur at 5 °C and at depths between 200 and 400 m (Figure 3.2 s&t). Combined predictions of the delta gamma models indicate that snow crab biomass is higher in the north of the Banks, with a hotspot located in the northeast, and in the southeastern edge of the Banks (Figure 3.2 g). The yellowtail flounder biomass hotspot is found south of the Banks (Figure 3.2 n). Finally, Atlantic cod biomass is higher in the north and periphery of the Banks, as well as in the southeast (Figure 3.2 u).

3.4.2 Biomass indices

A decline in the snow crab relative biomass index was observed over time, reaching a minimum of 33.72 t in 2016 (Figure 3.3 a). Although there has been a small recovery since then, the current biomass index of snow crab was 85% lower in 2019 than at the beginning of the time series in 1996. Yellowtail flounder relative biomass has fluctuated over time, peaking in 2006 (597.88 t), 2012 (538.31 t) and 2008 (424.83 t) (Figure 3.3 b). However, the biomass plummeted to its lowest value in 2016 (119.96 t) and has remained relatively low since then, with a biomass of 171.12 t in 2019. Similarly, Atlantic cod biomass has fluctuated over time, reaching its highest value in 2013 (150.07 t), with smaller peaks in 1999 (100.6 t) and 2006 (100.04 t) (Figure 3.3 c). Since 2014, the relative biomass of Atlantic cod has declined, hitting

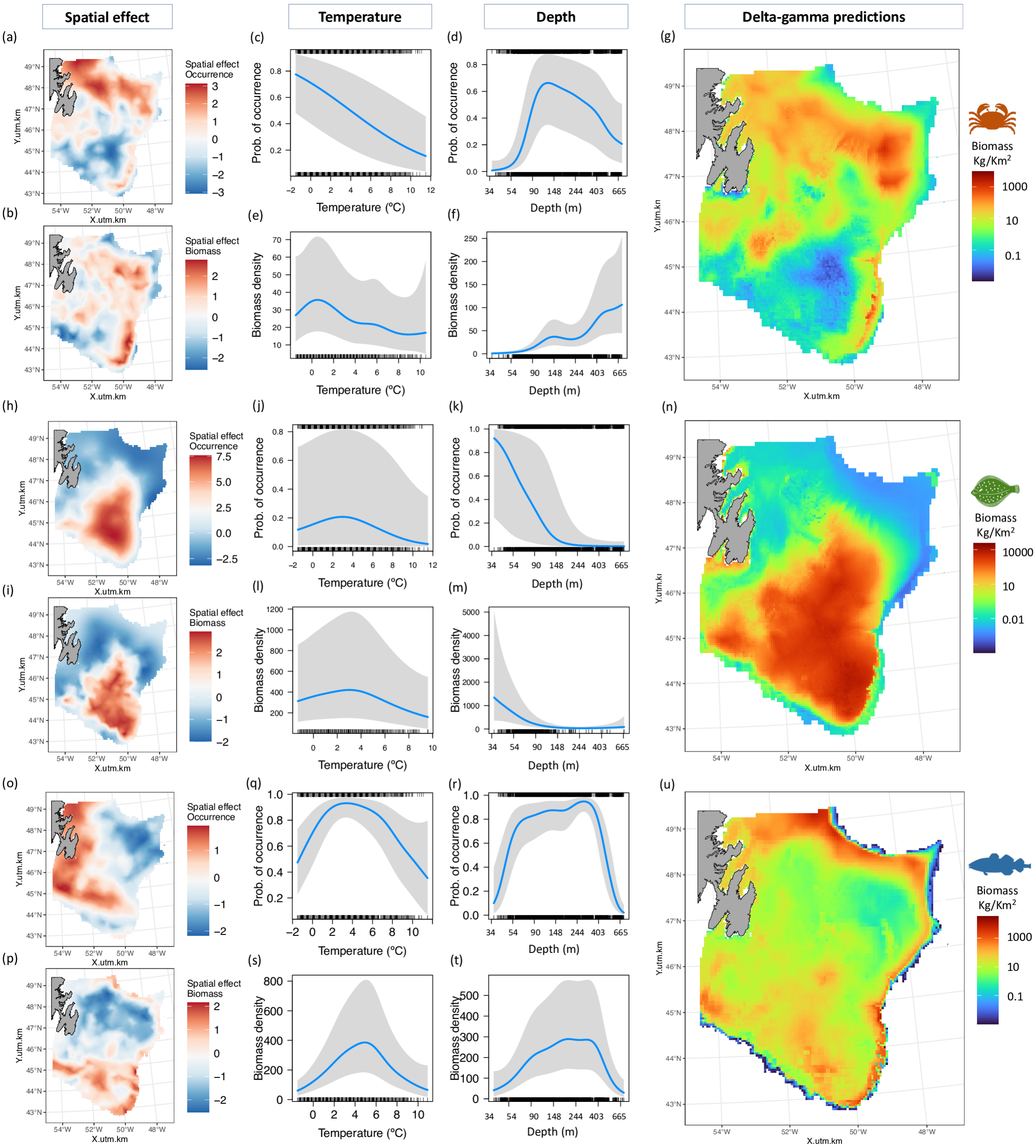


FIGURE 3.2: Spatial random field deviations summed across all years of snow crab probability of occurrence (a) and biomass (b), yellowtail flounder probability of occurrence (h) and biomass (i), and Atlantic cod probability of occurrence (o) and biomass (p). Temperature smoothed effects on snow crab probability of occurrence (c) and biomass (d), yellowtail flounder probability of occurrence (j) and biomass (k), and Atlantic cod probability of occurrence (q) and biomass (r). Depth smoothed effect on snow crab probability of occurrence (e) and biomass (f), yellowtail flounder probability of occurrence (l) and biomass (m), and Atlantic cod probability of occurrence (s) and biomass (t). Note that depth has been log-transformed. Biomass density units are kg/25 km2. Delta gamma combined biomass prediction of snow crab (g), yellowtail flounder (n) and Atlantic cod (u) over the Grand Banks. Predictions made on a 5x5 km grid.

a record low of 19.30 t in 2017, a similar biomass level when the stock collapsed in the mid-1990s (31.12 and 20.39 t in 1996 and 1997, respectively). As of 2019, the biomass of Atlantic cod on the Grand Banks was rather low compared to the historical series (43.17 t). My model effectively generated an environmental-informed biomass index that showed trends consistent with strata-based indices reported in the stock assessments of the studied species. For yellowtail flounder, my biomass index had a high correlation ($R^2 = 0.92$), with the strata-based index falling within the confidence interval. For snow crab, the correlation with the strata-based index was also high ($R^2 = 0.84$). However, some disparities were evident between the indices, as my analysis indicates slightly higher biomass estimates, particularly at the beginning of the time series. Note that I am comparing the biomass index created using spring data with the strata-based biomass index created using fall data. Unfortunately, no established index exists for Atlantic cod in the 3LNO division since this species is considered two separate stocks (i.e., 2J3KL and 3NO). As a result, I compared my biomass index to the index used to assess the 3NO stock, as it more accurately represents cod biomass within the Grand Banks, resulting in a correlation of $R^2 = 0.63$.

3.4.3 Centre of gravity

The Centre of gravity indicates the central point of a population distribution. In the case of snow crab, the centre of gravity shifted slightly toward the northwest of the Grand Banks over time (Figure 3.4 a). The centre of gravity of yellowtail flounder has remained relatively stable (Figure 3.4 b). Atlantic cod had the greatest changes in the centre of gravity, first moving eastward and then northward at the end of the time series (Figure 3.4 c). I also calculated the species centre of gravity directly from the data using mean weight, which displayed similar trends but are slightly more spread out in Figure A.8. This difference can be attributed to the

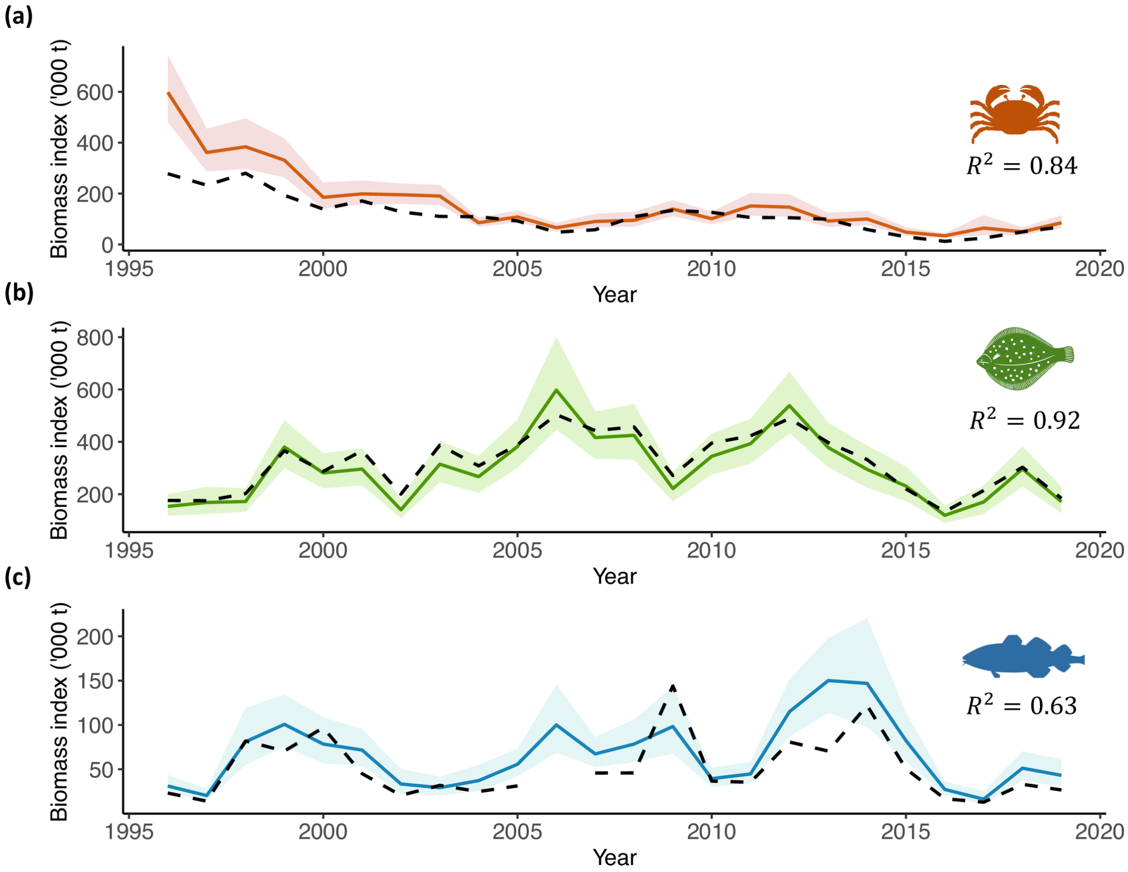


FIGURE 3.3: Biomass indices of snow crab (orange), yellowtail flounder (green) and Atlantic cod (blue) on the Grand Banks of Newfoundland (3LNO division) estimated from the spatio-temporal delta gamma GAM. Shaded areas indicate the 95% confidence interval. The black dashed line indicates the strata-based index of the species (units in tonnes x1000). R^2 is the coefficient of determination.

spatio-temporal model predicting biomass in years and locations with sampling gaps.

3.4.4 Fishing effect

My findings suggest a negative relationship between snow crab biomass and fishing (measured as catch) in divisions 3L and 3N, although these relationships were not statistically significant (p = 0.1 and 0.9, respectively). Similarly, I observed a negative relationship between yellowtail flounder biomass and fishing in divisions 3N and 3O. These relationships were also not statistically significant, although the

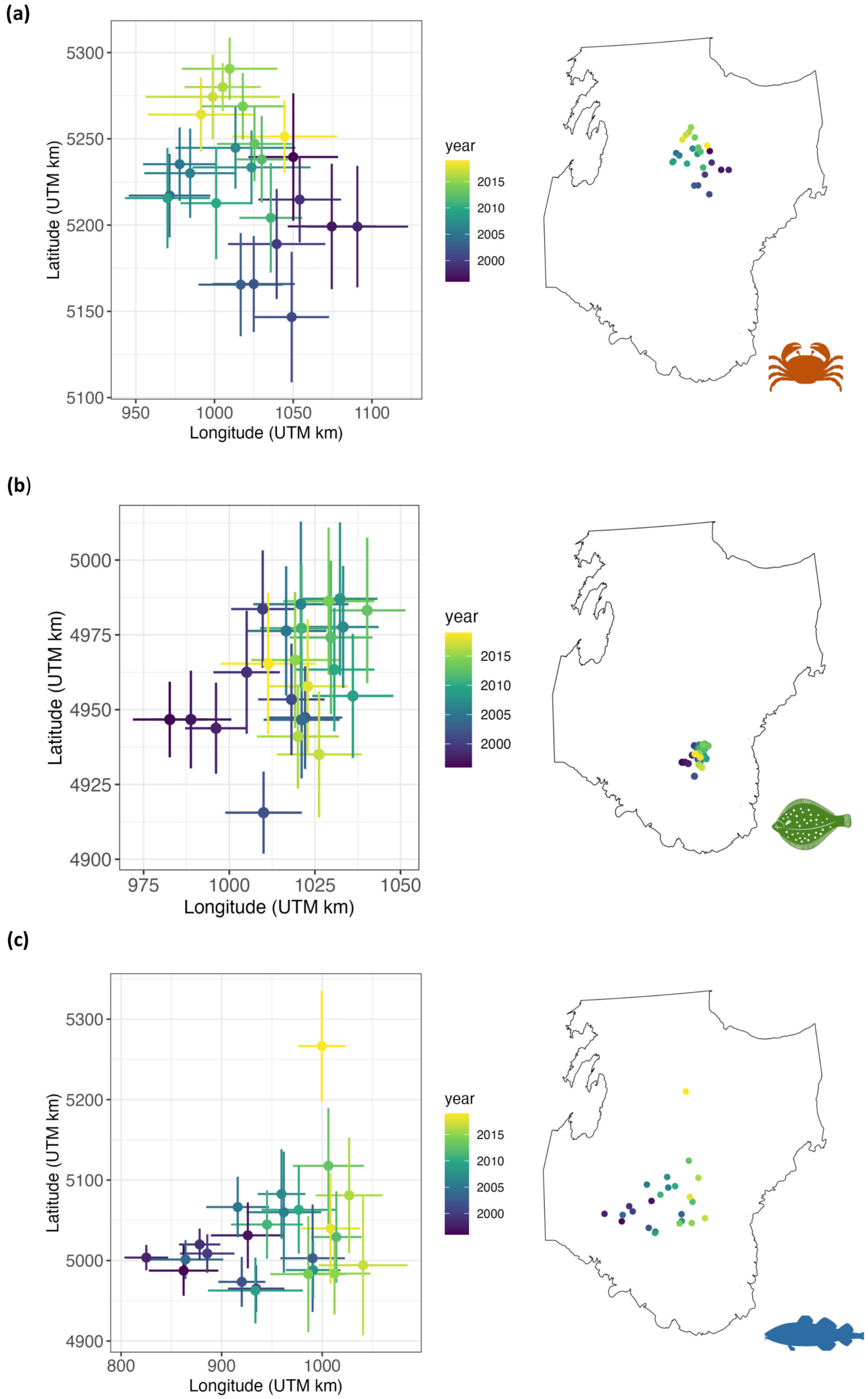


FIGURE 3.4: Centre of gravity of snow crab (a), yellowtail flounder (b) and Atlantic cod (c) on the Grand Banks of Newfoundland. Points indicate mean values and bars indicate variance. Colours represent years (from 1996 to 2019), with more recent years in yellow.

fishing effect was more pronounced in division 3N ($p = 0.08$ and 0.48, respectively) (Figure A.4).

3.5 Discussion

My findings highlight the importance of considering spatial heterogeneity in fisheries survey data, as the spatial component accounted for the majority of observed variance for all three species (Table 3.2). The spatial component explains variance that is not accounted for by the covariates depth and temperature. I observed that spatial effects differed between the occurrence and biomass processes for snow crab and Atlantic cod, but not for yellowtail flounder. These differences have been found in other studies and may be indicating spatial differences between species life stages, which are ignored in the occurrence analysis but get weighed in the biomass analysis (Izquierdo et al., 2021). Likewise, I noted a disparity in the relationship between biomass and depth for snow crab in both the occurrence and biomass processes, which is likely linked to the preference of adult snow crab for deeper waters (Mullowney et al., 2018). Biomass hotspots are more restrictive than occurrence hotspots since biomass is higher only in areas with suitable conditions (e.g., environmental, reduced competition, prey availability), whereas individuals have a wide spatial range where they can be found (Izquierdo et al., 2021).

The new biomass indices presented in this study overcome issues related to gaps in sampling by interpolating among missing data points. Missing data were important in the years 2015 and 2017 due to incomplete sampling during those periods (Rideout and Ings, 2019; Brodie and Stansbury, 2007). They also account for species habitat-presence (i.e., depth and temperature) when predicting in unsampled locations and address spatio-temporal correlation. Predicted model biomass estimates align closely with those obtained using strata-based methods, with some disagreements for snow crab and Atlantic cod. In the case of snow crab, the assessment of the stock is done using data from the fall trawl survey. This is because spring data are considered to be less reliable because certain population components may be sampled relatively poorly during this time, coinciding with the mating and moulting periods (Mullowney et al., 2014a). In my analysis, I applied the conversion factor used to account for the low catchability of snow crab in the fall bottom trawl survey (Dawe et al., 2010; Mullowney et al., 2018). The development of this conversion factor was created using data from 2000 to 2016. Thus, the disparities observed in the biomass indices, particularly during the early stages of the temporal series, could potentially be explained by the exclusion of certain years and differences between fall and spring data. Spring data correspond to the pre-fishing season; the higher biomass observed in the new biomass index compared to the fall index could also be attributed to this. For Atlantic cod, differences are mostly due to the comparison of 3NO to 3LNO Atlantic cod.

The models used in the assessment of all stocks included in my analysis, except 3NO Atlantic cod, require biomass indices as input (snow crab assessment uses biomass trends, yellowtail flounder a Schaefer surplus production model and 2J3KL Atlantic cod a state-space model). Therefore, the new biomass indices developed in the present study could be used in the assessment of the species. The use of spatio-temporal indices to fit stock assessments has been shown to improve estimate precision compared to design-based indices (Shelton et al., 2014; Cao et al., 2017). Consequently, this approach has been adopted by governmental bodies such as DFO and the United States National Oceanic and Atmospheric Administration (NOAA) to conduct the assessment of species such as northern shrimp (*Pandalus borealis*) (DFO, 2023b) and yelloweye rockfish (*Sebastes ruberrimus*) (Haggarty et al., 2021). However, it is important to acknowledge that calculating these indices is computationally intensive and presents implementation challenges. For example, spatial confounding (i.e., unaccounted spatial effects influencing the relationships between predictors and response variables) may exist, leading to bias in predictions

(Clayton et al., 1993). Thus, accurately defining the spatial component is crucial in spatio-temporal models (Commander et al., 2022).

The centre of gravity has been used to evaluate the impacts of climate, fishing pressure and other anthropogenic factors on the average location of marine populations (Adams et al., 2018; Friedland et al., 2021). A shift in species' centre of gravity may create challenges and risks for managing resources when species move outside of historical fishing areas or management boundaries (Ojea et al., 2020; Sumaila et al., 2020). The temperature distribution over the Grand Banks is not uniform, with the south and the north warmer than the centre. Additionally, this area undergoes natural cyclical periods of cold and warmth (Cyr et al., 2022). Changes in species distribution (here reflected as changes in the centre of gravity) can be an early sign of water warming on the Grand Banks due to natural variability and/or to climate change (Gonçalves Neto et al., 2021; Saba et al., 2016). However, shifts in species distribution may also be influenced by other factors such as competition, prey availability, habitat degradation and fishing (Adams et al., 2018; Robinson et al., 2017). My results indicate that snow crab is the most sensitive species to warming as its biomass declined as temperature increases, in agreement with other observations in Newfoundland and Labrador, where cold events have been associated with higher recruitment of snow crab (Dawe et al., 2008; Marcello et al., 2012).

I found that yellowtail flounder tolerates a wide range of temperatures, with a preference for 3 °C. This interpretation agrees with the literature, stating that yellowtail flounder can survive wide fluctuations in temperature (Perry and Smith, 1994; Walsh, 1992). The persistence in the yellowtail centre of gravity on the Grand Banks is likely related to a weak current regime allowing for the retention of eggs and larvae in the southern part of the Grand Banks (Simpson and Walsh, 2004)—hypothesized as a nursery ground (Brodie et al., 2010). Atlantic cod has a preference for warmer waters compared to yellowtail flounder and snow crab, favoring temperatures around 5 °C. The northward shift in the center of gravity of Atlantic cod could be explained by a faster recovery of the 3L component of the 2J3KL northern stock, or it may indicate a northern shift of the southern 3NO stock as a response to warming in the region due to a northern shift of the Gulf Stream (Gonçalves Neto et al., 2021).

Management of natural resources is a complex task that should consider ecological processes and how they relate to administrative boundaries. When management units are solely defined based on these administrative boundaries, decisions can have unintended consequences for the ecosystem (Kerr et al., 2014). My analysis of Atlantic cod showed a continuous distribution over the Grand Banks during years of higher biomass (Figure A.7), indicating hyperaggregation behaviour (i.e., aggregation of fish in a location during a period of low abundance (Rose and Kulka, 1999). While this behaviour can decrease individual competition and maximize fitness, it can also increase the vulnerability of the species to fishing because of range contraction (Burgess et al., 2017). Previous studies have documented the mixing of Atlantic cod stocks (Smedbol et al., 2002; Tulk et al., 2017), suggesting that a joint assessment of the population and management decisions at the 2J3KL and 3NO management units, similar to the approach taken with snow crab, would be prudent. However, the pursuit of such collaborative efforts may face institutional barriers, given that these two Atlantic cod stocks fall under the purview of distinct regulatory bodies, namely DFO and NAFO. NAFO is a regional fisheries management organization responsible of the management of high seas fishery resources, while DFO manages resources within the Canadian economic exclusive zone. Both entities apply the precautionary approach and reference points to manage the resources (DFO, 2006; NAFO, 2004), however, differences in management strategies, regulatory frameworks, and governance structures across these governing entities may exist. Fostering this joint assessment would require both the DFO and NAFO to engage in collaborative workshops to share best practices, align priorities, and agree on management strategies.

Ocean warming (natural or driven by climate change) has been identified as the primary driver of snow crab decline in Newfoundland, while fishing and competition may have had localized impacts (Mullowney et al., 2014b). Overfishing is generally blamed for the decline of yellowtail flounder stocks in the early 1990s, but the productivity of the species was also strongly influenced by climatic conditions during the collapse and subsequent recovery (Brodie et al., 2010). In the present analysis, even though I could not directly account for the fishing effect in my models, I assessed the effect of fishing on species biomass at a coarser spatial resolution—the NAFO division level. I found that, even though the negative effect of fishing (i.e., landed catches) on species biomass was important in certain divisions (such as 3L and 3N for snow crab, and 3N for yellowtail flounder), these relationships were not statistically significant (refer to Figure A.4). The divisions with the strongest fishing effect overlapped with those in which species had a biomass hotspot. This result is not surprising since fishers harvest on aggregations of individuals and not homogeneously across the entire area. However, the non-significance ($p > 0.05$) of the fishing effect on the new biomass indices suggests that additional factors likely contribute to the observed decline in species biomass.

My analysis is based on spring survey data, and therefore, the distribution patterns I observed may differ during other seasons. Species distribution is highly influenced by seasonal cycles, particularly in temperate areas, due to variations in environmental factors, light availability, and nutrient supply (Kaiser et al., 2011; Lloret-Lloret et al., 2020). Atlantic cod of the 2J3KL stock seek refuge near the continental shelf edge in winter and move to shallow coastal waters and onto the Grand Banks plateau during spring and summer for feeding (DFO, 2022b). It is possible that the difference in the timing of the survey could affect the trends in species distribution found in this study. This could be addressed by incorporating survey timing as a fixed or random effect in the model to adjust for variations in survey dates. Similarly, snow crab undergo seasonal migrations related to moulting and mating (Mullowney et al., 2018). It is likely that I am missing information on species affinity for habitats that rely on seasonal variations. In addition, I used aggregated size and sex information of species to predict biomass. Distribution differences among species life stages may exist, including potential shifts in habitat preferences between juvenile and adult stages (Tanaka et al., 2019).

As species range shift in different directions and rates, it is likely that predator-prey interactions will also change (Selden et al., 2018). The availability and abundance of prey directly impact the population dynamics and distribution of predators (Sydeman et al., 2015; Richardson et al., 2014). When prey species become scarce, predators may experience declines in body condition and overall population size (Petrie et al., 2022). The diminishing abundance of capelin, the primary prey of Atlantic cod, has been identified as a contributing factor to the decline in Atlantic cod growth potential (Petrie et al., 2022) and body condition (Regular et al., 2022) of the 2J3KL stock. Fisheries harvest of other prey items of the Atlantic cod (i.e. snow crab and northern shrimp) could further exacerbate the issue of food limitation, hampering stock recovery (Petrie et al., 2022; Regular et al., 2022). On the other hand, predators like Atlantic cod can play a regulatory role in shaping prey populations. In the Barents Sea, Atlantic cod has been identified as a regulator of the snow crab population, impacting both its distribution and productivity (Durant et al., 2023; Holt et al., 2021). A comparable phenomenon could potentially exist between these species on the Grand Banks. The examination of the distribution maps (Figure 3.2 g and u) reveals limited overlap between Atlantic cod and snow crab in the Grand Banks. The limited overlap could be primarily attributed to the preference of snow crab for lower temperatures (below 0 °C), however, snow crab distribution may also be regulated by Atlantic cod presence.

Future studies could explore predator-prey dynamics and species competition using alternative methodologies such as joint species distribution models (Clark et al., 2014; Pollock et al., 2014). Additionally, incorporating substrate type in future research could provide valuable insights into the habitat preferences of demersal and benthic species of the Grand Banks. Future research could enhance ecosystem understanding by incorporating predation-prey interactions (Rutterford et al., 2023; Laman et al., 2018), integrate multiple sources of data (Grüss and Thorson, 2019) and forecast climate change impacts on the Grand Banks under different emissions scenarios (Thompson et al., 2023). My work could serve as a foundation for the development of spatial management strategies since it provides fine-scale information on biomass distribution. This information is crucial for establishing effective conservation areas and spatial closures (Lawler et al., 2010; Abad et al., 2020).

3.6 Conclusions

The introduction of novel indices offers a practical avenue for informed decision-making and underscores the importance of comprehensive approaches to fisheries management. My study revealed a continuous distribution of Atlantic cod across the Grand Banks and a possible northern shift of the species, emphasizing the need for joint management of the 2J3KL and 3NO stocks. The research presented here holds promise for enhancing sustainability of Canadian fisheries by improving our understanding of the interactions between environmental variables and species distributions.

CHAPTER 4

Forecasting species biomass to 2100

4.1 Abstract

Species Distribution Models (SDMs) are tools for understanding climate-induced habitat changes, yet their outcomes depend heavily on climate model selection. This study compares biomass projections for three key species on the Grand Banks of Newfoundland—snow crab, yellowtail flounder, and Atlantic cod—known to be responsive to warming. We use Earth system models (GFDL-ESM4, IPSL-CM6A-LR) and a regional ocean model system (Atlantic Climate Model (ACM)) under varying emissions scenarios to assess long-term biomass trends and distributional shifts driven by future ocean warming on the Grand Banks. Results indicate declining biomass for snow crab and yellowtail flounder with rising temperatures, whereas Atlantic cod is anticipated to exhibit biomass gains, particularly in the southern Grand Banks. Variations in biomass projections among climate models were noticeable, with IPSL forecasting the most drastic decline. ACM and GFDL biomass projections were more similar to each other than GFDL and IPSL projections, likely because ACM was downscaled from GFDL. The difference between GFDL and ACM likely arises from the coarse spatial resolution of ESMs, leading to insufficient resolution of the bathymetry and incorrect current patterns, which, in turn, affect the bottom temperature field. These findings underscore the important role of climate model selection in SDM-derived biomass projections. We also partitioned uncertainty by sources and found that the relative contribution of variability by component changes by species. As temperatures continue to rise, the

urgency of implementing adaptive management strategies to minimize impacts on Newfoundland and Labrador fisheries becomes increasingly evident, including, for example, adjustments of fishing quotas, area closures and gear restrictions (Pinsky and Mantua, 2014). SDM outputs can aid in strategic decision-making, providing valuable insights for medium and long-term planning in fisheries management.

4.2 Introduction

Species distribution models (SDMs) have become increasingly important as the marine environment changes rapidly. Distributions of species in space and/or time are modelled as a function of a range of physical, environmental, and ecological variables. SDMs have been implemented with a diverse range of statistical tools, including classic regression models (e.g., generalized linear models- GLMs, generalized additive models- GAMs, and generalized linear mixed models GLMM) (Becker et al., 2020), machine learning algorithms (e.g., random forest and artificial network analysis) (Luan et al., 2020), climatic envelope methods (e.g., dynamic bioclimatic envelope models) (Fernandes et al., 2013; Cheung et al., 2016) and decision tree methods (e.g., boosted regression trees) (Yu et al., 2020). To forecast climate change impacts on species distributions, environmental outputs from Earth system models (ESMs) and regional ocean modelling systems (ROMS) are commonly used to forecast into the future (Cheung et al., 2016; Florko et al., 2021). ESMs simulate the Earth's entire climate system, focusing on global-scale interactions between the atmosphere, oceans, land surfaces, and ice. They provide insights into long-term climate trends and variability (Stock et al., 2011; Skogen et al., 2018). Variation in ESM projections can arise due to differences in forcing, process configuration, feedbacks, and horizontal and vertical resolutions (IPCC, 2021; Merrifield et al., 2023). In contrast, ROMS concentrate on specific regions or domains of the ocean, offering higher spatial resolutions to study fine-scale processes such as coastal dynamics, boundary currents, and mesoscale eddies (Drenkard et al., 2021; Kearney et al., 2021). The low spatial resolution of ESMs can make it challenging to adequately represent regional processes, as they are primarily designed to emphasize global-scale dynamics (Stock et al., 2011). ESMs also do not appropriately represent depths less than 50 m in shallow coastal regions (Stock et al., 2011). However, in many cases, these models are the only available information to project species distribution under climate change scenarios (IPCC, 2021).

Newfoundland and Labrador, located on the east coast of Canada, is a dynamic region that undergoes significant climatic variations, oscillating between warm and cold periods on decadal scales (Cyr and Galbraith, 2021). Within it, three major geographical subunits characterized by distinct productivity and a reasonably well-defined major marine community (aka ecosystem production units), have been identified: Newfoundland shelf (North Atlantic Fishery Organization (NAFO) divisions 2J3K), Grand Banks (3LNO) and Flemish Cap (3M) (Pepin et al., 2014; Koen-Alonso et al., 2019). A key feature of the Newfoundland system is the cold intermediate layer (CIL), consisting of a water layer below 0 °C. It forms during winter as a cold surface layer and remains as an intermediate layer separate from the surface (roughly 0-50 m) when waters warm in spring (Cyr and Galbraith, 2021). The presence of the CIL heavily impacts the Grand Banks because of the shallow depth of the oceanic plateau, creating distinct temperature patterns within the Banks. Moreover, recent observations suggest a trend of warming ocean temperatures on the Grand Banks (Cyr et al., 2022). This warming may be influenced not only by warmer air temperatures that increase the heat transfer to the upper layers of the oceans but also by a slowing down of the shelf-break jet, which reduces the supply of the fresh, cold and nutrient-rich waters of the Labrador Current to the Grand Banks slopes (Jutras et al., 2020; Garcia-Suarez et al., 2023; Rutherford et al., 2024).

In the Newfoundland and Labrador region, a shift from a warm to cold phase in the 1990s, coupled with intensive fishing, triggered alterations in ecosystem productivity, leading to a substantial decline in most groundfish stocks and a surge in invertebrate biomass on the Newfoundland Shelf (Pedersen et al., 2017) and the Grand Banks (Dempsey et al., 2017). Responding to the groundfish collapse, several fishing moratoria were imposed in 1992 and 1994 on the Newfoundland Shelf and the Grand Banks, respectively, to facilitate the recovery of groundfish stocks (e.g., Atlantic cod, yellowtail flounder, haddock, among others). The impact of the collapse was profound, affecting both harvesters and plant workers in the province, with over 35,000 individuals losing their source of livelihood (Mather, 2013). In the present study, we focused on three key fisheries species of the Grand Banks that exhibited distinct responses to the collapse: yellowtail flounder (*Limanda ferruginea*), Atlantic cod (*Gadus morhua*) and snow crab (*Chionoecetes opilio*).

The yellowtail flounder fishery was closed from 1994 to 1997 at the 3LNO division and rebounded, currently operating as a Marine Stewardship Council (MSC) certified fishery (Brodie et al., 2010; Knapman et al., 2020). Yellowtail flounder inhabits the east coast of North America, from Newfoundland to the Chesapeake Bay (Brodie et al., 2010), with biomass peaking on the Grand Banks at approximately 3 °C (in spring), and tolerating a wide temperature range 1-6 °C (Ruiz-Diaz et al., 2024). In contrast, Atlantic cod stocks (3NO and 2J3KL) remain at low levels compared to historical baselines, with only a modest increase in biomass observed in the 2J3KL stock, primarily driven by the 2J3K divisions (DFO, 2022). This situation has resulted in the persistent closure of the directed fishery for both stocks (Rideout et al., 2021; DFO, 2022b). Atlantic cod, found across the North Atlantic Ocean, avoids temperatures exceeding 12 °C (Drinkwater, 2005). In the Grand Banks, higher biomass of Atlantic cod is found at at 5-6 °C (in spring) on the Grand Banks (Ruiz-Diaz et al., 2024).

Following the collapse, Newfoundland and Labrador's fishing industry diversified its targets, focusing on invertebrate species like snow crab. Snow crab has become the province's most valuable species, with a value of $761 million CAD in 2022, representing 58% of the total landed value of all fisheries resources in NL (Mather, 2013; NL Government, 2023). A recent study found that the species is moving from Subarctic to Arctic environments (Mullowney et al., 2023). This suggests that with future warming, the species may experience biomass losses on the Grand Banks, where most of the Newfoundland and Labrador quota (59%) is currently allocated. In addition to potential biomass losses due to future warming, it is important to consider that species may also exhibit northward shifts on the shelf or migrate into deeper waters as they seek suitable habitats.

The climatological changes mentioned above may present a pressing issue for Newfoundland and Labrador's fishing sector, which in 2022 contributed $1.4 billion CAD to the local economy and currently employs over 17,000 people across 400 communities (NL Government, 2023). Thus, the objectives of this study are: i) to produce and compare biomass projections for three contrasting species on the Grand Banks of Newfoundland under two emission scenarios; and ii) to evaluate the importance of climate model choice in these types of projections. In particular, we compared species biomass projections using the Coupled Model Intercomparison Project (CMIP) 6 earth system models IPSL-CM6A-LR (Boucher et al., 2020) and the GFDL-ESM4 (Dunne et al., 2020) under low (SSP1-2.6) and high (SSP3-7.0) emissions scenarios, and the ROMS Atlantic Canada model (from now on referred as ACM) (Laurent et al., 2021; Rutherford et al., 2024) as climate forcings. The ACM model was forced by anomalies from the GFDL's high-resolution coupled model, CM2.6, with a rapid increase in CO2 that resembles the SSP4-6.0 scenario (Garcia-Suarez et al., 2023). While these results are only projections and should be interpreted with caution, they provide valuable guidance for fisheries management strategies by detecting changes in habitat suitability and anticipating future biomass trends. In assessing differences in biomass projections, we specifically analyzed the influence of climate model choice and emissions scenario, including variations in temperature fields under low (SSP1-2.6) and high (SSP3-7.0 and SSP4-6.0) emissions pathways.

4.3 Material and Methods

4.3.1 General approach

We used SDMs to characterize current species distributions, with temperature and depth as key drivers. These models aim to capture the general changes associated with climate-driven shifts in temperature. To achieve this objective, we defined temperature fields for the Grand Banks using various emissions scenarios (low - SSP1-2.6 and high – SSP3-7.0 and SSP4-6.0-) generated by multiple climate models (IPSL, GFDL and ACM), thereby capturing uncertainty surrounding these projections. Subsequently, we will utilize the SDMs and the projected temperature fields to forecast the expected distributions of the focal species between the present and 2100 under different climate change scenarios. Finally, we assessed variability as a function of climate models and emissions scenarios.

4.3.2 Oceanographic and biological survey data

Fisheries and Oceans Canada (DFO) has conducted annual stratified random multispecies trawl surveys in Newfoundland and Labrador since 1971, with these surveys experiencing important modifications in survey design, coverage, species recorded, and gear over time (Brodie and Stansbury, 2007). One major change in these surveys was the introduction of the Campelen trawl gear (i.e., 1800 shrimp trawl) in 1995-1996 (Brodie and Stansbury, 2007). The previous survey trawl was Engels. This change improved catches of small-sized fishes and marked the start of the time series recording for commercial shellfish species. Georeferenced data on presence/absence and biomass for the focal species of this study, as well as water temperature and depth, come from DFO spring surveys on the Grand Banks between 1996 and 2019. This survey do not collect environmental data other than temperature, that is why we focused on assessing temperature as a driver of species distribution. For predicting biomass, we created grids with a 5×5 km spatial resolution which included gridded bathymetry information with a 15 arc seconds spatial resolution from the general bathymetric chart of the oceans project (GEBCO) and spring bottom temperature data interpolated over the Grand Banks with a spatial resolution of $0.1° \times 0.1°$ (Cyr et al., 2022) (Figure 4.1). Bathymetry data represented depths from 35 to 750 m since those were the depths sampled in the RV trawl survey.

4.3.3 Climate models and emissions scenarios

We considered both low and high emissions scenarios to assess their impacts on snow crab, yellowtail flounder, and Atlantic cod distributions on the Grand Banks. We used three models to characterize these scenarios. The ACM uses ROMS version 3.5, a terrain-following, free-surface, primitive equation ocean model (Haidvogel et al., 2008; Laurent et al., 2021). It was configured with 30 vertical levels (layers are thinner in shallower water and thicker in deeper water), with a minimum water depth of 10 m, and an approximate horizontal resolution of 10 km (240×120 horizontal grid cells). The model encompass the Gulf of Maine, Scotian Shelf, East Newfoundland Shelf, Grand Banks, and the Gulf of St. Lawrence, has been demonstrated to accurately capture regional circulation patterns (Brennan et al., 2016), and represent biogeochemical properties well (Laurent et al., 2021). The ACM was calibrated to observed values (Laurent et al., 2021). In comparison, IPSL-CM6A-LR (Boucher et al., 2020) and GFDL-ESM4 (Dunne et al., 2020) are ESMs with a coarser spatial resolution of approximately 100 km. These models produce a much poorer agreement with observed temperatures, salinity, nitrate,

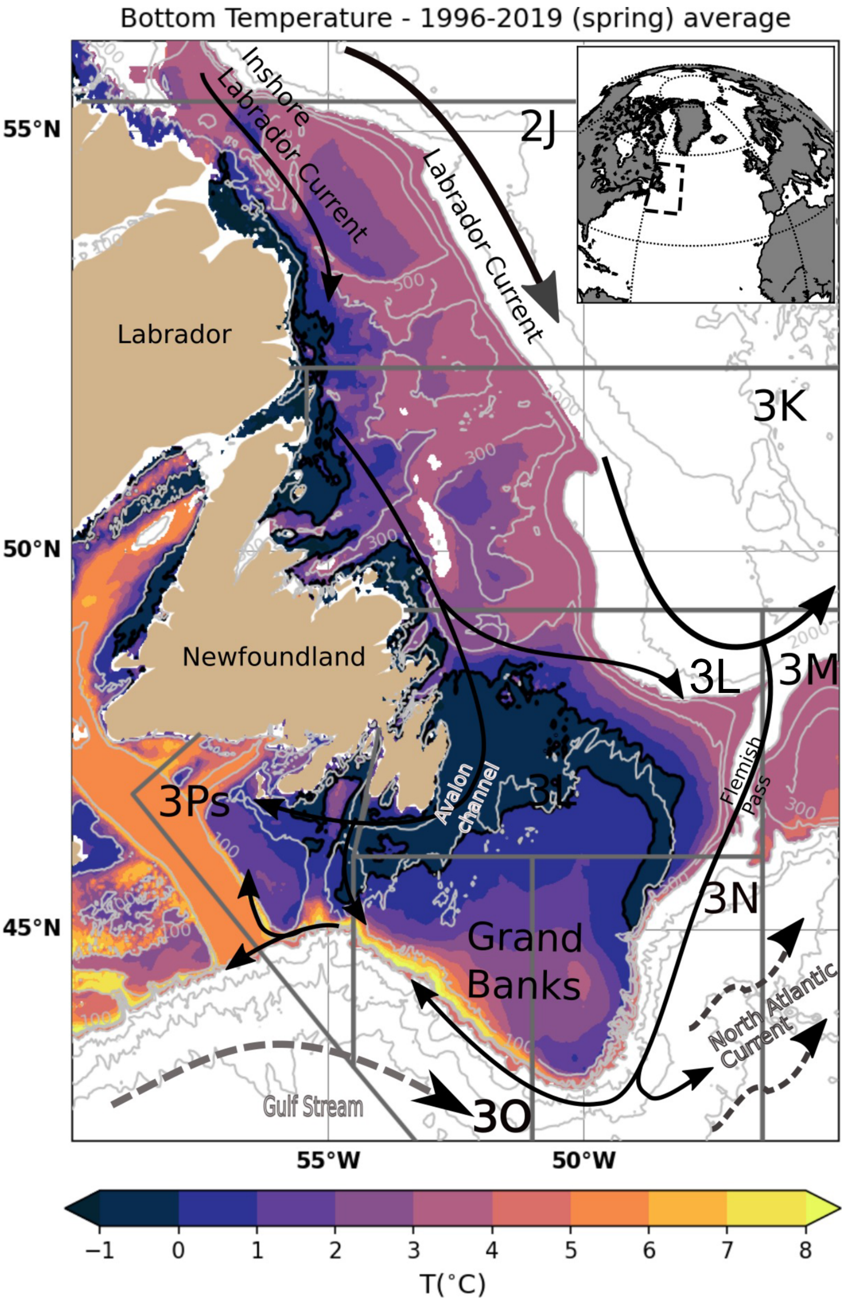


Figure 4.1: Map of the average spring bottom temperature during the historical period (1996-2019) interpolated over the Grand Banks. Isobaths are indicated in light grey; Northwest Atlantic Fisheries Organization NAFO divisions boundaries are indicated with grey rectangles. Black arrows show the main currents of the region.

and chlorophyll observation in the Grand Banks than the ACM (Laurent et al., 2021). ESMs also do not appropriately represent depths less than 50 m (Stock et al., 2011).

For biomass projections, we used annual averages of the sea bottom temperature (potential temperature on bottom – thetao_bot) sourced from the Coupled Model Intercomparison Project (CMIP) 6 ESMs IPSL-CM6A-LR (Boucher et al., 2020), GFDL-ESM4 (Dunne et al., 2020) and the ROMS ACM (Laurent et al., 2021; Rutherford et al., 2024). We used the shared socioeconomic pathway (SSP) and representative concentration pathways (RCP) scenarios SSP3-7.0 for IPSL and GFDL, and SSP4-6.0 for ACM as the high emissions scenarios due to availability, and the low emissions scenario SSP1-2.6 (van Vuuren et al., 2011). Unfortunately, the low emissions scenario was not available for ACM (Figure 4.2 a&b). Note that while the specifics of these scenarios do not align perfectly among models, they are similar enough for general comparisons and characterizations. Finally, we bias-corrected annual bottom temperatures projections of the climate models to the local spring observations by calculating the mean values from 2015 to 2019 and subtracting the difference between predictions and observations (see Figure B.9 and Figure B.10). We selected these years because the projections and observations time overlapped.

4.3.4 Modelling approach

Species distribution models

To build species distribution models, we used the R package sdmTMB (Anderson et al., 2022). sdmTMB fits models with maximum marginal likelihood through template model builder (TMB; (Kristensen et al., 2015)) and incorporates the stochastic partial differential equation approach (SPDE; (Lindgren and Rue, 2015)) for approximating spatial Gaussian random fields, drawing from the methodology

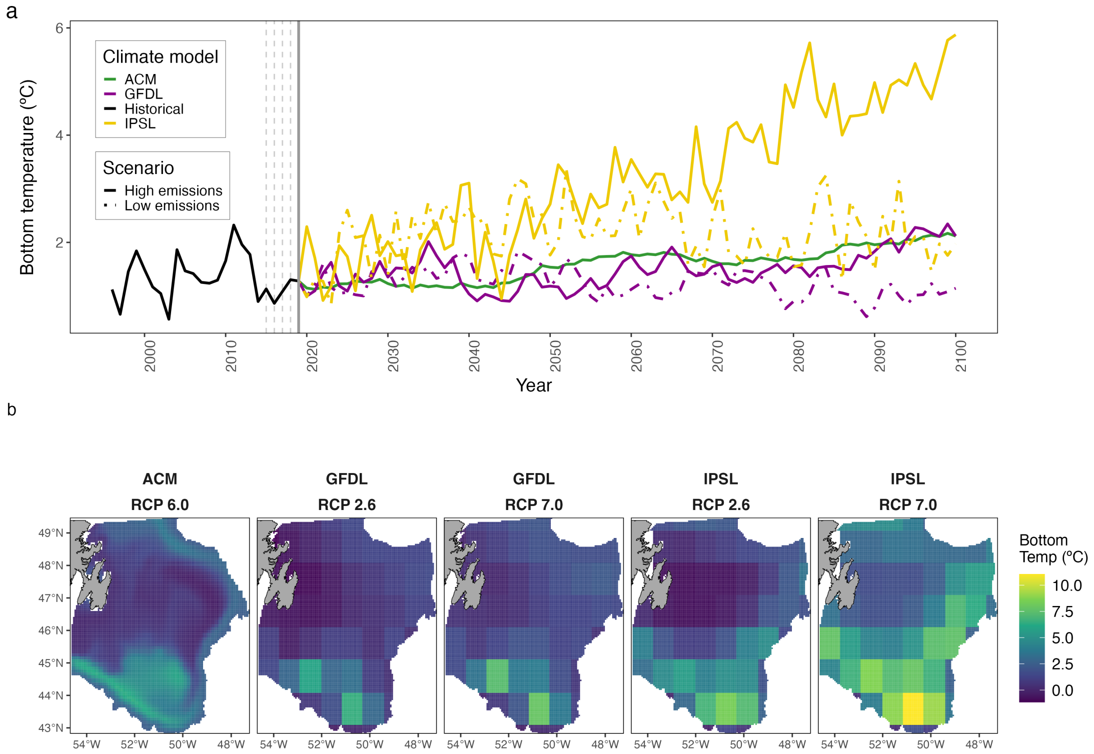


FIGURE 4.2: Maps and time series of average annual bottom temperature projection on the Grand Banks. a, Time series of average annual bottom temperature for the model domain. The historical period is represented by a black line, while the IPSL-CM6A-LR, GFDL-ESM4, and ACM models are indicated by yellow, purple and green lines, respectively. Dashed lines represent the low emissions scenario (SSP1-2.6), and solid lines depict the high emissions scenario (SSP4-6.0 for ACM, and SSP3-7.0 for GFDL and IPSL). b, Maps of mean annual bottom temperature projections by climate model (GFDL, IPSL and ACM) and RCP scenarios at the end of the century (period 2071-2100).

established in the integrated nested Laplace approximation (INLA) R package (Rue et al., 2009; Lindgren and Rue, 2015).

Two population variables were used as response variables to characterize the species distributions. Firstly, a presence/absence variable was considered to measure the probability of species occurrence. Secondly, species biomass was used as an indicator of the conditional-to-presence-biomass. Abiotic explanatory variables were bathymetry (here called depth) and bottom temperature. After some preliminary analysis, covariates were added to the model as curvilinear effects to account for their non-linear relationships. Finally, we included swept-area by the survey gear (log-transformed) as an offset in the model to account for sampling effort (Anderson et al., 2022).

The general form of the SDM is a delta (hurdle) generalized linear mixed effects model (GLMM). We test two different families, delta_gamma and delta_lognormal. We considered $Z(s,t)$ to be the occurrence and $W(s,t)$ the conditional-to-presence biomass at location s and time t. The model formulation can be written as follows:

$$Z(s,t) \sim \text{Bernoulli}(\pi(s,t)) \tag{4.1a}$$

$$W(s,t) \sim \text{Gamma}(\mu(s,t),\phi) \quad \text{or} \quad W(s,t) \sim \text{lognormal}(\mu(s,t),\sigma^2) \tag{4.1b}$$

$$\text{logit}(\pi(s,t)) = \beta_Z + \sum_{i=1}^{I} f_i(X_i(s,t)) + V_Z(s,t) \tag{4.1c}$$

$$\log(\mu(s,t)) = \beta_W + \sum_{i=1}^{I} f_i(X_i(s,t)) + V_W(s,t) \tag{4.1d}$$

where $\pi(s,t)$ represents the probability of occurrence at location s and time t; $\mu(s,t)$ is the mean; and ϕ and σ are the variance of the conditional-to-presence biomass for the gamma and lognormal distribution respectively. The linear predictors, which represent the intercept of each variable associated with the parameter $\pi(s,t)$ and $\mu(s,t)$, are represented by β_Z and β_W, respectively. f_i represents any function applied to the covariate X_i, which in the present study was a second-degree polynomial function. $V_Z(s,t)$ and $V_W(s,t)$ refer to the spatial structure of the occurrence and conditional-to-biomass model, respectively.

Our model aimed to identify the optimal average spatial relationships that describe the distribution patterns, treating individual years as replicates. We created a mesh with a cutoff of 15 km, which resulted in 761 nodes. We refrained from incorporating spatiotemporal variations (i.e., autoregressive model of order one (AR1) and random walk (RW)) as well as fixed temporal covariates (i.e. year as a fixed effect) into the model because of challenges in projecting these effects over an extended period into the future (Liu et al., 2023).

Model selection

We compared four different model configurations (Table B.1, Table B.2 and Table B.3). To select the best fitting, we calculated model Akaike information criteria (AIC), an estimator of model prediction error commonly used in model selection (Burnham and Anderson, 2002). We also quantified the percent deviance explained when comparing model configurations to an intercept-only null model, using relative log-likelihood between models (Liu et al., 2023). Finally, we visually inspected the quantile residual plots (Figure B.1, Figure B.3 and Figure B.5).

Additionally, we assessed model performance during the historical period by comparing mean biomass values observed to those predicted and calculated the area under the curve (AUC) and the Pearson correlation (R). We assessed future predictability by implementing the leave-future-out strategy in which we trained our model with data from 1996 to 2016 and tested it against the last 3 years of the time series (2017-2019).

Biomass projections to 2100

We analyzed time series projections of biomass as a percentage change between the historical period (1996-2019) and each future year. Then, we compared projections among climate models and low (SSP1-2.6) and high (SSP4-6.0 for ACM, and SSP3-7.0 for IPSL and GFDL) emissions scenarios. We ran simulations to the end of the century because temperature projections from RCPs scenarios increasingly diverge after 2050 (Pershing et al., 2021; Sobie et al., 2021). Changes in spatial patterns of species biomass were assessed by calculating the biomass difference:

$$\Delta\text{Biomass} = B_{\text{Fut},K}(i,j) - B_{\text{Hist}}(i,j) \tag{4.2}$$

Where $B_{\text{Fut},K}$ represents the biomass at the coordinates (i, j) for the end of century period (2077-2100) under the high emissions scenario for climate model K; $B_{\text{Hist}}(i, j)$ is the biomass at the same coordinates for the historical period (1996-2019).

We called this difference in biomass: ΔBiomass. To enhance visual clarity, distributions in the figure were constrained between the 0.1 and 99.9th percentiles range due to the presence of a few extreme values in ΔBiomass.

4.3.5 Biomass uncertainty evaluation

We assessed point-wise prediction uncertainty of species distribution models during the baseline period (1996-2019) by conducting 100 simulations based on the joint precision matrix of our model (Thompson et al., 2023). The precision matrix, often referred to as the inverse covariance matrix, characterizes the relationships between variables assuming a multivariate normal distribution (Anderson et al., 2022). The variability in these simulations, and hence the level of prediction uncertainty, is directly influenced by the precision matrix. We repeated this approach to assess biomass projections from each climate model under the high emissions scenarios at the end of the century (period 2077-2100). Finally, we partitioned uncertainty in the biomass estimates among climate models and RCPs by fitting a linear model, with annual biomass estimates as a response variable and climate models (GFDL, IPSL and ACM) and scenarios (low and high emissions) as covariates, allocating residual error to parameter uncertainty (e_i):

$$\text{Biomass}_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + e_i \tag{4.3}$$

Biomass_i represents the annual biomass estimate for the i-th observation; β_0 is the intercept term; β_1 and β_2 are coefficients corresponding to the predictor variables

X_1 (climate model) and X_2 (emissions scenario), respectively. Finally, e_i represents the residual error term, capturing unexplained variation in the biomass estimates.

Dominance analysis is a statistical technique used to assess the relative importance of predictor variables in explaining variance in a dependent variable, and was applied to evaluate the relative importance of each component (Morley et al., 2020; Brodie et al., 2022). We smoothed the results by computing 10-year averages to mitigate noise and highlight the underlying trends. We acknowledge that having three climate models and only two scenarios – only one in the case of the ACM model – may induce bias in assessing predictors' importance.

4.4 Results

For all species, models that best explained spatial patterns of biomass distribution included depth and temperature as fixed effects and the spatial random field (Table B.1, Table B.2 and Table B.3). The spatial random field represents biomass deviations in space that are not accounted for by covariates. Its inclusion substantially improved model performance, especially for yellowtail flounder and Atlantic cod. Models estimates are available in Table B.4.

We used the model fit to predict biomass estimates of the focal species on the Grand Banks of Newfoundland in 1996 and 2019 (Figure 4.3, Figure 4.4 and Figure 4.5). Then, we forecasted to 2100 under the low and high emissions. The predictive capacity of the models varies among species, with highest predictability in yellowtail flounder (Pearson correlation = 0.74; AUC = 0.97), followed by snow crab (Pearson correlation = 0.55, AUC = 0.89) and Atlantic cod (Pearson correlation = 0.55, AUC = 0.82) (Figure B.7). We also assessed the out-of-sample predictability, training our model with data from 1996 to 2016 and testing it for the period 2017:2019. The predictability was (Pearson correlation = 0.7; AUC = 0.97) for yellowtail flounder, (Pearson correlation = 0.41, AUC = 0.89) for snow crab and (Pearson correlation = 0.47, *AUC* = 0.79) for Atlantic cod (Figure B.8).

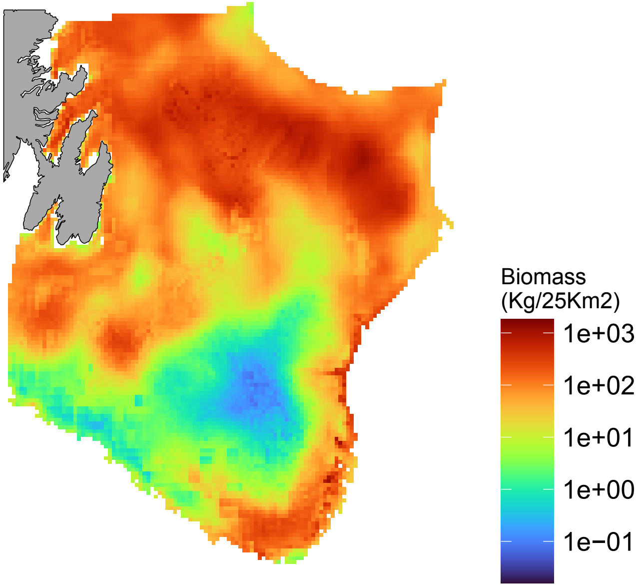


FIGURE 4.3: Map of snow crab biomass distribution over the Grand Banks obtained from the combined prediction of the delta_lognormal model. Biomass is in log scale.

Our findings underscored a long-term decline in the projected biomass of snow crab for all climate models and scenarios except for GFDL under the low emissions scenario (Figure 4.6). If we focus on the values at the end of the century (2077-2100), greater losses were observed for the high emissions scenario, especially for IPSL model -47% [± 1.67% SD], followed by ACM -10.4% [± 1.59% SD] and GFDL -14.68% [± 1.59% SD]. Under the low emissions scenario, biomass trends fluctuate around the historical average. Values at the end of the century (2077-2100) for IPSL projected biomass losses of -3.8% [± 1.6% SD], whereas GFDL projected biomass gains of 3.7% [± 1.57% SD].

We also observed a long-term decline in yellowtail flounder biomass for the IPSL model under the low and high emissions scenarios -8.4% [± 0.38% SD] and -29% [± 0.36% SD], respectively (Figure 4.7). Biomass projections at the end of the

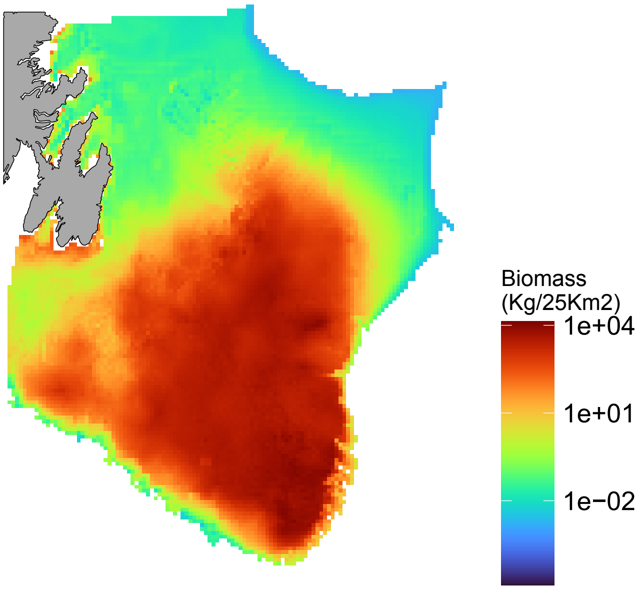


FIGURE 4.4: Map of yellowtail biomass distribution over the Grand Banks obtained from the combined prediction of the delta_gamma model. Biomass is in log scale.

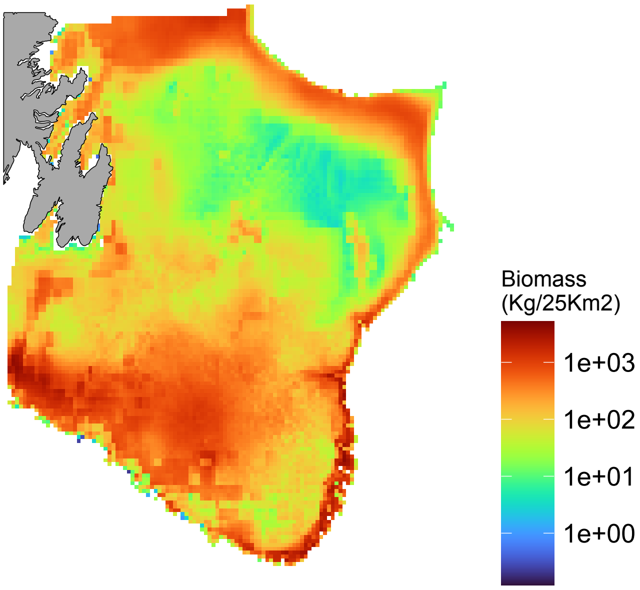


FIGURE 4.5: Map of Atlantic cod biomass distribution over the Grand Banks obtained from the combined prediction of the delta_lognormal model. Biomass is in log scale.

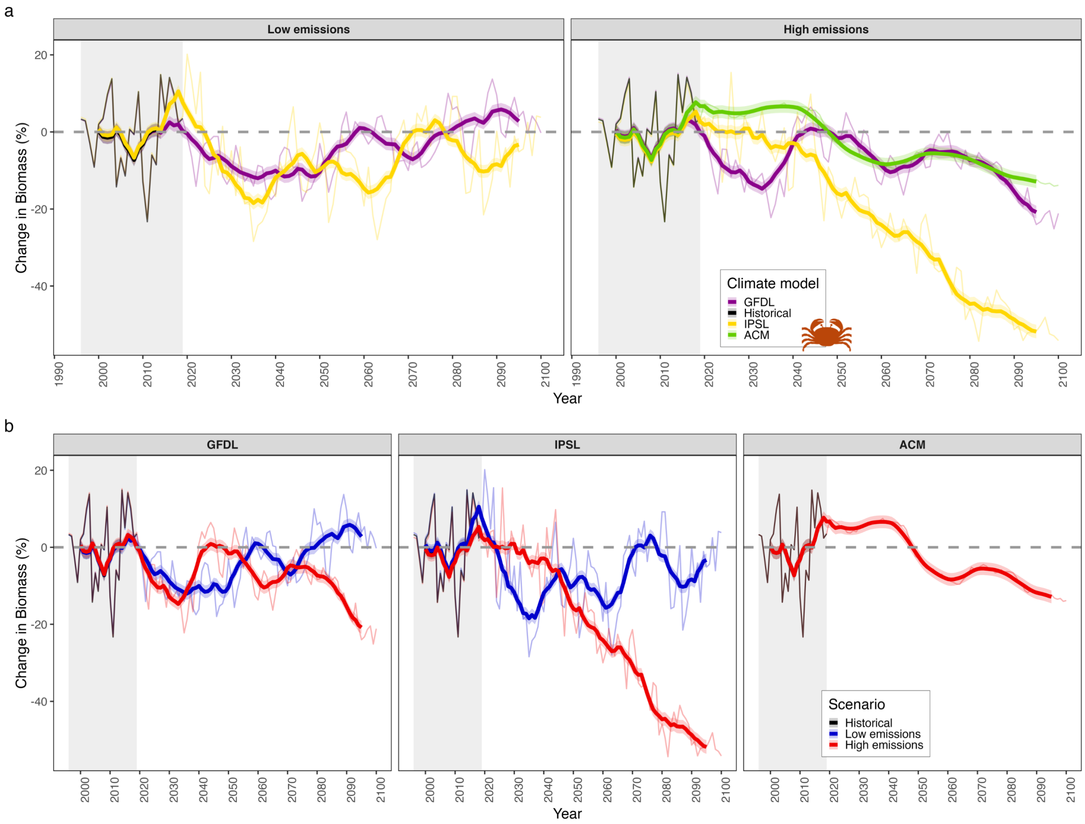


FIGURE 4.6: Projections of snow crab biomass by climate model and emissions scenario. a, Projections under low emissions (SSP1-2.6, left) and high emissions scenarios (SSP4-6.0 for ACM and SSP3-7.0 for IPSL-CM6A-LR and GFDL-ESM4 scenario, right). b, Projections by climate models for low and high emissions scenarios. Biomass changes are relative to the predicted values of the reference period (1996-2019), indicated by the shaded grey area. Solid coloured lines depict average projected biomass, while shaded areas indicate standard deviations based on the precision matrix runs. Zero change is represented by a horizontal dashed line.

century (2077-2100) for the GFDL model under both emissions scenarios indicated biomass values close to the historical average, -1.4% [± 0.38% SD] for the low emissions and 0.39% [± 0.38% SD] for the high emissions scenario. Finally, the ACM model suggests a small increase in biomass at the end of the century (period 2077-2100) of 4.45% [± 0.34% SD].

SDMs projected a long-term decline in Atlantic cod biomass for the GFDL-low emissions scenario of -11.9% [± 0.53% SD] at the end of the century (2077-2100), and an increase in biomass for the rest of models and scenarios (Figure 4.8).

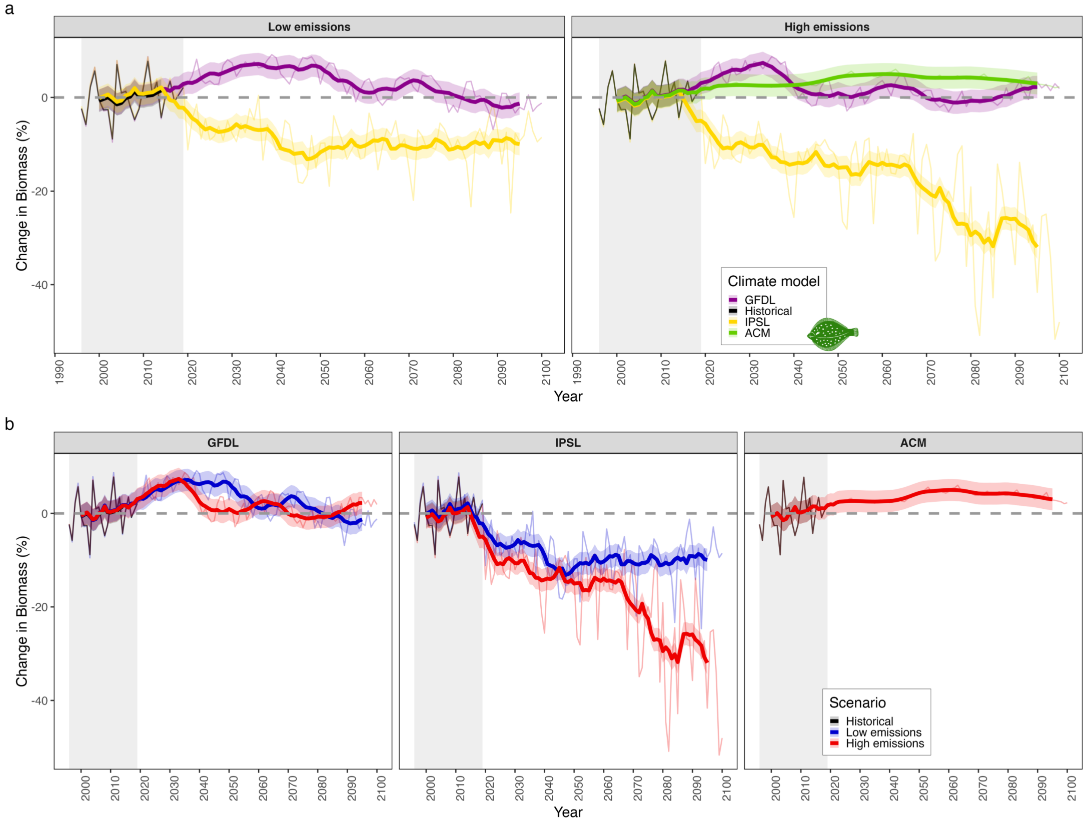


FIGURE 4.7: Projections of yellowtail flounder biomass by climate model and emissions scenario. a, Projections under low emissions (SSP1-2.6, left) and high emissions scenarios (SSP4-6.0 for ACM and SSP3-7.0 for IPSL-CM6A-LR and GFDL-ESM4 scenario, right). b, Projections by climate models for low and high emissions scenarios. Biomass changes are relative to the predicted values of the reference period (1996-2019), indicated by the shaded grey area. Solid coloured lines depict average projected biomass, while shaded areas indicate standard deviations based on the precision matrix runs. Zero change is represented by a horizontal dashed line.

Biomass projection for IPSL-low emission scenario indicates a gain of almost 18% [± 0.53% SD] at the end of the century. Under the high emissions scenario, GFDL oscillates around the historical average but showed an increase of 6.22% [± 0.53% SD] at the end of the century (period 2077-2100). IPSL and ACM both showed a similar trend of biomass gain at the end of the century, reaching values of 28.6% [± 0.54% SD] and 23.8% [± 0.52% SD], respectively.

The analysis revealed a consensus among earth system models (IPSL and GFDL) regarding the locations with the most pronounced losses in snow crab biomass,

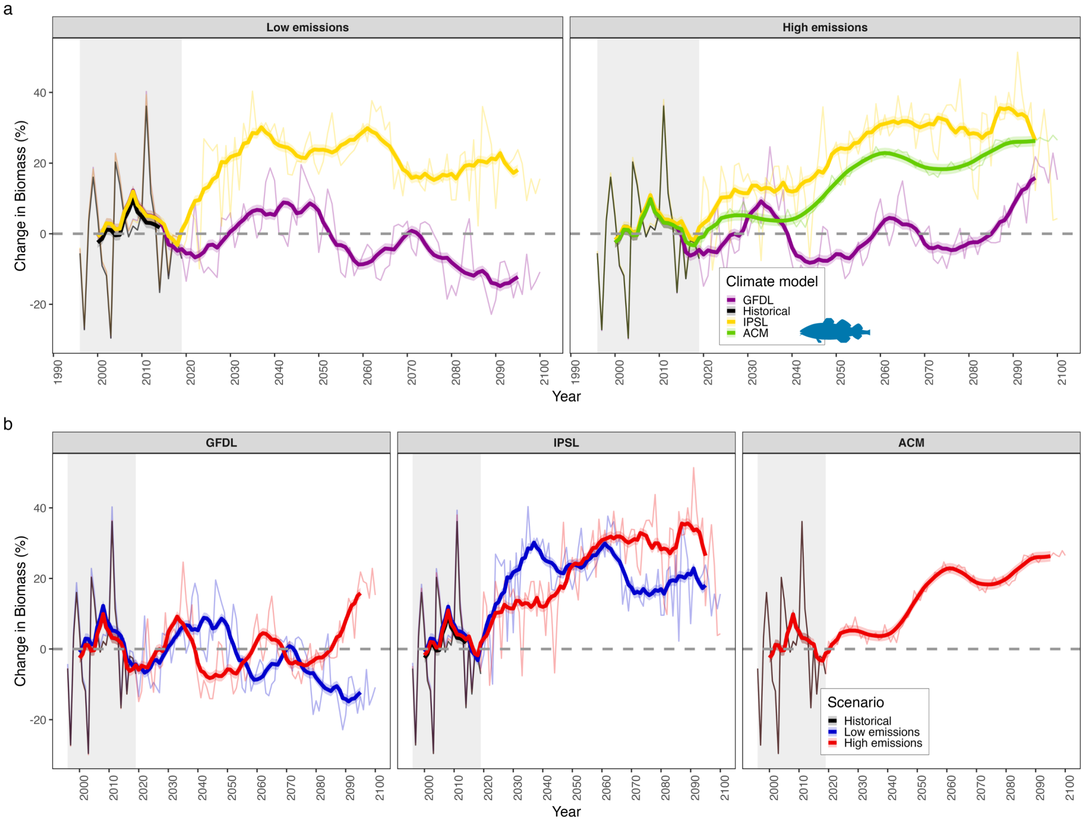


FIGURE 4.8: Projections of Atlantic cod biomass by climate model and emissions scenarios. a, Projections under low emissions (SSP1-2.6, left) and high emissions scenarios (SSP4-6.0 for ACM and SSP3-7.0 for IPSL-CM6A-LR and GFDL-ESM4 scenario, right). b, Projections by climate models for low and high emissions scenarios. Biomass changes are relative to the predicted values of the reference period (1996-2019), indicated by the shaded grey area. Solid coloured lines depict average projected biomass, while shaded areas indicate standard deviations based on the precision matrix runs. Zero change is represented by a horizontal dashed line.

specifically at the north and south of the Grand Banks. However, ACM depicted a less pronounced decline (Figure 4.9 a).

The majority of yellowtail flounder biomass changes were observed on the southeast shoal of the Grand Banks. GFDL and ACM mostly agreed on projected spatial biomass changes. In contrast, IPSL suggested a stronger decline in the southern part of the southeast shoal (Figure 4.9 b). Spatial biomass patterns for Atlantic cod showed the biggest disagreement among climate models (Figure 4.9 c). GFDL

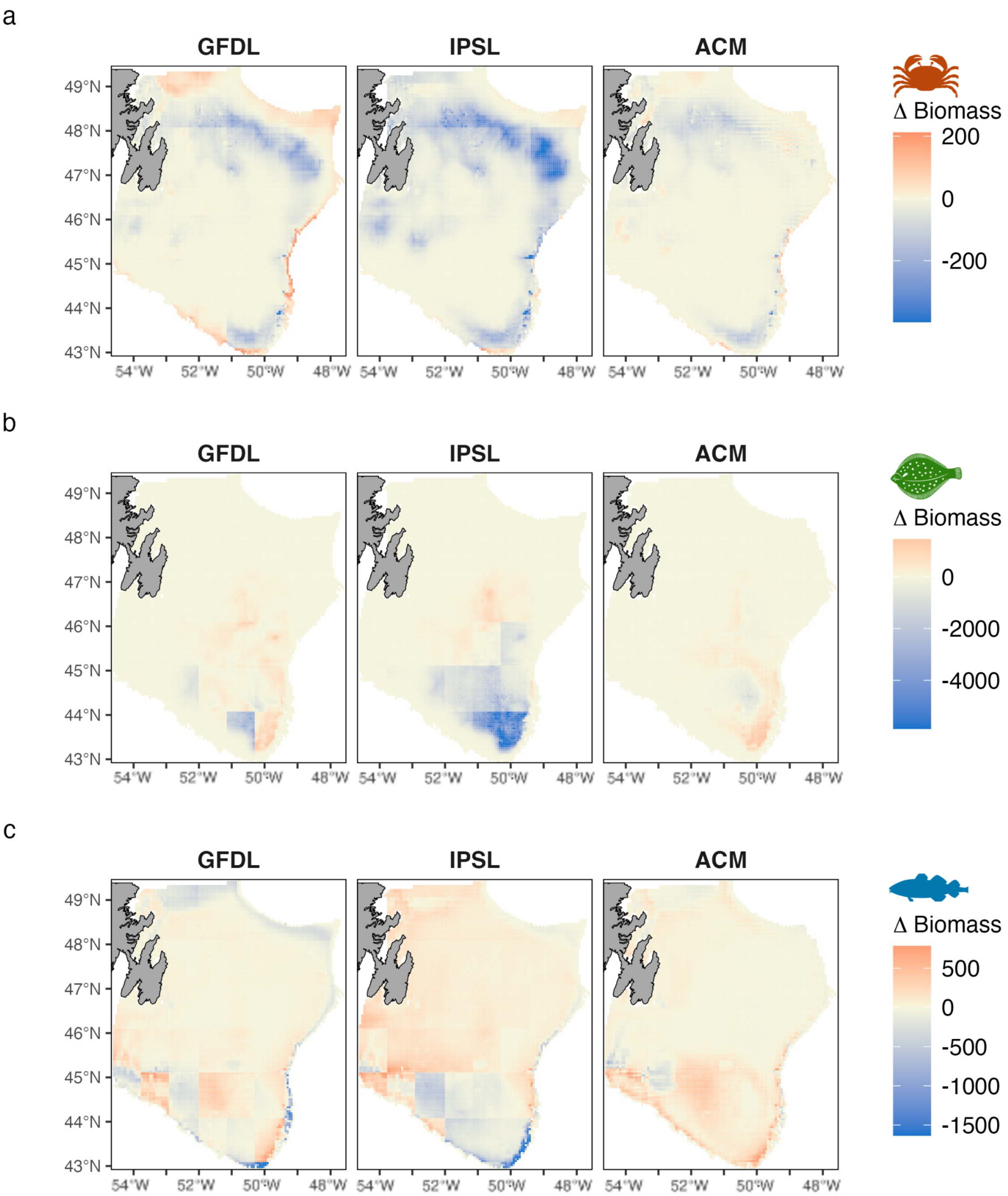


FIGURE 4.9: Spatial patterns of species biomass changes (in $kg/25km^2$) for a, snow crab; b, yellowtail flounder and c, Atlantic cod on the Grand Banks of Newfoundland by climate model (GFDL-ESM4, IPSL-CM6A-LR and ACM) under the high emissions scenarios (SSP4-6.0 for ACM and SSP3-7.0 for IPSL and GFDL) during the 2077-2100 period relative to the historical period (1996-2019). The Avalon Peninsula is the southern piece of land (in grey).

predicted losses in the north and southern edge, with some gains on the southern shoal. IPSL indicated biomass losses on the southeastern shoal and gains on the rest of the Banks. Finally, ACM projected gains mostly in the south of the Banks.

4.4.1 Uncertainty

We observed marked spatial variability in SDM biomass projections during the historical period (1996-2019), with standard deviations of biomass ranging from 0 to 4 $kg/25km^2$ for snow crab, yellowtail flounder and Atlantic cod (Figure 4.10-SDM). For snow crab, the periphery and the southeast shoal of the Grand Banks showed high variability (Figure 4.10 a). For yellowtail flounder, variability was higher in the northern part of the Banks and on the periphery (Figure 4.10 b). In the case of Atlantic cod, variability was pronounced around the Avalon Peninsula and on the periphery of the Banks (Figure 4.10 c).

Variability in biomass projections amplified between the historical period to the end of the century (2077-2100), where the standard deviation of the biomass increased, especially for yellowtail flounder ($30\,kg/25\,km^2$) (Figure 4.10 and Figure 4.11).

Uncertainty partitioning

We partitioned uncertainty to assess the relative contribution of each component: climate model, scenario and SDM parameters (Figure 4.12). For all three species—snow crab, yellowtail flounder, and Atlantic cod—climate model uncertainty was the dominant factor contributing to biomass uncertainty across all years, consistently showing the highest influence (above 50%). However, the contribution of SDM parameters and scenarios varied over time. For snow crab and yellowtail flounder, the influence of SDM parameters and scenarios increased slightly after 2050, indicating that assumptions and parameterizations in SDMs, along with specific future scenarios, become more critical for determining biomass uncertainty as projections extend further into the future (Figure 4.12 a & b). A similar trend was

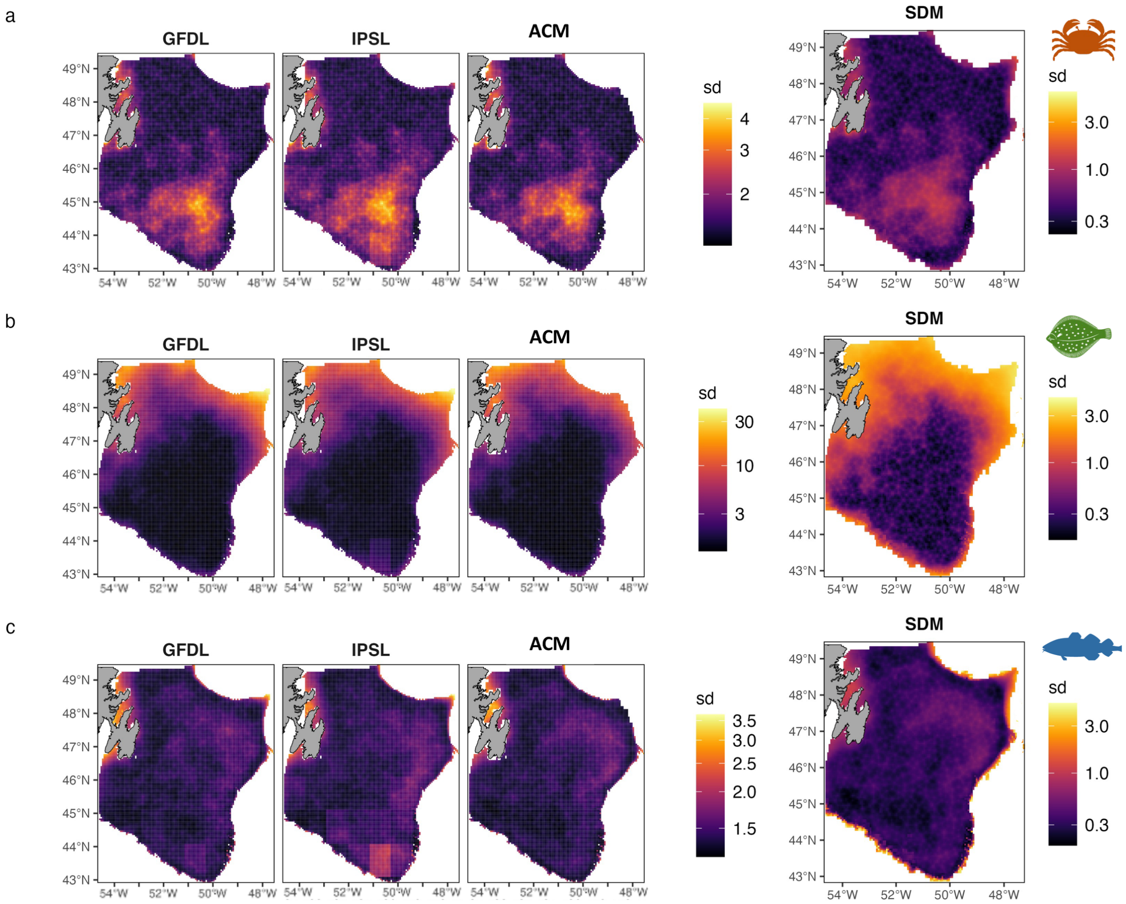


FIGURE 4.10: Spatial uncertainty of SDM biomass estimates (historical period; 1996-2019) and climate models projections (GFDL, IPSL and ACM) at the end of the century (2077-2100) measured as the standard deviation from 100 simulation draws ($kg/25\,km^2$) for (a) snow crab, (b) yellowtail flounder and (c) Atlantic cod projected biomass.

observed for Atlantic cod, with increasing contributions from SDM parameters and scenarios over time, though the changes were less pronounced compared to snow crab and yellowtail flounder (Figure 4.12 c).

4.5 Discussion

Depth and temperature are known to be key factors that determine the distribution and survival of many species, including snow crab (Windle et al., 2012), yellowtail flounder (Simpson and Walsh, 2004; Colbourne and Walsh, 2006) and Atlantic cod (Drinkwater, 2005; Linner and Chen, 2022). As expected, both depth and

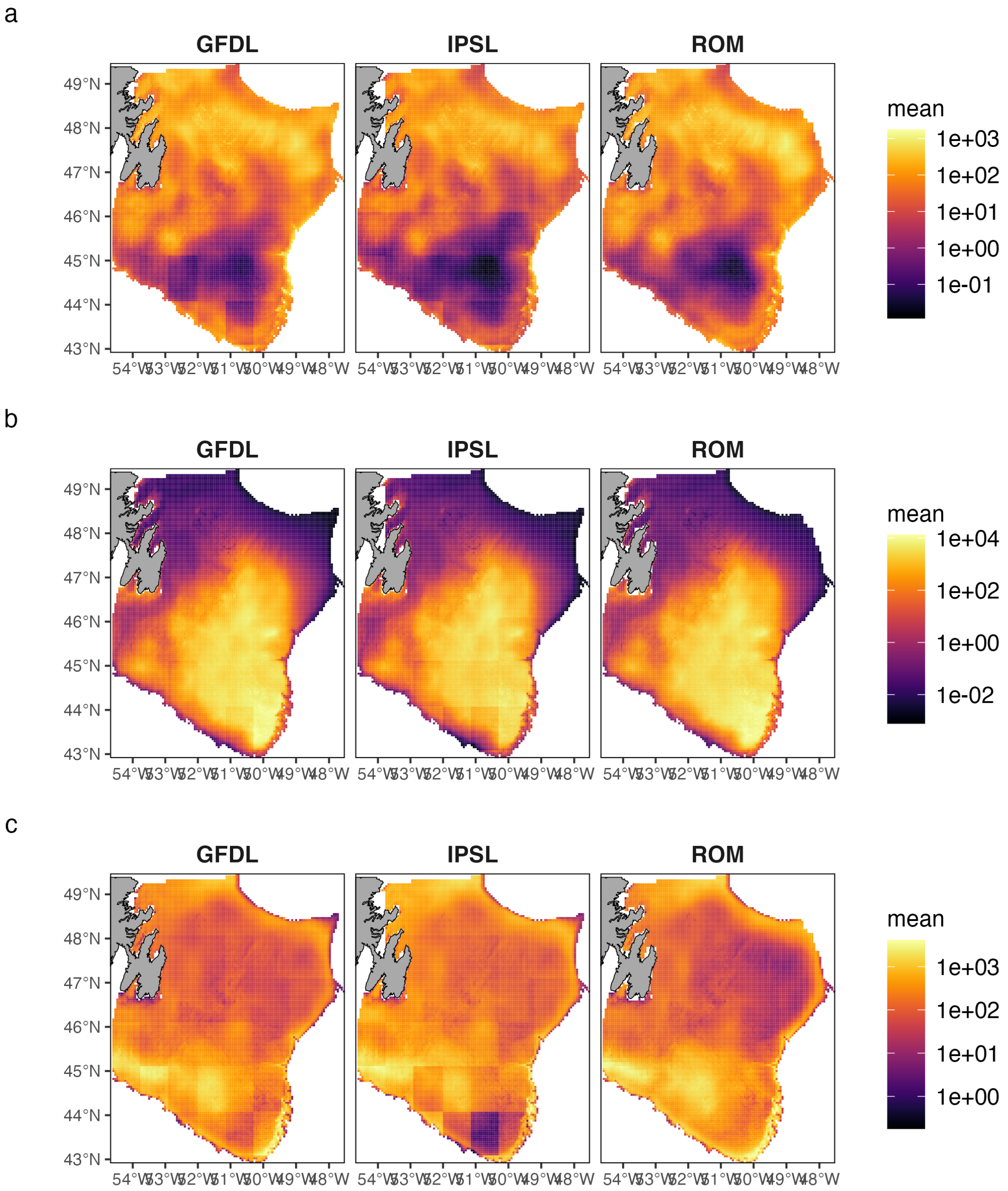


FIGURE 4.11: SDM biomass estimates (historical period; 1996-2019) and climate models projections (GFDL, IPSL and ACM) at the end of the century (2077-2100) measured as the mean from 100 simulation draws ($kg/25\,km^2$) for (a) snow crab, (b) yellowtail flounder and (c) Atlantic cod projected biomass. Log scale for better interpretation of spatial differences.

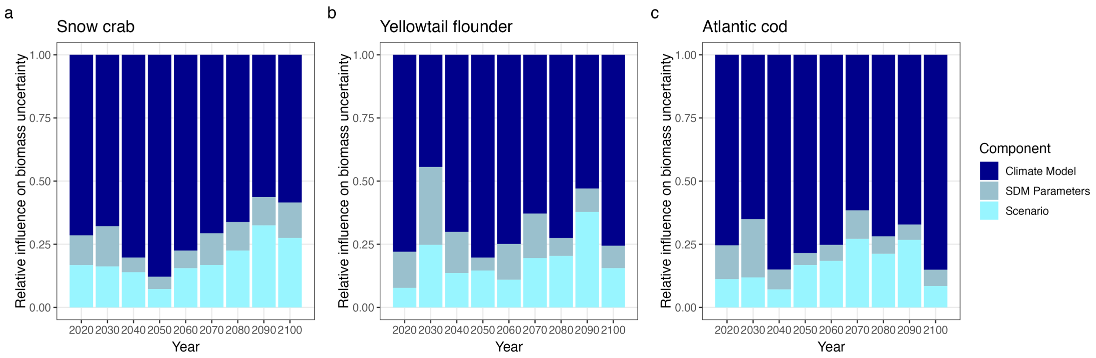


FIGURE 4.12: Relative uncertainty in biomass projections for a, snow crab; b, yellowtail flounder and c, Atlantic cod, partitioned across climate models (i.e., IPSL, GFDL and ACM), emissions scenarios (low-SSP1-2.6 and high-SSP4-6.0 & SSP3-7.0) and SDM parametrization.

temperature were relevant variables to explain spatial distribution. The best fitting models also included the spatial random field that explains variability not captured by the covariates.

Projected changes in species biomass to 2100 under low and high emissions scenarios showed an overall decline in snow crab and yellowtail flounder biomass compared to the historical period (1996-2019), whereas Atlantic cod is expected to gain biomass across the 21st century under the high emissions scenario. However, in the GFDL simulation, biomass declines through the mid-century before increasing. While there are differences in the magnitude of biomass projections across climate models, a consensus in the direction of changes was evident in all models except for GFDL-low emissions scenarios. This divergence can be attributed to the GFDL-low emissions scenario forecasting a decline in bottom temperature by the end of the century, in contrast to temperature increases projected by the other models and scenarios. The IPSL model projected the biggest warming on the Grand Banks.

Changes in species' geographic distributions can be analyzed by focusing on their range boundaries. At leading edges, species expand into new territories as environmental conditions improve, while at trailing edges, population extirpations lead to range contractions (Pinsky et al., 2020). Marine ectotherm species tend to fully use their potential latitudinal ranges in relation to their thermal tolerance limits (Sunday et al., 2012), and distribution shifts are thought to be higher at the leading edge than at the trailing edge (Poloczanska et al., 2013), although this is case specific (Robinson et al., 2015). Snow crab commonly occurs in subpolar and Arctic regions, favouring cold water environments below 5 °C (Foyle et al., 1989). On the Grand Banks of Newfoundland, higher biomass has been observed at temperatures close to 0 °C (in spring) (Ruiz-Diaz et al., 2024). As stenothermics, snow crabs respond strongly to changes in bottom temperature, particularly during their juvenile period (Dionne et al., 2003). Snow crabs on the Grand Banks of Newfoundland are at the trailing edge of their distribution, corresponding to their upper thermal threshold, making them particularly susceptible to ocean warming. A recent study detected a general shift in snow crab distribution from the Newfoundland region into the Arctic (Mullowney et al., 2023). Here, all models predicted that snow crab biomass on the Grand Banks will decline throughout the 21st century under the high emission scenarios while remaining close to the historical period under the low emissions scenario.

On the Grand Banks, yellowtail flounder thrive in sea bottom temperatures ranging from 1-6 °C in spring (Ruiz-Diaz et al., 2024). Despite their ability to tolerate a broad range of temperatures, there is evidence that stock productivity declines significantly at both extremes of the temperature range (Brodie et al., 2010). The case of yellowtail flounder is interesting as spatial uncertainty widely amplifies over time, which was not the case for snow crab and Atlantic cod. Yellowtail flounder distribution is centred around the southeast shoal of the Grand Banks due to the presence of a mild current system, facilitating the retention of eggs and larvae (Brodie et al., 2010). This region is considered as a nursery ground for yellowtail flounder (Simpson and Walsh, 2004), and is the area in which higher warming is expected on the Grand Banks (Figure 4.2 b). We found that yellowtail flounder biomass projections are expected to remain close to the historical average for GFDL and slightly higher for ACM, but to be negatively impacted for the IPSL model under high and low emissions scenarios.

Atlantic cod tolerate higher temperatures than the other two species, with a peak in biomass at 5 ºC on the Grand Banks in spring (Ruiz-Diaz et al., 2024). Our analysis indicates that, by the end of the century, most climate models (excluding the GFDL-low emissions scenario) predict an increase in Atlantic cod biomass on the Grand Banks. In particular, the ACM showed the greatest biomass gains. These results contrast with findings in the Gulf of Maine, where biomass decrease was noted with ocean warming (Fogarty et al., 2008; Pershing et al., 2015), but are in agreement with forecasted thermal habitat for cod on the Newfoundland and Labrador shelf (Cote et al., 2021). The difference can be attributed to the distinct thermal environments of these regions. The Gulf of Maine has an average bottom temperature of 7.1 °C (Fogarty et al., 2008), while the Grand Banks experiences significantly cooler temperatures, averaging 1.34 °C during our historical period (1996-2019). This movement suggests that Atlantic cod could potentially benefit from moderate warming in the Grand Banks, while those in the Gulf of Maine may be experiencing temperatures beyond their physiological limits, leading to declines in biomass (Pinsky et al., 2020). Gains in Atlantic cod biomass are expected to occur mostly in the southern Grand Banks (3NO stock).

Variability in the predictive capacities of the SDMs directly impacts the reliability of biomass projections. For instance, our leave-future-out cross-validation showed that yellowtail flounder model exhibited the highest predictability (Pearson correlation = 0.7; $AUC = 0.97$), indicating more confidence in its biomass projections. Conversely, Atlantic cod model showed lower predictability (Pearson correlation = 0.47; $AUC = 0.79$), suggesting greater uncertainty in biomass projections for this species. Snow crab falls in between with moderate model predictability (Pearson correlation = 0.41; $AUC = 0.89$).

The low spatial uncertainty of the SDMs indicated consistency in the biomass predictions during the historical period (1996-2019). However, projecting to 2100 under the high emissions scenario (SSP3-7.0 for IPSL and GFDL and SSP4-6.0 for ACM) showed increased uncertainty, especially for yellowtail flounder. This finding aligns with other species distribution studies (Thuiller et al., 2019; Thompson et al., 2023), reflecting challenges in extrapolating predictions to novel conditions and/or the model's capacity to capture the underlying mechanisms governing species distributions (Brodie et al., 2022). In all species, there is a notable overlap between regions with biomass absence and areas of high uncertainty (see Figure B.2, Figure B.4 and Figure B.6). Furthermore, observation uncertainty, linked to bias in the sampling coverage, can lead to an incomplete depiction of a species' entire environmental niche (Reum et al., 2020). While the Grand Banks region has relatively comprehensive sampling coverage, we anticipate observation uncertainty to be more pronounced near the Avalon Peninsula since, in this area, independent inshore sampling is performed, and at the periphery of the Grand Banks, corresponding to deeper waters that are less sampled (Rideout and Ings, 2019). Depth sampling limitation may contribute to the higher uncertainty observed in the biomass predictions for the three species at the periphery of the Grand Banks. Another possible explanation relates to the spatial resolution of the climate models, which increases bias near the slope of the banks.

Variation in spatial warming among climate models is crucial to understanding uncertainty surrounding species distribution projections. In the present analysis, we found greater variation among climate models than among scenarios. We also found differences in the variability of the temperature projections, with ACM temperature increasing steadily, while the ESMs, GFDL and IPSL showed high variability. This is likely due to the low spatial resolution of ESM, leading to incorrect circulation patterns due to inaccuracies in the bathymetry (Figure B.11 and

Figure B.12). In a dynamic coastal region like the Grand Banks, changes in circulation patterns, particularly the strength of the shelf break current, play a crucial role in determining sea bottom temperature on the Grand Banks (Garcia-Suarez et al., 2023; Rutherford et al., 2024). These small-scale circulation features are poorly captured by ESMs, and can even vary among ROMs (Rutherford et al., 2024). In the same way, the cold intermediate layer is a key feature of the Banks that also affects the temperature pattern distribution, with colder waters prevailing in the northern Grand Banks due to the advection of winter-origin waters from the Labrador shelf, and warmer temperatures observed in the southern Grand Banks, including the shallow southeast shoal (Cyr and Galbraith, 2021). The CIL falls within a specific depth range (50-200 m); thus, models with high bathymetry bias would likely misrepresent the CIL.

4.5.1 Model caveats and assumptions

The SDMs used here do not capture mechanistic drivers of species distribution based on functional traits and physiological constraints – thus, reducing confidence in the projections. For instance, in the Bering Sea, the recent collapse of the snow crab population has been linked to elevated water temperatures (Szuwalski et al., 2023). Despite these temperatures not exceeding the thermal limits of the species, they heightened the crabs' caloric requirements. This, together with a restricted distributional range, resulted in a mass starvation event (Szuwalski et al., 2023). Therefore, it is important to acknowledge that ocean warming can trigger unforeseen ecological responses. Moreover, when including the spatial component in our model, we are assuming that the biotic and abiotic conditions (all but temperature and depth) are going to remain the same in the future. This assumption may not be correct. For instance, seasonality affects marine species in terms of reproduction, feeding, and migration. Shifts in seasonal timing, such as earlier phytoplankton blooms due to warming, can disrupt these processes. For demersal species, this may lead to mismatches in prey availability, affecting feeding success and growth rates. Ultimately, these changes can impact species distribution and biomass. Shifts in species distributions can affect predator-prey dynamics, community structure, and ecosystem structure and functioning (Albouy et al., 2014; Selden et al., 2018). However, neglecting to consider unexplained spatial correlation in species distribution modelling can result in several problems, including an increased likelihood of false positive findings, misinterpretation of the relationships between environmental factors and species distribution, and decreased model accuracy (Laxton et al., 2023). The inclusion of the spatial random field could impact the estimates of fixed effects due to spatial confounding, which refers to a situation where predictors in the model are correlated with spatial or spatio-temporal effects, potentially leading to bias (Clayton et al., 1993). When confounding exits, spatial random fields may absorb variability associated with climate variables, potentially leading to an underestimation of the true impacts of climate change on species biomass (Thompson et al., 2023). A key caveat of this analysis is the limited number of environmental predictors used in the species distribution models. While temperature and depth were included, other important factors, such as primary productivity, which may change dramatically under climate change, were not considered. This narrows the focus to primarily thermal changes, while other oceanographic variables, such as nutrient availability and deoxygenation, may also have significant impacts on species distributions in the future. Incorporating a broader range of environmental variables could provide a more comprehensive view of potential changes.

As fish populations shift, it's important to consider how fisheries management efforts can be adapted to more effectively manage and conserve marine resources (Ruiz-Díaz, 2023; Pinsky et al., 2021). The projections generated by our SDMs offer a broad overview of potential changes in thermal habitat suitability, providing initial insights into the types of changes that could occur. It is important to note that while these projections indicate projected biomass changes, they should not be interpreted as definitive predictions. Nonetheless, these results hold significant relevance for fisheries management. Firstly, they confirm that changes in habitat suitability are indeed anticipated with warming waters, which could have varying impacts on different fisheries. While some fisheries may face challenges due to these changes, severely depleted stocks like 3NO cod may potentially benefit. Secondly, our findings underscore the potential of SDMs to inform medium and long-term planning for fisheries management. Projections of species biomass and spatial distributions offer valuable insights into the spatial dimension of these changes, aiding in strategic decision-making.

CHAPTER 5

Top-down vs bottom-up ecosystem control

5.1 Abstract

The Grand Banks of Newfoundland is a highly dynamic and productive ecosystem that has sustained important fisheries for centuries. However, a regime shift occurred in the early 1990s, altering community structure and leading to the imposition of moratoria on many fisheries. There is contrasting evidence about whether the Grand Banks of Newfoundland ecosystem is bottom-up (resource driven) or top-down (predator driven) controlled. Using a multispecies size spectrum model, this study assesses the direct and indirect ecological consequences of changing biomass of the target species capelin, sand lance (forage species) and Atlantic cod (top predator), to evaluate their importance for food web stability. Changing biomass of target species leads to shifts in biomass and mean body weight across trophic levels both above and below the target species. All species show a linear relationship between mortality and biomass except for the Atlantic cod, which showed a non-linear response with increasing mortality. On the one hand, an increase in forage fish biomass led to a gain in piscivores, large benthivores and losses in medium benthivores, whereas a decrease in forage fish biomass resulted in the opposite trend. These changes are also mirrored in the species mean body weight. On the other hand, increasing biomass of Atlantic cod led to larger changes in the community, with increases in the main prey species (capelin, sand lance and northern shrimp), snow crab and thorny skate, while the other species declined. Reducing Atlantic cod biomass resulted in increases in redfish, snow crab and medium

benthivores, and a decline in main prey items, large benthivores and piscivores. Again, these changes were mirrored in the species' body weight. When Atlantic cod biomass increased by 17%, a drastic shift in the system was observed, with the main prey species going functionally extinct. We discuss the ecological reasons behind these changes and conclude that Atlantic cod may play a more important role in maintaining the Grand Banks's food web stability than forage fish.

5.2 Introduction

The question of whether food webs are bottom-up (resource) or top-down (predator) driven is one of the most fundamental in ecology (Frank et al., 2006, 2007; Lynam et al., 2017). This topic has been actively debated on the Grand Banks, with studies suggesting both top-down (Bundy, 2001) and bottom-up control (Buren et al., 2014; Cyr et al., 2024).

Forage fishes are central to the productivity of marine ecosystems, playing a crucial role in the marine food web by transferring energy from lower trophic levels, such as plankton, to higher trophic levels that can include commercially important fish species, marine mammals, and seabirds (Pikitch et al., 2012; Eddy et al., 2021). Forage fish are typically short-lived and experience large cyclical fluctuations in population size (also known as boom-and-bust cycles) driven by environmental conditions and density-dependent processes (Lewis et al., 2019). On the one hand, fluctuations in forage fish populations can greatly impact dependent predators, affecting food web structure (Gjøsæter et al., 2009; Cury et al., 2011). On the other hand, top predators play an important role in marine ecosystems by regulating the population dynamics of prey species and maintaining the balance of the food web (Frank et al., 2005). This predatory pressure has been found to foster biodiversity and contribute to the stability of the marine community (Ellingsen et al., 2015). Shifts in forage fish and top predator abundance can trigger large changes in community structure known as trophic cascades, which can propagate up and down in trophic levels (Andersen and Pedersen, 2010). Trophic cascades produce indirect effects that extend two or more links away from the primary interaction (Pace et al., 1999; Frank et al., 2005).

The Grand Banks of Newfoundland, situated southeast of the Island of Newfoundland, are a series of submerged seamounts with an average depth of 200 meters (DFO, 2007b). This dynamic system is shaped by the colder, nutrient-rich Labrador Current from the north and the warmer, nutrient-poor North Atlantic Current, the northern branch of the Gulf Stream from the south (Cyr and Galbraith, 2021). The Grand Banks experience pronounced seasonal variation in primary production, marked by a robust spring bloom and a moderate fall bloom. These variations are driven by changes in light availability and nutrient mixing above the thermocline (Cyr et al., 2024). Additionally, the region undergoes milder and colder winters, which typically occur on a decadal scale linked to the North Atlantic Oscillation, the principal driver of atmospheric variability in the North Atlantic (Cyr and Galbraith, 2021).

On the Grand Banks, the primary forage species consist of capelin (*Mallotus villosus*) and northern sand lance (*Ammodytes dubius*) (Winters, 1983). Capelin typically occupies offshore areas of the northern Grand Banks and undertakes inshore migrations during the summer months to spawn (Crook et al., 2017). The 2J3KL stock is commercially fished in an inshore roe fishery in coastal Newfoundland, and its status is evaluated annually by Fisheries and Oceans Canada (DFO) (DFO, 2022a). The southern stock, 3NO, is not commercially exploited and is assessed by the Northwest Atlantic Fisheries Organization, NAFO (Tretyakov, 2015). The species can be found to depths of 250 m and inhabits pelagic water with a temperature range from -1.5 to 6 °C (Rose, 2005). Diet studies indicate that capelin is an important prey for several abundant fishes in the region, including Atlantic cod

(*Gadus morhua*), as well as marine mammals and seabirds (Gonzalez et al., 2006; Tam and Bundy, 2019). Sand lance, while also an important prey (Gonzalez et al., 2006; NL Government, 2020), has received considerably less attention relative to capelin as it is not commercially fished (Boldt et al., 2022; Robertson et al., 2022). Two species of sand lance occur in this region: *A. dubius*, which occupies more offshore waters, and *A. americanus,* which occurs farther inshore but occasionally overlaps with *A. dubius* (Winters and Dalley, 1988). In contrast to capelin, sand lance inhabits shallower waters (generally < 100 m) and occurs in sandy areas of the Grand Banks (Staudinger et al., 2020). Spawning occurs in winter between November and March, and migratory behaviour is not as apparent as in capelin (Dalley and Winters, 1987; Morrison and Davoren, 2024). Both sand lance species burrow in sand to avoid predation and prefer waters ranging from 1 to 11 °C (NL Government, 2020).

Atlantic cod is a dominant predator in many ecosystems, including the Grand Banks (Link et al., 2009). In the Grand Banks, Atlantic cod inhabit waters with temperatures ranging from -2 to 11 °C and depths up to 400 m (Ruiz-Diaz et al., 2024). They are batch spawners, spawning from February to June and peaking in May (Myers et al., 1993). The species overwinters close to the edge of the continental shelf and migrates in spring and summer onto the plateau of the Grand Banks (DFO, 2022b). During the larval stage, they feed on phytoplankton and small zooplankton, particularly copepods (Myers et al., 1993). As they grow, Atlantic cod prey on a variety of smaller fish, invertebrates, and medium to large fish (Bundy et al., 2000; Gonzalez et al., 2006; Tam and Bundy, 2019). Adult cod are apex predators on the Grand Banks and have few natural predators, with harp seals being one of the most important (Stenson, 2013). During the fishing moratorium, which was announced following the stock collapse in the early 1990s, removals from the northern stock were permitted in stewardship and recreational inshore fisheries and as bycatch in the otter trawl fisheries of yellowtail flounder, skate and redfish (DFO, 2022b). The directed commercial fishery opened again in 2024 with a total allowable catch of 18,000 t (DFO, 2024). The southern Grand Banks stock, meanwhile, remains under moratorium (Rideout et al., 2021).

A dramatic decline in capelin biomass was observed during 1990-1991, with the northern stock dropping from 6 million tons in the late 80s to 0.02-0.06 million tons (99%) (Lewis et al., 2019). Similarly, a decline was noted in the southern stock in 1993, although the magnitude is less clear due to poor monitoring in this region (Tretyakov, 2015). Since then, both stocks have shown minimal recovery (Murphy et al., 2021, 2024; Tretyakov, 2015). Shifts in capelin life history traits before and after the collapse have also been detected, including declines in body condition size- and age-at-maturity and delayed spawning, the latter of which has been associated with weak year classes (Murphy et al., 2021; Buren et al., 2019). The low recovery of capelin has been related to changes in life-history traits and bottom-up processes, including early sea ice retreat, which determines spring bloom timing and, in turn, the dynamics of the main prey of capelin, the copepod *Calanus finmarchicus*, which is also the main prey of sand lance (Buren et al., 2014; Lewis et al., 2019; Staudinger et al., 2020). The decline in capelin biomass coincided with the collapse of groundfish populations, including Atlantic cod, American plaice, yellowtail flounder, and an increase in invertebrate biomass (i.e., snow crab, northern shrimp) (Koen-Alonso and Cuff, 2018). The groundfish collapse was attributed to a combination of overfishing and cooler environmental conditions (Dempsey et al., 2017). Several groundfish fisheries went into moratoria after the stock collapse, and some fisheries have yet to reopen (i.e., southern American plaice, southern Grand Banks Atlantic cod, capelin) (see Table C.1 for further details). Less is known about the response of sand lance before the collapse because it was not monitored. However, the species has been sampled in the bottom trawl survey since the fall of 1995, although its catchability is low (Brodie and Stansbury, 2007). A recent study improved the sand lance abundance index by combining trawl data with stomach content information, considering the consumption rates of Atlantic cod and American plaice (Robertson et al., 2022). The study found that sand lance abundance has fluctuated since 1995, with notable peaks in 1998-2000, 2004-2009, and 2012-2015.

Our research evaluates the direct and indirect ecological consequences of changing biomass on the following target species: capelin and sand lance (forage species) and Atlantic cod (top predator). We seek to determine which of these species leads to profound changes in community structure and stability. To achieve this, we developed a multispecies size spectrum food web model, a physiologically structured model that describes fish communities by accounting for variations in diet and ecological roles as individuals grow (Scott et al., 2014; Blanchard et al., 2017). Body growth and age-at-maturation are food-dependent, with processes formulated at the individual level. The primary components include growth, mortality, and reproduction driven by size-dependent predation and maturation (Scott et al., 2014). Using this model, we represented the major components of the Grand Banks fish community (see species included in Figure 5.1) and assessed how changes in the biomass of capelin and sand lance (both separately and jointly) and Atlantic cod may change biomasses and mean body weights of other species composing the food web. Through this research, we aim to elucidate bottom-up (driven by forage fish) vs top-down (driven by Atlantic cod) controls on the Grand Banks' food web.

5.3 Materials and Methods

5.3.1 General approach

To understand the roles of forage species and top predators in the Grand Banks community, we developed a multispecies size spectrum food web model using the mizer modelling framework (Scott et al., 2014). Mizer is a dynamic, size-based ecosystem model that represents predation interactions and growth processes at the

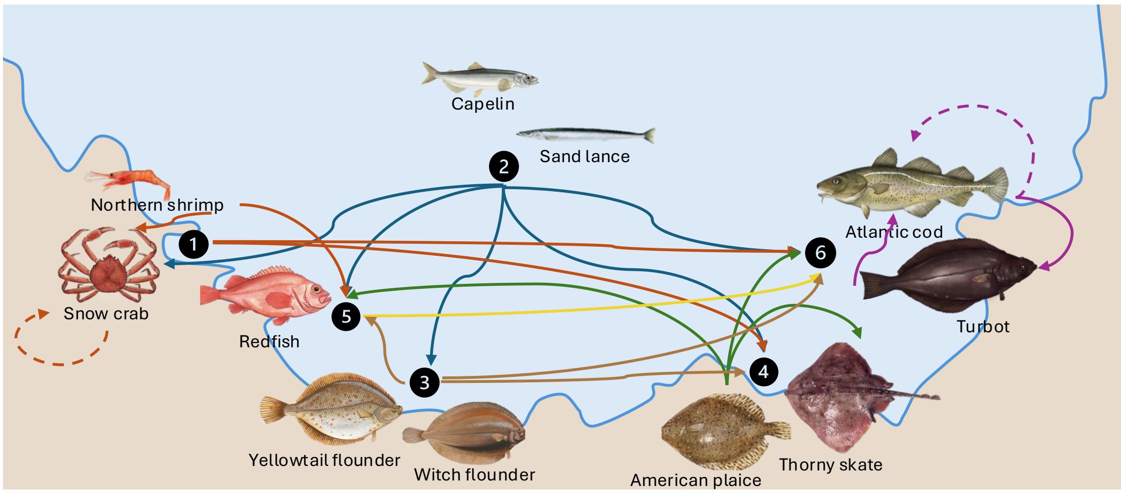


FIGURE 5.1: Species included in the size spectrum model. (1) Invertebrates, orange; (2) Planktivorous, blue; (3) medium benthivorous, brown; (4) large benthivorous, green; (5) Plank-piscivorous, yellow; (6) Piscivorous, purple. Solid lines indicate predator-prey links, with arrows pointing at predators. Dashed lines indicate cannibalism. Species image sources: Fisheries and Oceans Canada (DFO) and National Oceanic and Atmospheric Administration (NOAA).

individual level and fully resolves the size structure of species and the community (Scott et al., 2014). However, in our case, we only capture a fraction of the species in the ecosystem. The model was calibrated using 11 years of average biomass estimates (2000-2010) from the multispecies bottom trawl survey. Then, it was validated by forcing it with a time series of fishing mortality and evaluating how well the model was able to match yield and biomass trends from the entire period (1996-2019).

5.3.2 Multispecies size spectrum model description

The model used in this study relies on three key assumptions: (i) individual energy budgets drive community-level energy flows; (ii) predator-prey size ratios primarily determine trophic interactions; and (iii) vital rates are closely related to individual body sizes, following allometric scaling relationships used to estimate biological rates (Andersen et al., 2016). These assumptions enable dynamic growth, reproduction, and mortality rates to emerge from trophic interactions (Andersen and Beyer, 2006; Hartvig et al., 2011).

The model involves various biological processes, including prey selection (based on species-specific and size-based preferences) and energy allocation (encountered prey are assimilated, and energy is allocated to respiration, growth, and reproduction depending on individual size). The model formulates the size spectrum as a function of mortality (μ) and growth rate (g) using the McKendrick–von Foerster equation (McKendrick, 1926; Von Foerster and Stohlman, 1959); Equation (5.1). Recruitment introduces individuals into the size spectrum at the smallest body size, typically the egg size. This is represented as a boundary condition Equation (5.2). The feeding kernel, which determines the distribution of prey sizes that a predator feeds on, is governed by the size ratio between predators and prey and is described by a log-normal function (Scott et al., 2014). The model also includes a background resource spectrum, which feeds smaller individuals and planktivorous species. Dynamics of the size spectrum are governed by predation rates and a semi-chemostat equation, which determines the time evolution of the resource spectrum (De Roos et al., 2008; Scott et al., 2014) (see Table C.2 for full details in model equations).

$$\frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w)N_i(w)}{\partial w} = -\mu_i(w)N_i(w) \tag{5.1}$$

$$g_i(w_0)N_i(w_0) = R_i \tag{5.2}$$

where g_i is the growth rate (mass per time), μ_i the mortality (per time), N_i the size spectrum of species i, R_i the recruitment (number of recruits or eggs per time) of species i, and w_0 the individual's egg size.

For fishes and invertebrates, recruitment depends on egg production and follows a Beverton–Holt-type stock-recruit function, in which the maximum recruitment helps scale the abundance of species (see Table C.2). Body growth rates depend on prey availability, while death rates are influenced by predation, fishing, and external mortality. Further documentation on the model framework is available in the R package mizer (Scott et al., 2014).

In mizer, mortality not accounted for by fishing or predation is considered external morality and accounts for additional losses such as those due to disease or senescence. By default, mizer assumes that the external mortality is a species-specific constant $Z0_i$ independent of size. The value of $Z0_i$ is either specified as a species parameter or it is assumed to depend allometrically on the asymptotic size, w_{inf}; Equation (5.3) (Scott et al., 2014). Specifically, external mortality is calculated as:

$$Z0_i = Zp_i \times (w_{inf_i})^{Ze} \tag{5.3}$$

where Zp_i is pre-factor or base mortality rate for species i, representing mortality that is independent of body size (e.g., due to predation by unmodelled predators, disease, etc.) and is set to 0.6 by default; w_{inf_i} is the body size of an individual of species i; and Ze is the exponent that controls how external mortality scales with body size (w_{inf_i}) (Scott et al., 2014). This assumption conforms with life history theory such that larger, longer-lived species generally experience lower mortality rates than smaller, short-lived species (Thorson et al., 2017). Further, maintaining constant external mortality across size classes has the practical benefit of preventing an unrealistic buildup of large-bodied, high-trophic-level individuals (Andersen et al., 2016).

5.3.3 Parameterization

The model domain corresponds to the Northwest Atlantic Fisheries Organization (NAFO) divisions 3L, 3N and 3O (Figure 5.2). We obtained regional biomass estimates for groundfish from DFO spring trawl surveys of the Grand Banks between 1996 and 2019. Trawl surveys have been conducted by DFO in Newfoundland and Labrador annually since 1971 but with some modifications in survey design, sampling gear, and spatial coverage over time (Brodie and Stansbury, 2007). Of particular note, the survey was initially performed using Engels (145 high lift otter trawl) sampling gear but later changed to a Campelen trawl (i.e., 1800 shrimp trawl) in 1995-1996 (Brodie and Stansbury, 2007). This change improved catches of small-sized fish and enabled abundance estimates of commercial shellfish species. Biomass estimates were obtained for groundfishes using design-based methods implemented in the Rstrap package (Regular et al., 2020). For snow crab, we obtained biomass estimates from the stock assessment for the 3LNO divisions. This was done because the catchability of snow crab is low in the DFO trawl survey (Dawe et al., 2010). For forage fish, catchability in the trawl survey is also low. We, therefore, used a capelin biomass estimate from acoustic data, though this sampling only covers the 3L region of the stock, where most capelin occurs (DFO, 2022a). We used the biomass index from the bottom trawl survey for the northern sand lance.

Fixed and species-specific parameters, including maximum size, size at maturation, and length-weight relationship parameters, are detailed in Table C.3 and Table C.4. For groundfishes, we assumed maximum length, Linf, corresponding to the maximum observed length from the trawl survey over the calibration period 2000-2010, as recommended elsewhere (Delius et al., 2023). Age- and length-at-maturity were primarily obtained from stock assessments when available (see Table C.5). Size-at-maturation corresponds to females as they limit reproductive output and reach maturity at larger sizes than males. However, for snow crab, we used size-at-maturation values associated with males because males are larger than females and the fishery targets males only. Parameters for length-weight relationships were estimated from DFO trawl survey data. In the case of one fish species, thorny skate, we used values from Fishbase, corresponding to Flemish Cap thorny skate (Froese and Pauly, 2024). Shrimp length-weight relationships were provided by DFO.

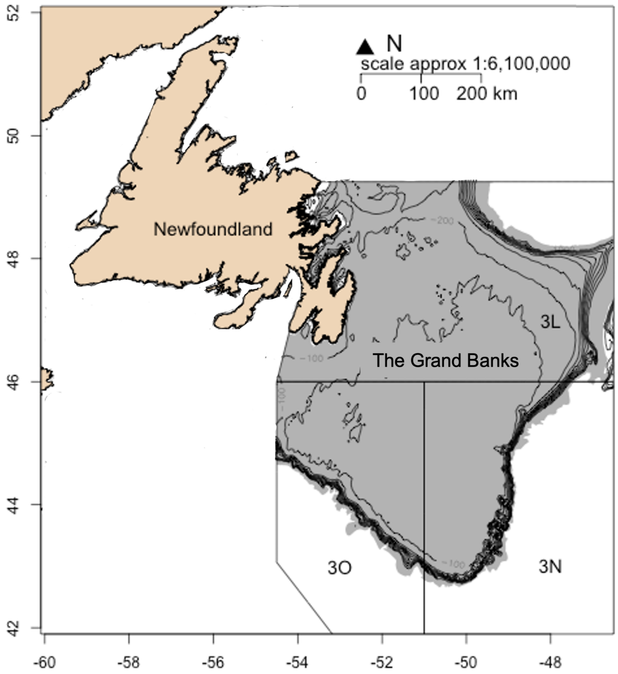


FIGURE 5.2: Map of the Grand Banks. Black rectangles represent the NAFO divisions 3L, 3N and 3O. Isobaths are indicated with backlines and show depths up to 1000 m.

Predation interactions in mizer are based on the size selectivity of predators, represented by a log-normal feeding kernel. The mean preferred predator-to-prey mass ratio and width are adjusted during calibration, with default values set to 100 and 1, respectively, for cod-like predators (Hartvig et al., 2011). These values were modified as needed: lower for piscivores and higher for omnivores and planktivores (Szuwalski et al., 2017; Jacobsen et al., 2017) (Table C.3).

To parameterize the prey species preference of predators, species interaction coefficients were assigned a value of 1 (present in predator diet) or 0 (absence in diet) based on stomach content information from Gonzalez et al. (2006) and a previously developed Ecopath model (Bundy et al., 2000) (Figure C.1). By adopting the default value of 1, the model implicitly assumes that prey is fed upon in proportion to their relative encounter rates by the predator (Hartvig et al., 2011).

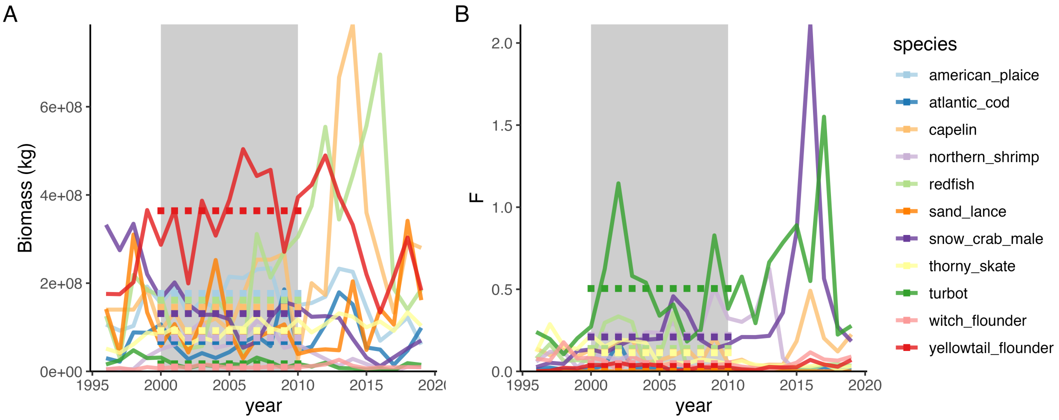


FIGURE 5.3: A) Historical time series of biomass (kg) for the whole model domain was calculated using RV trawl data, and B) fishing mortality rates were calculated as the ratio between catches and biomass. The time average period (2000-2010) is highlighted in grey, and average values are indicated by squares, with colour representing species.

The time series of species biomass was calculated using the bottom trawl data and the R-strap R package (Figure 5.3 A). Catches were obtained from stock assessments (Table C.6). Fishing effort was calculated using the ratio between catches and biomass (Figure 5.3 B) because several species were not assessed (e.g., sand lance), and others were assessed at different management units (e.g., Atlantic cod, redfish, turbot, capelin). To deal with the inconsistency between management units, we used the following approaches: in the case of Atlantic cod, we used the catches of the southern stock (3NO). We used catches in the 3O stock for redfish since this stock is the most exploited. In the case of turbot, we used catches from the 3KLMNO divisions. Finally, we used the NAFO STATLANT database for capelin to obtain catch information. Sand lance is not a commercial species; therefore, catches were assumed to be zero. Moreover, this species has low catchability as bycatch.

Fishing mortality, F, is imposed on individuals by size selective fishing gear. F is a product of size-dependent gear selectivity function (the ability of a gear to capture individuals by size, ranging from 0 to 1), fishing effort (a measure of the fishing intensity) and catchability (an additional scalar that relates population abundance to F) (Scott et al., 2014). We used a length-based sigmoid selectivity function based on two parameters, l25 and l50, which determine the length at which 25% and 50% of the stock are captured, respectively (Figure C.2). These parameters were estimated from the size distribution data collected from bottom trawl catches by calculating the 25th percentile and the 50th percentile of the length of the catches. Next, we calculated the average fishing mortality over the (2000-2010) calibration period and used it as a baseline in the calibration. We set catchability to 1, thus allowing the use of fishing effort as a direct measure of fishing mortality under constant selectivity (Benoit et al., 2022).

5.3.4 Model calibration

Model calibration proceeded in an iterative manner. First, we brought the model to equilibrium by adjusting initial reproduction efficiency values using the steady() function in mizer, exploring other parameters if unrealistic values (> 1) were returned. Next, we calibrated biomass by scaling initial species biomasses to match observed relative biomasses without altering the size structure. We then tuned growth by modifying intake and metabolism parameters if feeding levels were high, but growth was low (Audzijonyte et al., 2023). Reproductive parameters were calibrated by adjusting the maximum recruitment parameter ($Rmax$) while fixing reproductive efficiency ($erepro = 1$), using the quasi-Newton method with box constraints (L-BFGS-B) to minimize the sum of squared errors between modelled and empirical relative biomass, with a penalty to prevent species extinction (Blanchard et al., 2014). We ensured long-term species co-existence by running simulations for 100 years. Finally, we tested different reproduction levels to assess species' sensitivity to fishing and compared them to expected ranges based on species' life-history characteristics (Audzijonyte et al., 2023). The emergent diets, feeding levels and predation mortality were features of the model we intended to evaluate in the calibration procedure.

5.3.5 Model validation

To validate the model, we evaluated observed and modelled size-at-age values (Blanchard et al., 2014) for fish species using age-length keys obtained from Rstrap. We selected age-length keys corresponding to the year 2005, which is in the middle of our calibration period (2000-2010). This information was unavailable for snow crab, northern shrimp, northern sand lance and thorny skate. Additionally, we forced the model with time-varying fishing mortality to assess correlations between predicted and observed time series of biomass and catch (Blanchard et al., 2014).

5.3.6 Model scenario

We implemented four exploratory types of simulations to identify the relative importance of forage fish and Atlantic cod. In the first three scenarios, we evaluated the response of the Grand Banks' community to increases and decreases in external mortality on (1) capelin, (2) sand lance and (3) both capelin and sand lance. Specifically, under each scenario, we evaluated changes in biomass and mean body size when mortalities were increased/decreased by 5%, 10%, 15% and 30% (Table 5.1). The range of values used in the simulations was designed to account for a broad spectrum of possible outcomes. In the fourth scenario, we instead applied the same increases and decreases in mortality but to Atlantic cod. In doing so, we sought to identify the relative importance of forage fish and cod in governing community structure.

Using the calibrated model as our starting point, we adjusted the external mortality values ($Z0$) according to each scenario and projected 1000 years, ensuring equilibrium was reached. To account for small oscillations in biomass and weight, we calculated the 11-year average values at the end of the simulations (990-1000

TABLE 5.1: Values of external mortality used for running the simulations. The original represents the values in the calibrated model. The percentage values indicate the mortality increased and decreased relative to the original value

External mortality (Z0)	Capelin	Sand lance	Atlantic cod
original	0.24	0.216	0.045
Increasing external mortality			
5%	0.251	0.227	0.048
10%	0.263	0.238	0.05
15%	0.275	0.248	0.052
30%	0.311	0.281	0.059
Decreasing external mortality			
5%	0.23	0.2	0.043
10%	0.21	0.19	0.04
15%	0.2	0.18	0.038
30%	0.16	0.15	0.031

years). We then calculated the relative change in variables (biomass or mean body weight) between the calibrated model and the equilibrium values under the scenario as follows (Reum et al., 2024):

$$\Delta X_i = \frac{X\mathrm{sim}_{i,j} - X\mathrm{ori}_i}{X\mathrm{ori}_i} \times 100 \tag{5.4}$$

Where X represents the variable of interest (i.e., biomass or weight) of species i. Xsim correspond to the variable of interest during the simulation j, and Xori represents the variable of interest in the original (unmanipulated) simulation.

5.4 Results

5.4.1 Model calibration

The calibrated model produced biomass levels that closely matched average observed values (Pearson's correlation coefficient, $R = 0.8$) but were, on average, biased slightly higher than the observations (-0.28; Figure C.3 and Figure C.4).

The model also demonstrated plausible resilience to fishing, as indicated by the fishing mortality rate at maximum yield under equilibrium conditions (Figure C.5). Feeding levels ranged from 0.5 to 0.75 (Figure C.6). The model also produced plausible ontogenetic shifts in the diets of the species groups, with all species initially feeding on background resources and shifts towards invertivory and piscivory with size (Figure C.7). Predation pressure was highest on capelin, followed by sand lance and northern shrimp. Higher mortality rates were observed for capelin, followed by sand lance and northern shrimp (Figure C.8).

5.4.2 Model validation

Species growth rates predicted by the model were consistent with observed growth rates, achieving $R^2 > 0.9$ for all assessed species except American plaice, which was slightly lower, $R^2 = 0.89$ (Figure C.9). Additionally, when forced with F time series the model captured trends in yield and biomass (Figure C.10 and Figure C.12). For yield, species with relatively high Pearson's correlation between observed and modelled values ($R > 0.7$) included American plaice, Atlantic cod, yellowtail flounder, and thorny skate. Species with moderate correlation ($0.4 < R < 0.7$) were redfish, turbot, witch flounder, northern shrimp, and snow crab. Capelin exhibited a low correlation ($R < 0.1$). For biomass, most species showed a moderate correlation between modelled and observed values ($0.4 < R < 0.7$), including American plaice, turbot, yellowtail flounder, sand lance, northern shrimp, snow crab, and thorny skate. Correlations were lower ($R < 0.2$) for Atlantic cod, redfish, witch flounder, and capelin (Figure C.11 and Figure C.13).

5.4.3 Simulations

Scenarios involving increased or decreased mortality in capelin and sand lance resulted in linear, proportional changes in their biomasses (Figure 5.4 and Figure 5.5). For example, a 30% increase in mortality for both species led to declines in biomass of 15% for capelin and 11% for sand lance (Figure 5.4). Conversely, a 30% decrease in mortality resulted in increases in biomass of 21% for capelin and 15% for sand lance (Figure 5.5. The response of Atlantic cod biomass to external mortality increase was non-linear. Initially, cod biomass declined with increasing external mortality, with a maximum reduction of 16% for a 15% increase in mortality. However, when mortality reached 30%, the decline in biomass stabilized (Figure 5.4). A decrease in cod mortality resulted in a linear increase in biomass, with a 66% rise corresponding to a 30% reduction in mortality (Figure 5.5).

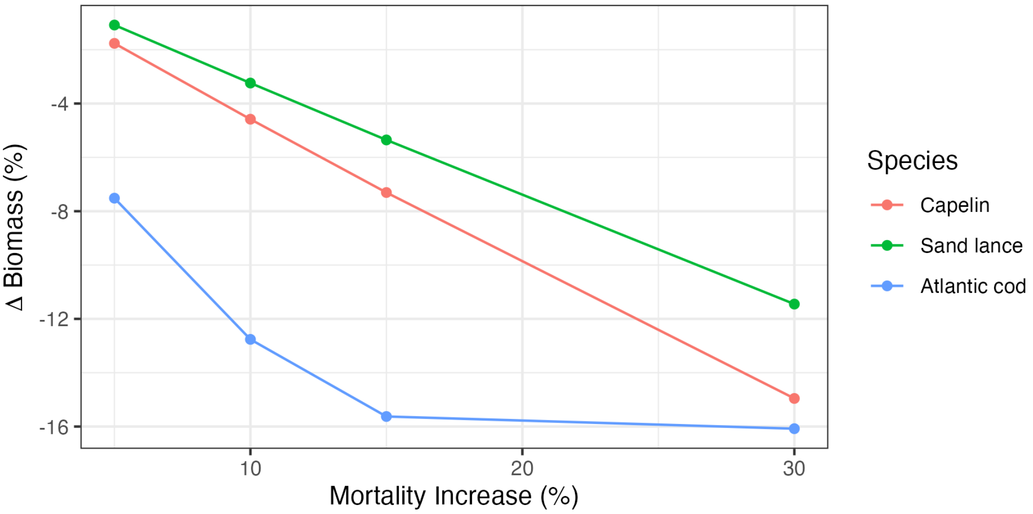


FIGURE 5.4: Increasing target species mortality. Change in biomass of capelin (orange), sand lance (green) and Atlantic cod (blue) as a result of the mortality scenarios. Mortality scenarios were run for each species individually.

5.4.4 Changing forage species biomass

Modifying capelin biomass led to larger changes in the biomass and mean body weight of non-target species compared to similar changes in sand lance biomass. These changes were even more pronounced when capelin and sand lance were modified simultaneously (Figure 5.6 and Figure 5.7).

Capelin Scenario

When capelin biomass declined by 15%, the species experiencing the largest reductions in biomass were turbot (-4%), American plaice (-1.7%), sand lance (-0.9%),

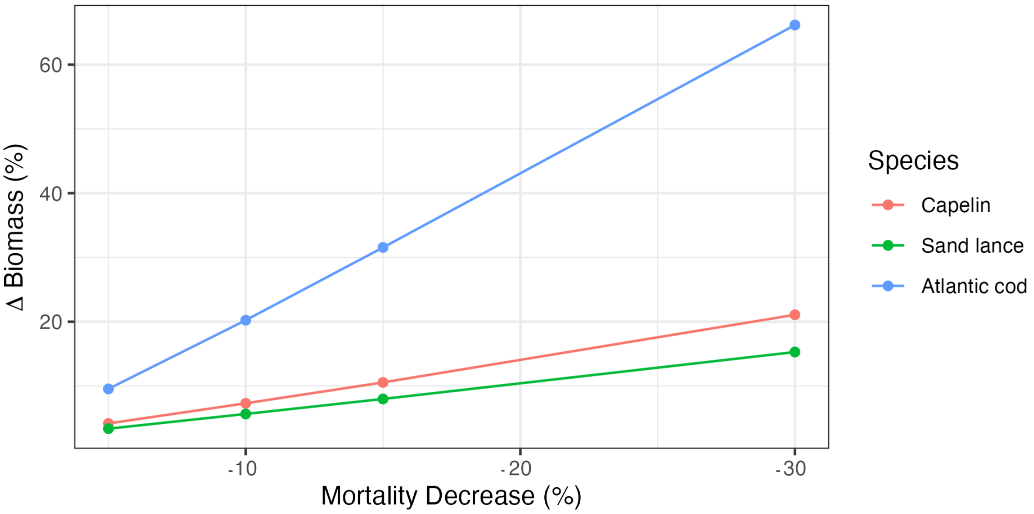


FIGURE 5.5: Decreasing target species mortality. Change in biomass of capelin (orange), sand lance (green) and Atlantic cod (blue) as a result of the mortality scenarios. Mortality scenarios were run for each species individually.

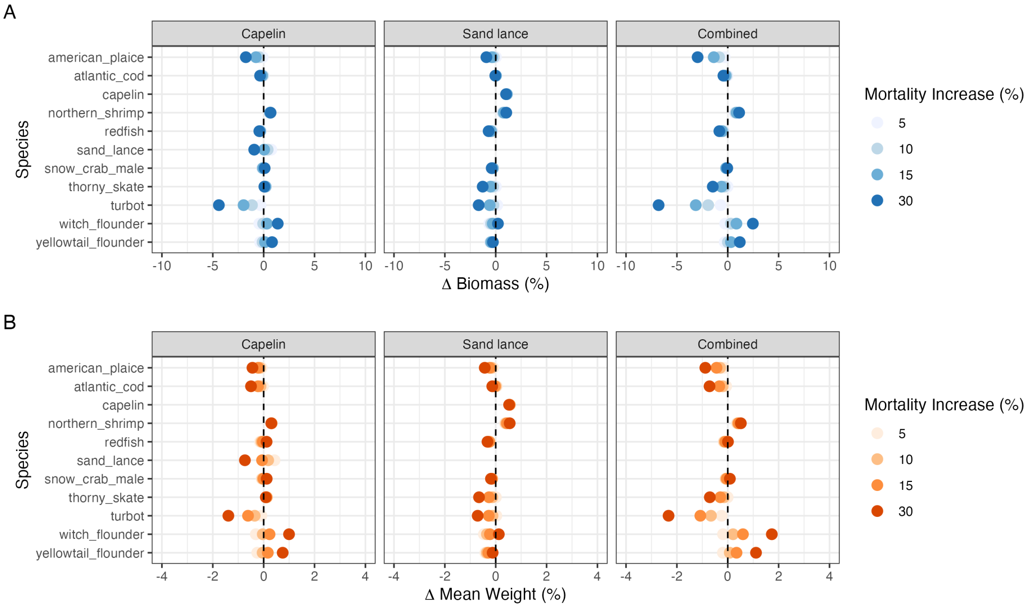


FIGURE 5.6: Decreasing forage fish biomass. Relative changes (in percentage) in A) biomass and B) mean body weight for species included in the Grand Banks' multi-species model under different mortality increase scenarios of the target forage species (capelin, sand lance and combined). The colour intensity indicates the level of mortality, with darker colours showing greater changes.

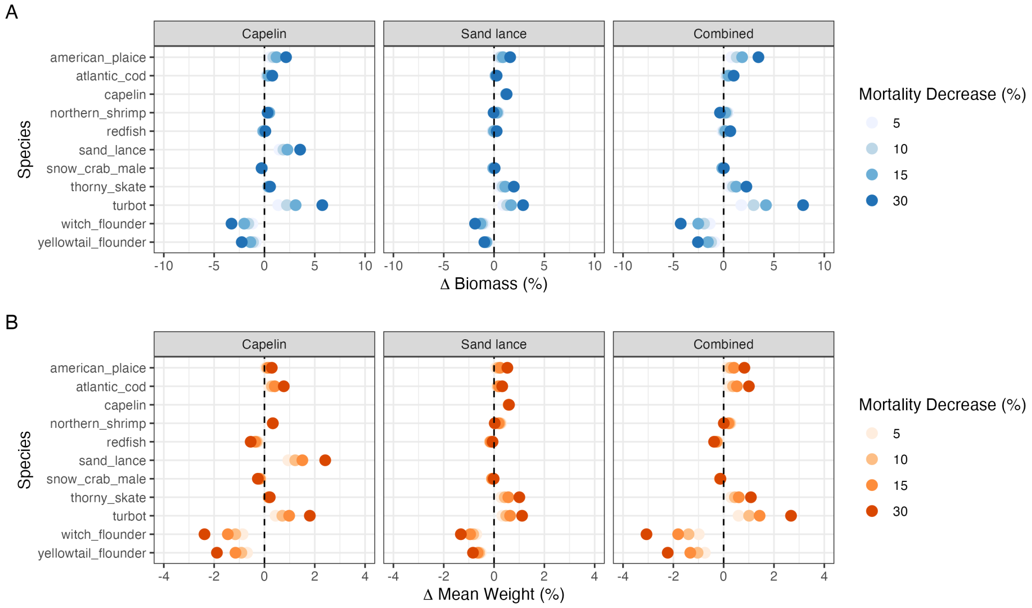


FIGURE 5.7: Increasing forage fish biomass. Relative changes (in percentage) in A) biomass and B) mean body weight for species included in the Grand Banks' multi-species model under different mortality decrease scenarios of the target forage species (capelin, sand lance and combined). The colour intensity indicates the level of mortality, with darker colours showing greater changes.

redfish (-0.42%), and Atlantic cod (-0.35%). In contrast, species that benefited from the decrease in capelin included witch flounder (1.4%), yellowtail flounder (0.8%), northern shrimp (0.7%), snow crab (0.09%), and thorny skate (0.06%) (Figure 5.6 A). Similar trends were observed in mean body weight. On the one hand, species with the greatest decreases in body weight included turbot (-1.4%), sand lance (-0.73%), Atlantic cod (-0.5%), and American plaice (-0.45%). On the other hand, witch flounder (1%), yellowtail flounder (0.75%), northern shrimp (0.3%), snow crab (0.12%), redfish (0.11%), and thorny skate (0.08%) increased in weight (Figure 5.6 B).

When capelin biomass increased by 21%, species that experienced declines in biomass included medium benthivores, witch flounder (-3.3%), yellowtail flounder (-2.2%), and snow crab (-0.28%). Species that saw an increase in biomass were turbot (5.7%), sand lance (3.5%), American plaice (2%), Atlantic cod (0.77%), thorny skate (0.55%), northern shrimp (0.3%), and redfish (0.09%) (Figure 5.7 A). In terms of body weight, the species with reductions were witch flounder (-2.4%), yellowtail flounder (-1.9%), redfish (-0.5%), and snow crab (-0.3%). Conversely, species that gained weight included sand lance (2.4%), turbot (1.8%), Atlantic cod (0.76%), northern shrimp (0.33%), American plaice (0.3%), and thorny skate (0.2%) (Figure 5.7 B).

Sand Lance Scenario

A 12% decline in sand lance biomass led to reductions in the biomass of turbot (-1.7%), thorny skate (-1.27%), American plaice (-0.9%), redfish (-0.7%), snow crab (-0.4%), yellowtail flounder (-0.3%), and Atlantic cod (-0.04%). Conversely, biomass increases were observed in northern shrimp (1%), capelin (1%), and witch flounder (0.2%) (Figure 5.6 A). In terms of body weight, the most notable decreases were seen in turbot (-0.7%), thorny skate (-0.65%), American plaice (-0.43%), redfish (-0.3%), snow crab (-0.18%), Atlantic cod (-0.13%), and yellowtail flounder (-0.12%). In contrast, species that experienced increases in mean body weight included northern shrimp (0.54%), capelin (0.52%), and witch flounder (0.12%) (Figure 5.6 B).

An increase in sand lance biomass by 17% resulted in declines in the biomass of witch flounder (-1.18%), yellowtail flounder (-0.9%), and northern shrimp (-0.05%). Species that gained biomass included turbot (2.9%), thorny skate (1.9%), American plaice (1.6%), capelin (1.25%), and, to a lesser extent, redfish (0.26%), Atlantic cod (0.25%), and snow crab (0.06%) (Figure 5.7 A). Regarding mean body weight, declines were observed in witch flounder (-1.3%), yellowtail flounder (-0.83%), redfish (-0.06%), and snow crab (-0.015%). Conversely, species that saw increases in mean body weight included turbot (1.1%), thorny skate (1%), capelin (0.6%), American plaice (0.52%), Atlantic cod (0.32%), and northern shrimp (0.03%) (Figure 5.7 B).

Combined Scenario

The effects became more pronounced when both capelin and sand lance biomasses declined simultaneously. Species that experienced the largest decreases in biomass included turbot (-6.8%), American plaice (-3%), thorny skate (-1.5%), redfish (-0.8%), Atlantic cod (-0.42%), and snow crab (-0.05%). Conversely, species that saw increases in biomass were witch flounder (2.5%), yellowtail flounder (1.2%), and northern shrimp (1.1%) (Figure 5.6 A). In terms of mean body weight, species with declines included turbot (-2.3%), American plaice (-0.9%), Atlantic cod (-0.72%), and thorny skate (-0.7%). Species that experienced increases in mean body weight were witch flounder (1.7%), yellowtail flounder (1.1%), northern shrimp (0.5%), snow crab (0.08%), and redfish (0.008%) (Figure 5.6 B).

An increase in both capelin and sand lance biomasses led to declines in witch flounder (-4.3%), yellowtail flounder (-2.5%), and northern shrimp (-0.36%). Species that gained biomass included turbot (7.9%), American plaice (3.5%), thorny skate (2.25%), Atlantic cod (1%), redfish (0.6%), and snow crab (0.02%) (Figure 5.7 A). Regarding mean body weight, declines were observed in witch flounder (-3%), yellowtail flounder (-2.2%), redfish (-0.4%), and snow crab (-0.12%). Species that gained weight were turbot (2.7%), thorny skate (1.1%), Atlantic cod (1%), American plaice (0.8%), and northern shrimp (0.006%) (Figure 5.7 B).

5.4.5 Changing Atlantic cod biomass

We observed a pronounced shift in the biomass of many non-target species in response to changes in Atlantic cod biomass (Figure 5.8 and Figure 5.9). When Atlantic cod biomass decreased by approximately 17%, substantial declines were seen in sand lance (-89.51%), northern shrimp (-87%), capelin (-79%), turbot (-77%), American plaice (-68%), and thorny skate (-6%). In contrast, biomass increased in redfish (79%), snow crab (69%), witch flounder (57%), and yellowtail flounder (47%) (Figure 5.8 A). Changes in mean body weight were also notable, with the largest decreases observed in sand lance (-58%), northern shrimp (-52%), capelin (-46%), American plaice (-26%), turbot (-17%), and thorny skate (-4%). Increases in body weight were recorded for witch flounder (55%), yellowtail flounder (50%), redfish (42%), and snow crab (36%) (Figure 5.8 B).

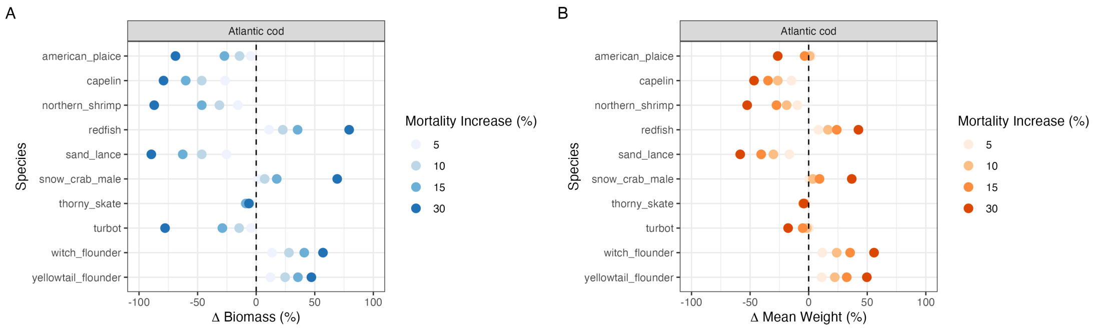


FIGURE 5.8: Decreasing Atlantic cod biomass. Relative changes (in percentage) in A) biomass and B) mean body weight for species in the Grand Banks' multi-species model under different mortality increase scenarios for Atlantic cod. The colour intensity indicates the level of mortality increase, with darker colours showing greater changes.

When Atlantic cod biomass increased by 66%, declines were observed in medium benthivores, yellowtail flounder (-82%) and witch flounder (-70%), redfish (-62%), turbot (-35%), and American plaice (-25%). In contrast, increases were seen in capelin (378%), sand lance (350%), and northern shrimp (98%), with moderate increases in thorny skate (25%) and snow crab (15%) (Figure 5.9 A). Changes in

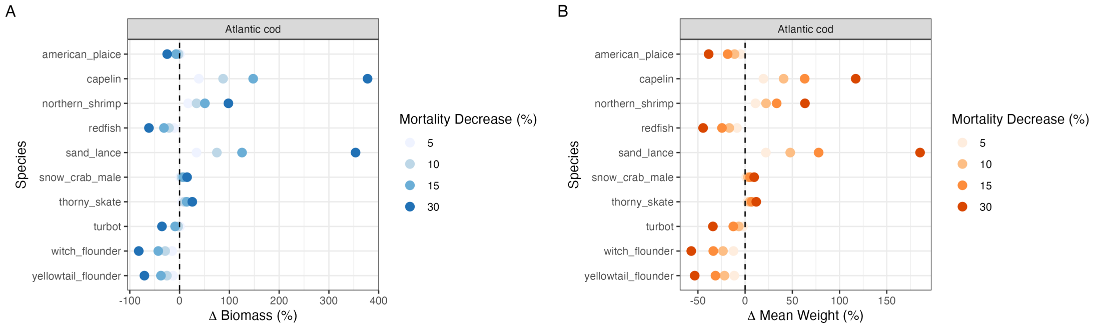


FIGURE 5.9: Increasing Atlantic cod biomass. Relative changes (in percentage) in A) biomass and B) mean body weight for species in the Grand Banks' multi-species model under different mortality increase scenarios for Atlantic cod. The colour intensity indicates the level of mortality decrease, with darker colours showing greater changes.

mean body weight were also pronounced, with the largest increases in sand lance (185%), capelin (117%), and northern shrimp (63%), and moderate increases in thorny skate (12%) and snow crab (9.5%). Meanwhile, moderate declines in mean body weight were observed in witch flounder (-57%), yellowtail flounder (-53%), redfish (-44%), American plaice (-38%), and turbot (-34%) (Figure 5.9 B).

5.4.6 Importance of the Target Species on the Food Web

In simulations where forage species biomass changes, other species in the community exhibited linear responses, with more substantial changes observed as capelin biomass decreases compared to sand lance (Figure 5.10 B). Similar linear responses were observed when forage fish biomass increased (Figure 5.11 B). However, the response differed when Atlantic cod biomass decreased, leading to more complex responses from non-target species. Once Atlantic cod mortality exceeded 16%, the non-target species drastically increased/decreased (Figure 5.10 A). This indicates that exceeding a 16% decline in cod biomass triggered a shift in community biomass. When we decreased Atlantic cod biomass above 18% (corresponding to an increase in external mortality of 40%), the system was not able to reach equilibrium, with the main prey species of the community (capelin, sand lance and northern shrimp) going functionally extinct. When we increased Atlantic cod biomass, we observed a linear response with non-target species, although capelin and sand lance showed a steep increase in biomass (above 300% gain) when cod biomass increased above 32% (Figure 5.11 A). After this point, the system did not reach equilibrium as Atlantic cod biomass kept increasing due to a functional extinction of medium benthivores.

5.5 Discussion

Using a multispecies size spectrum model, this study assesses the direct and indirect ecological consequences of changing the biomass of capelin and sand lance

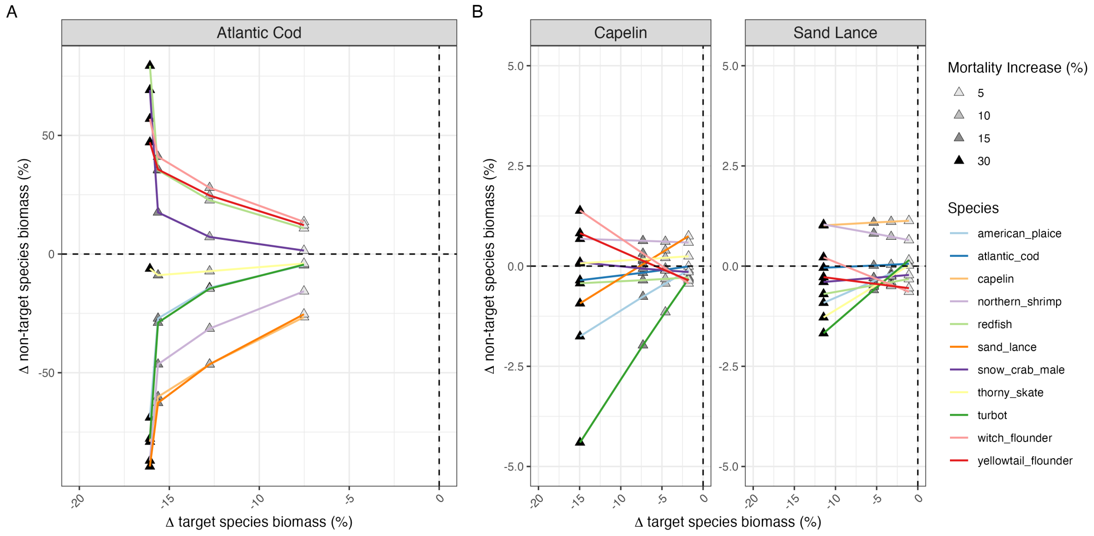


FIGURE 5.10: Decreasing target species biomass. Relative change (in percentage) in non-target species biomass relative to the decline in the target species (capelin, sand lance and Atlantic cod). The mortality increase scenario is indicated with grey triangles, with lighter colours representing lower mortality scenarios and darker colours representing higher mortality scenarios. Species are indicated by colour lines

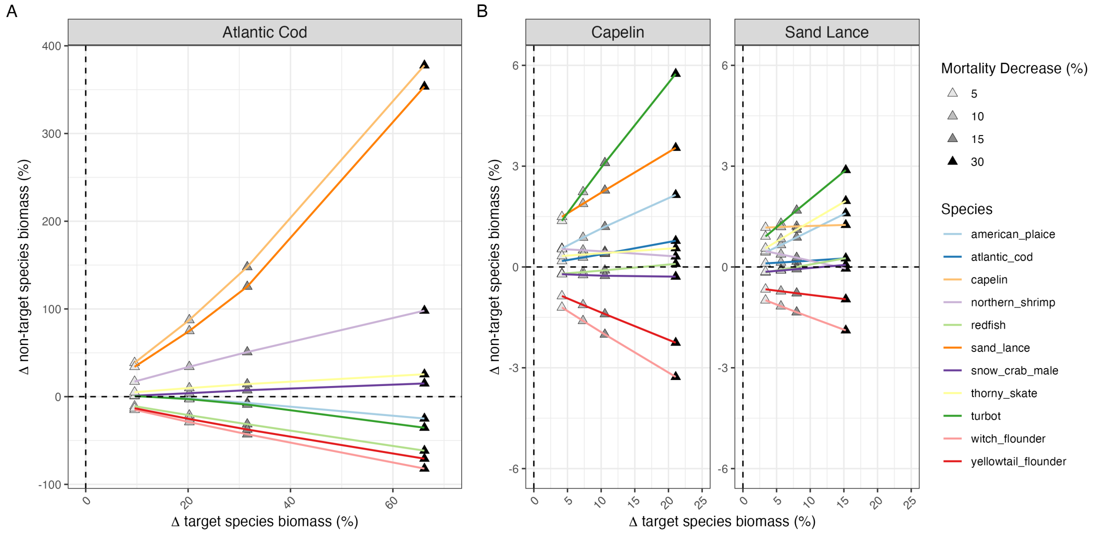


FIGURE 5.11: Increasing target species biomass. Relative change (in percentage) in non-target species biomass relative to the decline in the target species (capelin, sand lance and Atlantic cod). The mortality increase scenario is indicated with grey triangles, with lighter colours representing lower mortality scenarios and darker colours representing higher mortality scenarios. Species are indicated by colour lines

(forage species) and Atlantic cod (top predator), and evaluates their importance for the stability of the community. Our findings reveal that shifts in the biomass of these target species induce changes in both biomass and mean body weight across different trophic levels. In the bottom-up scenario, increases in forage fish biomass lead to higher biomass and mean body weight in piscivores and large benthivores species, while medium benthivores species decline. Overall, the decline in capelin had a more pronounced effect on non-target species within the Grand Banks community compared to a decline in sand lance. This suggests that capelin may have a more important role as an energy source in the Grand Banks food web, in line with many studies that highlight the critical role of capelin in the system (Buren et al., 2014; Regular et al., 2022). Moreover, capelin is smaller than sand lance, allowing it to be consumed by smaller predators which are more numerous in the system. Finally, a simultaneous increase in biomass of both forage fish species led to more pronounced changes in non-target species biomass and weight than simulating each species individually. This aligns with the portfolio theory (Figge, 2004; Schindler et al., 2010), suggesting that diversity among forage fish enhances the stability of Grand Banks communities by maintaining similar ecosystem functions.

Several studies have documented that Atlantic cod biomass often increases in response to a rise in capelin biomass in Newfoundland (Buren et al., 2014; Koen-Alonso et al., 2021). Our results support this trend but also indicate that other species may benefit more from increases in capelin biomass than Atlantic cod. For example, turbot experienced a 5.7% increase, sand lance saw a 3.5% increase, and American plaice rose by 2%. Increasing sand lance biomass had a greater positive effect on thorny skate biomass (1.9%) compared to the effect of increasing capelin biomass, which resulted in a smaller increase in thorny skate biomass (0.55%). This finding is in line with the literature highlighting the importance of sand lance in the diet of thorny skate (Gonzalez et al., 2006; Tam and Bundy, 2019). Atlantic cod was the only species for which the decline in mean body weight was notably greater than the decline in biomass in response to reductions in forage fish biomass. For example, in the capelin decline scenario, Atlantic cod's biomass declined by 0.35%, whereas its body weight dropped by 0.5%. Similarly, in the sand lance decline scenario, the biomass decreased by only 0.04%, while the body weight fell by 0.13%. One possible explanation is that the broad and omnivorous feeding habits of Atlantic cod (Link et al., 2009; Berard and Davoren, 2020) may enable them to maintain their overall biomass, but the strain on their high-energy resources (particularly capelin) can result in lower body weight. In fact, there are examples in the literature linking the poor body condition of Atlantic cod to capelin availability (Mullowney and Rose, 2014; Koen-Alonso et al., 2021; Regular et al., 2022). Thus, changes in forage fish biomass capelin and sand lance seem to have a larger effect on Atlantic cod individual growth and body condition than on its overall biomass.

In the top-down scenario, when we decreased Atlantic cod biomass, we observed big declines in the main prey items of the community, forage fish and northern shrimp, and a moderate decrease in piscivores and large benthivores. While the species expected to gain biomass are snow crab, redfish and medium benthivores. Snow crab is expected to see an increase in biomass of 69% with declining Atlantic cod biomass. Large increases in macroinvertebrates, such as snow crab and northern shrimp, have been reported to follow declines in Atlantic cod in nine continental shelf ecosystems (Worm and Myers, 2003). In the Northwest Atlantic Ocean, snow crab populations are primarily regulated by top-down mechanisms in the years leading up to fishery recruitment and by temperature in the post-settlement years (Boudreau et al., 2011). Similarly, Atlantic cod has been identified as a key regulator of snow crab populations in the Barents Sea, affecting their distribution and productivity (Durant et al., 2023; Holt et al., 2021). Our results for the Grand Banks suggest that Atlantic cod also plays an important role in controlling snow crab populations. However, we did not observe an increase in northern shrimp biomass, likely due to its position in the food web as a key prey for many species, particularly redfish (Gonzalez et al., 2006), whose biomass is also dramatically increasing in our simulations (79%). Redfish are characterized by long lifespan (> 50 years), slow growth, late maturation, and episodic production of large year classes (Cadigan et al., 2022b), and are heavily predated upon by Atlantic cod and turbot. They rely on zooplankton, shrimp, and other small invertebrates (Gonzalez et al., 2006; Cadigan et al., 2022b).

Turbot and American plaice are expected to experience biomass loss in response to changes in Atlantic cod biomass, with a more pronounced impact when cod biomass decreases. This might seem counterintuitive, suggesting that the system's responses are not straightforward and cannot always be anticipated. The decline in these large benthivores may be related to increases in redfish and snow crab populations, which heavily prey on capelin, sand lance, and shrimp. Large benthivores might compete with redfish at early life stages, with redfish potentially outcompeting them due to their plankt-piscivorous diet. As a predator of both species (Gonzalez et al., 2006; Tam and Bundy, 2019), an increase in cod biomass intensifies predation pressure, directly reducing the biomass of turbot and American plaice. Reducing Atlantic cod biomass can thus have complex, cascading effects throughout the food web, influencing various trophic levels differently (Frank et al., 2005). Bundy (2001) observed that the Newfoundland food web experienced larger fluctuations under top-down control than bottom-up control in Ecopath with Ecosystem simulations. Our results align with these findings, demonstrating that changes in forage fish biomass lead to variations in non-target species biomass of ±5%, with turbot experiencing slightly greater changes. In contrast, increasing or decreasing Atlantic cod biomass resulted in changes ranging from -90% to over 300%.

We also noted a non-linear response in Atlantic cod biomass with increasing external mortality. A 16% decline in cod biomass led to an important restructuring of the system, where cod biomass remained relatively stable while non-target species experienced drastic changes. However, when the decline in cod biomass exceeded 17%, the system failed to reach equilibrium due to the functional extinction of key prey species (driven by intense predation by redfish, snow crab and medium benthivores, which biomass drastically increased). This pattern indicates that moderate reductions in Atlantic cod biomass may trigger trophic cascades, which can take an extended period to propagate through the food web (Frank et al., 2005). In addition, reductions beyond this threshold can even lead to a regime shift, causing profound and irreversible changes within the community (Daskalov et al., 2007; Casini et al., 2008).

Strong (1992) argues that top-down structuring is atypical and signifies biological instability. Overfishing large predators disrupts the balance between predator and prey populations, hindering predator recovery due to increased predation and competition for food from prey, especially during the predators' early life stages (Frank et al., 2007). Continuing fishing and bycatch in low productivity conditions could also delay recovery (Shelton et al., 2006). Ecosystems under top-down control are particularly vulnerable to fishing exploitation compared to those regulated by bottom-up processes (Petrie et al., 2009). In the Northwest Atlantic, the collapse of cod has led to dramatic increases in invertebrate biomass (Dempsey et al., 2017; Koen-Alonso and Cuff, 2018) and significant cascading effects throughout the food web (Frank et al., 2005). Despite reductions in fishing pressure, the recovery of top predators like cod has not occurred in the Grand Banks, highlighting the complex and often unpredictable nature of ecosystem responses to such disturbances (Frank et al., 2006).

Our findings highlight the critical role of Atlantic cod in the Grand Banks, demonstrating that its decline can cause significant disruptions to ecosystem stability, potentially more so than changes in forage species alone. This emphasizes the need for ecosystem and multispecies models to inform management decisions. Size-spectrum models, in particular, offer valuable insights by capturing the ecological realism of size-structured vital processes, ontogenetic life-history traits, and tropho-dynamic interactions (Andersen et al., 2016). *Mizer* models are versatile tools for studying both top-down and bottom-up controls in ecosystems. Our findings underscore the significant top-down impact of Atlantic cod on ecosystem stability, aligning with Benoit et al. (2022), which demonstrated that top predator mortality has a stronger influence on community size structure than changes in smaller species. Conversely, *mizer* models also capture bottom-up effects. For example, Audzijonyte et al. (2023) found that increased plankton abundance positively affects fish biomass and yields. Thus, *mizer* models effectively illustrate the influence of both top-down and bottom-up controls, depending on the focus of the study.

As ecosystem approaches increasingly complement traditional single-species management frameworks (Link and Marshak, 2021; Pepin et al., 2022; Ruiz-Díaz, 2023), these models provide a comprehensive understanding of the broader impacts associated with targeting individual species within the ecosystem.

Limitations and future directions

The lack of comprehensive monitoring data for sand lance and capelin introduces uncertainty in their biomass estimates. In the case of sand lance, we had to rely on bottom trawl survey data, which have low catchability for this species (Tretyakov, 2015). For the capelin data, we used acoustic surveys that cover only part of the study area (the northern portion of the Banks), where most of the capelin is found (DFO, 2022a). Working with forage species can be challenging since their biomasses can be difficult to quantify due to large spatial variation and their strong population responses (i.e. changes in abundance and/or distribution) to environmental variability (Lewis et al., 2019). Future research should aim to address these limitations by incorporating more detailed and accurate data on forage species, which requires better monitoring. Additionally, my model predicted biomass for Atlantic cod, turbot and thorny skate higher than observed in the bottom-trawl survey, which may have implications on the model interpretation. While focusing on the recent post-collapse period is justified due to decreased productivity following the regime shift, it is important to recognize that excluding historical information may limit our understanding of potential changes in the ecosystem.

Bottom-up effects can be expected to be strongest in cases where a predator is a specialist relying to a great extent on the availability of the particular forage fish (Engelhard et al., 2014). In our model, we kept the predator-prey diet matrix relatively simple, based on presence and absence. Including information on the proportion of each prey in the diet would provide finer results, capturing these dependencies more accurately. This is an area where the model could be further improved. Moreover, our model does not consider changes in habitat, evolutionary changes, or Allee effects as a result of a drastic decline in species biomass (Hutchings and Reynolds, 2004).

Bottom-up studies in the region have explored how environmental conditions—such as temperature and the timing of the spring bloom—impact primary and secondary productivity, and how these effects scale up to forage fish and higher trophic levels. These studies have demonstrated that such environmental factors are important drivers of ecosystem dynamics (Cyr et al., 2024; Boyce et al., 2015). Our study focused exclusively on the direct effects of changes in forage fish biomass on the food web, without addressing the interactions between primary and secondary productivity. Hence, we could benefit from exploring how primary and secondary productivity drives bottom-up dynamics. The model could be further improved to account for the effect of climate change on the Grand Banks ecosystem, particularly associated with ocean warming -affecting species metabolic rates and predator-prey encounter- and changes in primary production (Reum et al., 2020; Woodworth-Jefcoats et al., 2019).

Finally, the inclusion of other apex predators like harp seals, which are known to be important predators of cod (Stenson, 2013), could help solve some of the questions regarding the lack of recovery of Atlantic cod and other groundfish species (Trzcinski et al., 2006; Chassot et al., 2009).

CHAPTER 6

General conclusions

Ecosystem-based fisheries management (EBFM) provides a framework for considering the broader ecological interactions and dependencies within marine ecosystems, aiming to maintain ecosystem function and structure. Unlike single-species fisheries management, which often focuses on individual species in isolation, EBFM accounts for the complex ecological systems in which fish exist. The severe consequences of overlooking ecosystem variability were evident in the Grand Banks and other regions of Atlantic Canada during the groundfish collapse, prompting initiatives like the Atlantic Zone Monitoring Program and other ecosystem-focused efforts by DFO since the late 1990s (Therriault et al., 1998). However, the recent collapse of the Bering Sea snow crab stock is a stark reminder that there is still work to be done to integrate ecosystem information into stock assessments. The sudden disappearance of 10 billion crabs was linked to neglected ecosystem factors: ocean warming reduced the cold pool, an essential refuge for young crabs from predation, and increased caloric intake led to mass starvation among the crabs (Szuwalski et al., 2023). Additionally, early warning signs, such as shifts in age and size at maturity, hinted at underlying issues within the population. Adopting an ecosystem-based approach enables us to better anticipate and address the risks associated with ecosystem changes, ultimately fostering more sustainable and resilient fisheries.

6.1 Implications for regional fisheries management

My research aims to advance EBFM of the Grand Banks of Newfoundland by exploring predator-prey dynamics, species habitat-preferences and response to ocean warming.

This thesis further proves that environmental variability and predator-prey interactions influence fish stock productivity and distribution. The Grand Banks ecosystem is influenced by a range of factors, including environmental variability (Cyr and Galbraith, 2021; Cyr et al., 2022), climate change (Gonçalves Neto et al., 2021; Saba et al., 2016), fishing pressure (Hutchings and Myers, 1994), and shifts in community structure (Pedersen et al., 2017; Dempsey et al., 2017; Koen-Alonso and Cuff, 2018). The historical analysis in Chapter 3 revealed the habitat preferences of snow crab, yellowtail flounder, and Atlantic cod concerning temperature and depth. Snow crab was found to be particularly sensitive to temperature, favouring waters close to 0 °C. Yellowtail flounder preferred temperatures around 3 °C while Atlantic cod favoured warmer waters, approximately 5 °C. Additionally, a northward shift in Atlantic cod biomass was observed over time, suggesting either a distributional shift or an increase in the northern stock's biomass. In contrast, the biomass centers of gravity for snow crab and yellowtail flounder remained relatively stable. Snow crab's sensitivity to temperature increases makes it particularly vulnerable to the future impacts of climate change in the region. Projections indicate a rise in bottom temperatures from 1.6 °C to 2.2 °C by the end of the century. An even more drastic scenario is expected under the IPSL climate model, which projects an increase in temperature of 5 °C. Climate change significantly affects fisheries productivity, with ocean warming already leading to a reduction in global fisheries production (Free et al., 2019). The projections for the Grand Banks in Chapter 4 suggest that ocean warming will decrease the biomass of snow crab while increasing the biomass of Atlantic cod under high emission scenarios. In the case of yellowtail flounder, declines in biomass were observed under the IPSL model, while GFDL and ACM revealed biomass increase. In contrast, under low-emission scenarios, species biomass tends to fluctuate around historical averages. The increase in Atlantic cod biomass, coupled with its strong predation pressure on snow crabs (Durant et al., 2023; Holt et al., 2021), will exacerbate the decline in snow crab populations. All these changes pose considerable challenges for the snow crab fishing sector in the long term.

The choice of climate model greatly influences the projected magnitude of changes in biomass. Earth system models predict larger biomass losses than regional oceanographic models, likely due to the misrepresentation of the cold intermediate layer caused by bathymetry biases in earth system models (Stock et al., 2011; Rutherford et al., 2024). This contrast highlights the importance of using regional oceanographic models over earth system models, when available, to achieve more accurate biomass projections. Despite differences in the magnitude of changes, all models agreed on the direction of these changes. The findings from Chapter 4 can inform the development of Climate-Resilient Fisheries Policies, which are designed to explicitly address the impacts of climate change and incorporate long-term environmental forecasts (Holsman et al., 2019). This approach can help anticipate and mitigate future challenges in the fishing industry through, for example, proactive adjustments of quotas, spatial closures, and gear restrictions (Pinsky and Mantua, 2014)

The spatio-temporal models used in Chapter 3 enabled the identification of species biomass hotspots and the calculation of environmentally informed biomass indices. This approach is currently being adopted by organizations such as DFO and NOAA for calculating standardized biomass indices (DFO, 2023b; Haggarty et al., 2021). The new spring biomass indices for snow crab, yellowtail flounder, and Atlantic cod in the 3LNO division could be used as inputs in future stock assessment models. These indices are particularly noteworthy for snow crab, as previous assessments focused only on fall data, and for Atlantic cod, which is managed as two separate stocks (2J3KL and 3NO). Hence, no index exists for the 3LNO division. Overall, the findings from Chapter 3 provide valuable insights about the stocks and can inform management and spatial conservation strategies.

6.2 Bottom-up vs top-down influences

The multispecies size spectrum model of Chapter 5 demonstrated that changes in the biomass of capelin, sand lance, and Atlantic cod causes shifts in biomass and mean body weight across both higher and lower trophic levels. Notably, these changes are more pronounced under the top-down scenario, highlighting the crucial role of Atlantic cod in maintaining the stability of the Grand Banks ecosystem. When Atlantic cod biomass declined more than 17%, a dramatic shift in the system occurred, with many prey species going functionally extinct. These findings indicate a stronger top-down control on the Grand Banks of Newfoundland than bottom-up control. However, it is important to note that the bottom-up effect was tested by altering the biomass of forage species rather than primary and secondary productivity, which has been shown to be important for the region in other studies (Buren et al., 2014; Cyr et al., 2024). Hence, it is likely that both processes play a role in controlling the system.

Regional-scale studies suggest that temperature, species diversity, and exploitation pressure all influence trophic control in marine ecosystems (Worm and Myers, 2003; Frank et al., 2006, 2007). Boyce et al. (2015) identified temperature as the most significant factor driving the spatial patterns of trophic control across marine ecosystems, both directly and indirectly, through its effects on primary production, biodiversity, and omnivory. Strong consumer control has been found in cold ecosystems, where temperatures are below 5 °C(Boyce et al., 2015). In these ecosystems, apex consumers limit the abundance of other consumers, and their removal can cause cascading effects down the food chain.

Ecosystems under top-down control are particularly vulnerable to fisheries exploitation compared to those regulated by bottom-up processes (Petrie et al., 2009). In the Grand Banks, the collapse of cod and other groundfish species in the early 1990s triggered cascading effects throughout the food web (Frank et al., 2005), with low recovery observed for many groundfish stocks despite the implementation of moratoria. While evidence suggests that reducing fishing pressure alone can lead to species recovery (Hilborn et al., 2020), the situation in the Grand Banks reveals a more complex reality. This system has undergone a restructuring of the community (Koen-Alonso and Cuff, 2018), altering predator-prey interactions. For example, increases in invertebrates and medium benthivores may lead to potential predation on or competition with the early life stages of cod (Hutchings and Rangeley, 2011). Moreover, alterations in species' life history traits, such as reduced age and size at maturity, have been documented in the region (DFO, 2022b; Murphy et al., 2021). These changes may increase natural mortality and reduce the ability of species to respond to environmental variability, making recovery more difficult even when fishing pressure is reduced (Planque et al., 2010; Hutchings and Rangeley, 2011). Therefore, understanding food web dynamics is crucial for developing effective management plans that ensure the sustainability of both target and non-target species.

6.3 Future research directions

The insights gained from understanding the impacts of climate change and predator-prey dynamics on the Grand Banks are essential for informing fisheries management strategies. This thesis also contributes to the promotion of EBFM implementation globally by synthesizing and outlining methods to integrate ecosystem information into current advisory practices (Chapter 2). Effective management requires an adaptive approach that incorporates ecological complexity and environmental variability to minimize negative impacts on the stocks (Gaines et al., 2018). Actions taken over the next decade can help us adapt to species redistributions and minimize negative impacts on fisheries and dependent communities, promoting a sustainable future (Free et al., 2020; Melbourne-Thomas et al., 2021). I suggest the following directions to move this thesis further, from strategic insights to tactical applications:

Precautionary approach Given the uncertainties associated with environmental variability, adopting a precautionary approach is prudent. This means erring on the side of caution in decision-making to prevent overexploitation and ensure the long-term health of marine ecosystems. My findings reveal that snow crab is particularly sensitive to increasing bottom temperature compared to yellowtail flounder and Atlantic cod. One way to implement this is by adding a precautionary buffer to biological reference points based on ecosystem conditions (Mildenberger et al., 2022). Additionally, the new biomass indices we developed can be utilized in stock assessments to better inform these reference points. Such measures will help safeguard against unforeseen adverse effects and support ecosystem resilience.

Dynamic management Fisheries management must be flexible and responsive to changing environmental conditions. This involves continuously updating management plans based on the latest scientific data and projections. Adaptive management allows for adjustments in fishing quotas, seasons, and protected areas to align with current ecosystem states (Pinsky and Mantua, 2014). In my thesis, I focused on the long-term effect of climate change on the target species. However, species distribution models (SDMs) can be used in a more tactical way. For example, they have been used with sub-seasonal environmental forecasts to facilitate dynamic spatial management, which can help identify optimal times and areas for fisheries to maximize target catch and avoid bycatch (Roberts et al., 2023).

Multispecies models for informed fisheries management Multispecies models offer a comprehensive approach to understanding the complex interactions within marine ecosystems, making them particularly necessary for fisheries management in situations where there are strong dependencies between predators and prey, as these interactions influence stocks productivity. In the Barents Sea, a multi-model approach improved understanding of trophic interactions between cod, capelin, polar cod and copepods under varying fishing pressures, helping managers predict how changes in prey stocks affect predator stocks like Atlantic cod (Nilsen et al., 2022). In practice, multispecies models could be used as the operational model in the management strategy evaluation, allowing the testing of different management strategies that are ecologically informed (Hollowed et al., 2020). They could also be used to refine single-species reference points with ecosystem information (Townsend et al., 2019; Howell et al., 2021).

The MIZER multispecies model developed in this thesis underscores the crucial role of Atlantic cod in maintaining ecosystem stability and the risks associated with their overexploitation. This model could be enhanced by incorporating seals into the system. Seals have been identified as a factor contributing to the slow recovery of Atlantic cod (Bundy, 2001). By adding seals to the model, we can better understand their effects on prey species and gain a clearer picture of the overall ecosystem dynamics. Additionally, the model can be re-calibrated with the therMIZER version, which accounts for the effect of temperature on species metabolism (Woodworth-Jefcoats et al., 2019; Reum et al., 2024). Warming accelerates species metabolism, increasing their intake requirements and thereby affecting community dynamics. Moreover, the size spectrum model could integrate primary productivity outputs from climate models to simulate ecosystem responses to future bottom-up processes (Reum et al., 2020; Rose et al., 2024).

6.4 Final remarks

Overall, this thesis advances ecosystem-based fisheries management by enhancing our understanding of predator-prey dynamics, species habitat preferences, and responses to ocean warming on the Grand Banks of Newfoundland. By examining the complex interactions within the entire ecosystem, my research provides compelling evidence that environmental variability and predator-prey relationships influence fish stock productivity and distribution. The projected impacts of climate change on the Grand Banks ecosystem present a complex scenario with significant implications for fisheries management. The potential decline in snow crab biomass and the increasing predation pressure from growing cod biomass underscore the need for a holistic approach to managing these species. The size spectrum model also indicates that rising Atlantic cod biomass will lead to a decline in large and medium benthivores, as well as piscivorous and plank-piscivorous species. However, given the strong top-down control detected in the Grand Banks, the reopening of the northern cod stock (2J3KL), which is currently just above the critical zone, could have unintended consequences for the food web. These findings reinforce the importance of incorporating ecosystem information into fisheries management decisions. Future research should focus on refining these models, integrating emerging data, and exploring innovative management strategies to address the ongoing challenges facing the Grand Banks of Newfoundland effectively.

Bibliography

Abad, E., Pennino, M. G., Valeiras, J., Vilela, R., Bellido, J. M., Punzón, A., and Velasco, F. (2020). Integrating spatial management measures into fisheries: The lepidorhombus spp. case study. *Marine Policy*, 116:103739. 53

Adams, C. F., Alade, L. A., Legault, C. M., O'Brien, L., Palmer, M. C., Sosebee, K. A., and Traver, M. L. (2018). Relative importance of population size, fishing pressure and temperature on the spatial distribution of nine northwest atlantic groundfish stocks. *PLoS One*, 13(4):e0196583. 49

Akaike, H. (1981). Likelihood of a model and information criteria. *Journal of econometrics*, 16(1):3–14. 38

Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D., and Gravel, D. (2014). From projected species distribution to food-web structure under climate change. *Global change biology*, 20(3):730–741. 83

Andersen, K. H. and Beyer, J. E. (2006). Asymptotic size determines species abundance in the marine size spectrum. *The American Naturalist*, 168(1):54–61. 91

Andersen, K. H., Jacobsen, N. S., and Farnsworth, K. D. (2016). The theoretical foundations for size spectrum models of fish communities. *Canadian Journal of Fisheries and Aquatic Sciences*, 73(4):575–588. 91, 93, 113

Andersen, K. H. and Pedersen, M. (2010). Damped trophic cascades driven by fishing in model marine ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 277(1682):795–802. 87

Anderson, S. C., Ward, E. J., English, P. A., and Barnett, L. A. (2022). sdmtmb: an r package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. *BioRxiv*, pages 2022–03. 36, 37, 38, 63, 65, 67

Armstrong, J. B., Fullerton, A. H., Jordan, C. E., Ebersole, J. L., Bellmore, J. R., Arismendi, I., Penaluna, B. E., and Reeves, G. H. (2021). The importance of warm habitat to the growth regime of cold-water fishes. *Nature Climate Change*, 11(4):354–361. 7

Audzijonyte, A., Delius, G. W., Stuart-Smith, R. D., Novaglio, C., Edgar, G. J., Barrett, N. S., and Blanchard, J. L. (2023). Changes in sea floor productivity are crucial to understanding the impact of climate change in temperate coastal ecosystems according to a new size-based model. *PLoS Biology*, 21(12):e3002392. 97, 113

Bakun, A., Babcock, E. A., Lluch-Cota, S. E., Santora, C., and Salvadeo, C. J. (2010). Issues of ecosystem-based management of forage fisheries in "open" non-stationary ecosystems: the example of the sardine fishery in the gulf of california. *Reviews in Fish Biology and Fisheries*, 20:9–29. 13

Balbi, S., del Prado, A., Gallejones, P., Geevan, C. P., Pardo, G., Pérez-Miñana, E., Manrique, R., Hernandez-Santiago, C., and Villa, F. (2015). Modeling trade-offs among ecosystem services in agricultural production systems. *Environmental Modelling & Software*, 72:314–326. 17

Barange, M., Bahri, T., Beveridge, M., Cochrane, K. L., Funge-Smith, S., Poulain, F., et al. (2018). Impacts of climate change on fisheries and aquaculture. *United Nations' Food and Agriculture Organization*, 12(4):628–635. 15

Barnett, L. A., Jacobsen, N. S., Thorson, J. T., and Cope, J. M. (2019). Realizing the potential of trait-based approaches to advance fisheries science. *Fish and Fisheries*, 20(5):1034–1050. 20, 28

Becker, E. A., Carretta, J. V., Forney, K. A., Barlow, J., Brodie, S., Hoopes, R., Jacox, M. G., Maxwell, S. M., Redfern, J. V., Sisson, N. B., et al. (2020). Performance evaluation of cetacean species distribution models developed using generalized additive models and boosted regression trees. *Ecology and evolution*, 10(12):5759–5784. 56

Bell, R. J., Grieve, B., Ribera, M., Manderson, J., and Richardson, D. (2022). Climate-induced habitat changes in commercial fish stocks. *ICES Journal of Marine Science*, 79(8):2247–2264. 7

Benoit, D. M., Chu, C., Giacomini, H. C., and Jackson, D. A. (2022). Size spectrum model reveals importance of considering species interactions in a freshwater fisheries management context. *Ecosphere*, 13(7):e4163. 97, 113

Bentley, J. W., Lundy, M. G., Howell, D., Beggs, S. E., Bundy, A., De Castro, F., Fox, C. J., Heymans, J. J., Lynam, C. P., Pedreschi, D., et al. (2021). Refining fisheries advice with stock-specific ecosystem information. *Frontiers in Marine Science*, 8:602072. 22

Berard, M. T. and Davoren, G. K. (2020). Capelin (mallotus villosus) availability influences the inshore summer diet of atlantic cod (gadus morhua) in coastal newfoundland. *Environmental Biology of Fishes*, 103(6):771–782. 110

Berkes, F. (2012). Implementing ecosystem-based management: Evolution or revolution? *Fish and Fisheries*, 13(4):465–476. 14

Blanchard, J. L., Andersen, K. H., Scott, F., Hintzen, N. T., Piet, G., and Jennings, S. (2014). Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model. *Journal of Applied Ecology*, 51(3):612–622. 97, 98

Blanchard, J. L., Heneghan, R. F., Everett, J. D., Trebilco, R., and Richardson, A. J. (2017). From bacteria to whales: using functional size spectra to model marine ecosystems. *Trends in ecology & evolution*, 32(3):174–186. 90

Boldt, J. L., Murphy, H. M., Chamberland, J.-M., Debertin, A., Gauthier, S., Hackett, B., Hagel, P. S., Majewski, A. R., McDermid, J. L., Merette, D., et al. (2022). Canada's forage fish: an important but poorly understood component of marine ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, 79(11):1911–1933. 88

Boucher, O., Servonnat, J., Albright, A. L., Aumont, O., Balkanski, Y., Bastrikov, V., Bekki, S., Bonnet, R., Bony, S., Bopp, L., et al. (2020). Presentation and evaluation of the ipsl-cm6a-lr climate model. *Journal of Advances in Modeling Earth Systems*, 12(7):e2019MS002010. 59, 61, 63

Boudreau, S. A., Anderson, S. C., and Worm, B. (2011). Top-down interactions and temperature control of snow crab abundance in the northwest atlantic ocean. *Marine Ecology Progress Series*, 429:169–183. 110

Boyce, D. G., Frank, K. T., Worm, B., and Leggett, W. C. (2015). Spatial patterns and predictors of trophic control in marine ecosystems. *Ecology Letters*, 18(10):1001–1011. 114, 120

Briton, F., Shannon, L., Barrier, N., Verley, P., and Shin, Y.-J. (2019). Reference levels of ecosystem indicators at multispecies maximum sustainable yield. *ICES Journal of Marine Science*, 76(7):2070–2081. 16

Britten, G., Dowd, M., Kanary, L., and Worm, B. (2017). Extended fisheries recovery timelines in a changing environment. *Nature communications*, 8:15325. 13, 15

Brodie, S., Smith, J. A., Muhling, B. A., Barnett, L. A., Carroll, G., Fiedler, P., Bograd, S. J., Hazen, E. L., Jacox, M. G., Andrews, K. S., et al. (2022). Recommendations for quantifying and reducing uncertainty in climate projections of species distributions. *Global change biology*, 28(22):6586–6601. 68, 81

Brodie, W. and Stansbury, D. (2007). A brief description of Canadian Multispecies Survey in SA2+ Divisions 3KLMNO from 1995–2006. Technical report, Northwest Atlantic Fisheries Organization. NAFO SCR 2007 Doc. 07/18. 33, 47, 60, 89, 94

Brodie, W. B., Walsh, S. J., and Maddock Parsons, D. (2010). An evaluation of the collapse and recovery of the yellowtail flounder (limanda ferruginea) stock on the grand bank. *ICES Journal of Marine Science*, 67(9):1887–1895. 49, 51, 58, 79

Bryndum-Buchholz, A., Tittensor, D. P., and Lotze, H. K. (2021). The status of climate change adaptation in fisheries management: Policy, legislation and implementation. *Fish and Fisheries*, 22(6):1248–1273. 20, 27

Bundy, A. (2001). Fishing on ecosystems: the interplay of fishing and predation in newfoundland labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(6):1153–1167. 86, 111, 123

Bundy, A., Lilly, G. R., and Shelton, P. A. (2000). A mass balance model of the Newfoundland-Labrador Shelf. Technical report, Fisheries and Oceans Canada. Can. Tech. Rep. Fish. Aquat. Sci. 2310:xiv + 157 p. 88, 95

Buren, A. D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Ollerhead, N., and Montevecchi, W. A. (2014). Bottom-up regulation of capelin, a keystone forage species. *PLoS One*, 9(2):e87589. 86, 89, 109, 120

Buren, A. D., Murphy, H. M., Adamack, A. T., Davoren, G. K., Koen-Alonso, M., Montevecchi, W. A., Mowbray, F. K., Pepin, P., Regular, P. M., Robert, D., et al. (2019). The collapse and continued low productivity of a keystone forage fish species. *Marine Ecology Progress Series*, 616:155–170. 89

Burgess, M. G., Costello, C., Fredston-Hermann, A., Pinsky, M. L., Gaines, S. D., Tilman, D., and Polasky, S. (2017). Range contraction enables harvesting to extinction. *Proceedings of the National Academy of Sciences*, 114(15):3945–3950. 50

Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference. A practical information-theoretic approach.* Springer, New York, NY. 66

Burnham, K. P. and Anderson, D. R. (2004). Multimodel inference: understanding aic and bic in model selection. *Sociological methods & research*, 33(2):261–304. 38

Cadigan, N., Rideout, R., and Regular, P.M., . (2022a). A state-space assessment model for 3NO cod. Technical report, Northwest Atlantic Fisheries Organization. NAFO SRC Doc. 22/039. 6

Cadigan, N. G., Duplisea, D. E., Senay, C., Parent, G. J., Winger, P. D., Linton, B., and Kristinsson, K. (2022b). Northwest atlantic redfish science priorities for managing an enigmatic species complex. *Canadian Journal of Fisheries and Aquatic Sciences*, 79(9):1572–1589. 111

Cao, J., Thorson, J. T., Richards, R. A., and Chen, Y. (2017). Spatiotemporal index standardization improves the stock assessment of northern shrimp in the gulf of maine. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(11):1781–1793. 48

Casini, M., Lövgren, J., Hjelm, J., Cardinale, M., Molinero, J.-C., and Kornilovs, G. (2008). Multi-level trophic cascades in a heavily exploited open marine ecosystem. *Proceedings of the Royal Society B: Biological Sciences*, 275(1644):1793–1801. 112

Chassot, E., Duplisea, D., Hammill, M., Caskenette, A., Bousquet, N., Lambert, Y., and Stenson, G. (2009). Role of predation by harp seals pagophilus groenlandicus in the collapse and non-recovery of northern gulf of st. lawrence cod gadus morhua. *Marine Ecology Progress Series*, 379:279–297. 115

Cheung, W. W., Jones, M. C., Reygondeau, G., Stock, C. A., Lam, V. W., and Frölicher, T. L. (2016). Structural uncertainty in projecting global fisheries catches under climate change. *Ecological Modelling*, 325:57–66. 56

Christie, P., Bennett, N. J., Gray, N. J., Wilhelm, T., Lewis, N., Parks, J., Ban, N. C., Gruby, R. L., Gordon, L., Day, J., et al. (2017). Why people matter in ocean governance: Incorporating human dimensions into large-scale marine protected areas. *Marine Policy*, 84:273–284. 24

Clark, J. S., Gelfand, A. E., Woodall, C. W., and Zhu, K. (2014). More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications*, 24(5):990–999. 53

Clayton, D. G., Bernardinelli, L., and Montomoli, C. (1993). Spatial correlation in ecological analysis. *International journal of epidemiology*, 22(6):1193–1202. 49, 83

Colbourne, E. and Walsh, S. (2006). The Distribution and Abundance of Yellowtail Flounder (Limanda ferruginea) in Relation to Bottom Temperatures in NAFO Divisions 3LNO Based on Multi-Species Surveys from 1990–2005. Technical report, Northwest Atlantic Fisheries Organization. NAFO SCR 2006 Doc. 06/23. 34, 76

Coll, M., Shannon, L., Kleisner, K. M., Juan-Jordá, M. J., Bundy, A., Akoglu, A., Banaru, D., Boldt, J. L., Borges, M., Cook, A., et al. (2016). Ecological indicators to capture the effects of fishing on biodiversity and conservation status of marine ecosystems. *Ecological Indicators*, 60:947–962. 16

Collie, J. S., Botsford, L. W., Hastings, A., Kaplan, I. C., Largier, J. L., Livingston, P. A., Plagányi, É., Rose, K. A., Wells, B. K., and Werner, F. E. (2016). Ecosystem models for fisheries management: finding the sweet spot. *Fish and Fisheries*, 17(1):101–125. 18

Commander, C. J., Barnett, L. A., Ward, E. J., Anderson, S. C., and Essington, T. E. (2022). The shadow model: how and why small choices in spatially explicit species distribution models affect predictions. *PeerJ*, 10:e12783. 49

Cote, D., Konecny, C. A., Seiden, J., Hauser, T., Kristiansen, T., and Laurel, B. J. (2021). Forecasted shifts in thermal habitat for cod species in the northwest atlantic and eastern canadian arctic. *Frontiers in Marine Science*, 8:764072. 80

Cressie, N. and Wikle, C. (2015). *Statistics for Spatio-Temporal Data*. John Wiley & Sons. 31

Crook, K. A., Maxner, E., and Davoren, G. K. (2017). Temperature-based spawning habitat selection by capelin (mallotus villosus) in newfoundland. *ICES Journal of Marine Science*, 74(6):1622–1629. 87

Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J., Furness, R. W., Mills, J. A., Murphy, E. J., Österblom, H., Paleczny, M., et al. (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science*, 334(6063):1703–1706. 86

Cvitanovic, C., Hobday, A. J., van Kerkhoff, L., Wilson, S. K., Dobbs, K., and Marshall, N. A. (2015). Improving knowledge exchange among scientists and decision-makers to facilitate the adaptive governance of marine resources: a review of knowledge and research needs. *Ocean & Coastal Management*, 112:25–35. 24

Cyr, F. and Galbraith, P. (2021). A climate index for the newfoundland and labrador shelf. *Earth System Science Data, 13*, 13:1807–1828. xxi, 2, 4, 57, 82, 87, 118

Cyr, F., Lewis, K., Bélanger, D., Regular, P., Clay, S., and Devred, E. (2024). Physical controls and ecological implications of the timing of the spring phytoplankton bloom on the newfoundland and labrador shelf. *Limnology and Oceanography Letters*, 9(3):191–198. 1, 86, 87, 114, 120

Cyr, F., Snook, S., Bishop, C.and Galbraith, P., Chen, N., and Han, G. (2022). Physical Oceanographic Conditions on the Newfoundland and Labrador Shelf during 2021. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Res. 2022 Doc. 2022/040. 2, 35, 49, 57, 61, 118

Dahood, A., Klein, E. S., and Watters, G. M. (2020). Planning for success: leveraging two ecosystem models to support development of an antarctic marine protected area. *Marine Policy*, 121:104109. 25

Dalley, E. and Winters, G. (1987). Early life history of sand lance(ammodytes), with evidence for spawning of a. dubius in fortune bay, newfoundland. *Fishery Bulletin*, 85(3):631–641. 88

Daskalov, G. M., Grishin, A. N., Rodionov, S., and Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences*, 104(25):10518–10523. 112

Dawe, E., Parsons, D., and Colbourne, E. (2008). Relationships of sea ice extent and bottom water temperature with abundance of snow crab (Chionoecetes opilio) on the Newfoundland—Labrador Shelf. Technical report, ICES CM (2008): B02. 49

Dawe, E. G., Walsh, S. J., and Hynick, E. M. (2010). Capture efficiency of a multispecies survey trawl for snow crab (chionoecetes opilio) in the newfoundland region. *Fisheries Research*, 101(1-2):70–79. 38, 48, 94

De Roos, A. M., Schellekens, T., Van Kooten, T., Van De Wolfshaar, K., Claessen, D., and Persson, L. (2008). Simplifying a physiologically structured population model to a stage-structured biomass model. *Theoretical population biology*, 73(1):47–62. 92

Delius, G., Scott, F., Blanchard, J., and Andersen, K. (2023). mizer: Dynamic multi-species size spectrum modelling. r package version 2.5.0. 94

Dempsey, D., Koen-Alonso, M., Gentleman, W., and Pepin, P. (2017). Compilation and discussion of driver, pressure, and state indicators for the grand bank ecosystem, northwest atlantic. *Ecological Indicators*, 75:331–339. 5, 32, 58, 89, 112, 118

Denit, K. (2016). Noaa fisheries ecosystem-based fisheries management road map. Technical report, NMFS policy directive 01–120-01. National Oceanic and Atmospheric Administration. 21

DFO (2006). A Harvest Strategy Compliant with the Precautionary Approach. Technical report, Fisheries and Oceans Canada. Can. Sci. Advis. Sec. Sci. Advis. Rep. 2006/023. 50

DFO (2007a). Canada's Oceans State. A description of Canada's maritime zones. Technical report, Fisheries and Oceans Canada. DF0/2007-1199. 5

DFO (2007b). The Grand Banks of Newfoundland: Atlas of Human Activities. DFO/2007-1238. Technical report, Fisheries and Oceans Canada, Newfoundland and Labrador Region. 1, 87

DFO (2019). Groundfish Newfoundland and Labrador Region NAFO Subarea 2 + Divisions 3KLMNO. Technical report, Fisheries and Oceans Canada. 5, 40

DFO (2022a). Assessment of 2J3KL Capelin in 2020. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2022/013. 6, 87, 94, 113

DFO (2022b). Stock assessment of Northern cod (NAFO Divisions 2J3KL) in 2021. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2022/041. 6, 51, 58, 88, 89, 121

DFO (2023a). Assessment of Newfoundland and Labrador (Divisions 2HJ3KLNOP4R) Snow Crab in 2022. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2023/044. 6, 36, 39

DFO (2023b). Assessment of Northern Shrimp (Pandalus borealis) and Striped Shrimp (Pandalus montagui) in the Eastern and Western Assessment Zones. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2023/013. 48, 119

DFO (2024). 2J3KL Northern cod fishery management approach. Technical report, Fisheries and Oceans Canada. 89

Dichmont, C. M., Ellis, N., Bustamante, R. H., Deng, R., Tickell, S., Pascual, R., Lozano-Montes, H., and Griffiths, S. (2013). Editor's choice: Evaluating marine spatial closures with conflicting fisheries and conservation objectives. *Journal of Applied Ecology*, 50(4):1060–1070. 22

Dichmont, C. M., Fulton, E. A., Gorton, R., Sporcic, M., Little, L. R., Punt, A. E., Dowling, N., Haddon, M., Klaer, N., and Smith, D. C. (2017). From data rich to data-limited harvest strategies—does more data mean better management? *ICES Journal of Marine Science*, 74(3):670–686. 22

Dionne, M., Sainte-Marie, B., Bourget, E., and Gilbert, D. (2003). Distribution and habitat selection of early benthic stages of snow crab chionoecetes opilio. *Marine Ecology Progress Series*, 259:117–128. 79

Drenkard, E. J., Stock, C., Ross, A. C., Dixon, K. W., Adcroft, A., Alexander, M., Balaji, V., Bograd, S. J., Butenschön, M., Cheng, W., et al. (2021). Next-generation regional ocean projections for living marine resource management in a changing climate. *ICES Journal of Marine Science*, 78(6):1969–1987. 56

Drinkwater, K. F. (2005). The response of atlantic cod (gadus morhua) to future climate change. *Ices journal of marine science*, 62(7):1327–1337. 34, 58, 76

Dunne, J. P., Horowitz, L., Adcroft, A., Ginoux, P., Held, I., John, J., Krasting, J. P., Malyshev, S., Naik, V., Paulot, F., et al. (2020). The gfdl earth system model version 4.1 (gfdl-esm 4.1): Overall coupled model description and simulation characteristics. *Journal of Advances in Modeling Earth Systems*, 12(11):e2019MS002015. 59, 61, 63

Duplisea, D. E., Roux, M.-J., Hunter, K. L., and Rice, J. (2021). Fish harvesting advice under climate change: A risk-equivalent empirical approach. *PLoS One*, 16(2):e0239503. 23, 27

Durant, J. M., Holt, R. E., Ono, K., and Langangen, Ø. (2023). Predatory walls may impair climate warming-associated population expansion. *Ecology*, 104:e4130. 52, 110, 119

Eddy, T. D., Bernhardt, J. R., Blanchard, J. L., Cheung, W. W., Colléter, M., Du Pontavice, H., Fulton, E. A., Gascuel, D., Kearney, K. A., Petrik, C. M., et al. (2021). Energy flow through marine ecosystems: confronting transfer efficiency. *Trends in Ecology & Evolution*, 36(1):76–86. 86

Ellingsen, K. E., Anderson, M. J., Shackell, N. L., Tveraa, T., Yoccoz, N. G., and Frank, K. T. (2015). The role of a dominant predator in shaping biodiversity over space and time in a marine ecosystem. *Journal of Animal Ecology*, 84(5):1242–1252. 86

Engelhard, G. H., Peck, M. A., Rindorf, A., C. Smout, S., Van Deurs, M., Raab, K., Andersen, K. H., Garthe, S., Lauerburg, R. A., Scott, F., et al. (2014). Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine Science*, 71(1):90–104. 114

Essington, T. E. and Punt, A. E. (2011). Implementing ecosystem-based fisheries management: Advances, challenges and emerging tools. *Aquaculture, Fish and Fisheries*, 12(2):123–124. 14

EU (2008). Directive 2008/56/ec of the european parliament and of the council. *Official Journal of the European Union*. 21

FAO (2020). *The state of world fisheries and aquaculture 2020: Sustainability in action*. Food and Agriculture Organization of the United Nations. 12

Fernandes, J. A., Cheung, W. W., Jennings, S., Butenschön, M., de Mora, L., Frölicher, T. L., Barange, M., and Grant, A. (2013). Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic bioclimate envelope model. *Global change biology*, 19(8):2596–2607. 56

Figge, F. (2004). Bio-folio: applying portfolio theory to biodiversity. *Biodiversity & Conservation*, 13:827–849. 109

Fisheries Act (1985). Fisheries act (cf-14). government of canada. 6

Florko, K. R., Tai, T. C., Cheung, W. W., Ferguson, S. H., Sumaila, U. R., Yurkowski, D. J., and Auger-Méthé, M. (2021). Predicting how climate change threatens the prey base of arctic marine predators. *Ecology Letters*, 24(12):2563–2575. 56

Fogarty, M., Incze, L., Hayhoe, K., Mountain, D., and Manning, J. (2008). Potential climate change impacts on atlantic cod (gadus morhua) off the northeastern usa. *Mitigation and Adaptation Strategies for Global Change*, 13:453–466. 80

Fogarty, M. J. (2014). The art of ecosystem-based fishery management. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(3):479–490. 26

Fogarty, M. J., Rosenberg, A. A., Cooper, A. B., Dickey-Collas, M., Fulton, E. A., Gutiérrez, N. L., Hyde, K. J., Kleisner, K. M., Kristiansen, T., Longo, C., et al. (2016). Fishery production potential of large marine ecosystems: A prototype analysis. *Environmental development*, 17:211–219. 16

Forestier, R., Blanchard, J. L., Nash, K. L., Fulton, E. A., Johnson, C., and Audzijonyte, A. (2020). Interacting forces of predation and fishing affect species' maturation size. *Ecology and Evolution*, 10(24):14033–14051. 20, 28

Foyle, T. P., O'Dor, R. K., and Elner, R. W. (1989). Energetically defining the thermal limits of the snow crab. *Journal of Experimental Biology*, 145(1):371–393. 79

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. (2005). Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308(5728):1621–1623. 86, 87, 111, 112, 121

Frank, K. T., Petrie, B., and Shackell, N. L. (2007). The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology & Evolution*, 22(5):236–242. 86, 112, 120

Frank, K. T., Petrie, B., Shackell, N. L., and Choi, J. S. (2006). Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecology Letters*, 9(10):1096–1105. 86, 112, 120

Free, C. M., Mangin, T., Molinos, J. G., Ojea, E., Burden, M., Costello, C., and Gaines, S. D. (2020). Realistic fisheries management reforms could mitigate the impacts of climate change in most countries. *PloS one*, 15(3):e0224347. 122

Free, C. M., Thorson, J. T., Pinsky, M. L., Oken, K. L., Wiedenmann, J., and Jensen, O. P. (2019). Impacts of historical warming on marine fisheries production. *Science*, 363(6430):979–983. 118

Friedland, K. D., Smoliński, S., and Tanaka, K. R. (2021). Contrasting patterns in the occurrence and biomass centers of gravity among fish and macroinvertebrates in a continental shelf ecosystem. *Ecology and Evolution*, 11(5):2050–2063. 49

Froese, R. and Pauly, D. (2024). Fishbase. world wide web electronic publication. version (06/2024). 94

Fulton, E. and Gorton, R. (2014). Adaptive futures for se australian fisheries & aquaculture: climate adaptation simulations. *Australia: CSIRO*. 20, 22

Fulton, E. A. (2021). Opportunities to improve ecosystem-based fisheries management by recognizing and overcoming path dependency and cognitive bias. *Fish and Fisheries*, 22(2):428–448. 23, 25

Fulton, E. A., Punt, A. E., Dichmont, C. M., Harvey, C. J., and Gorton, R. (2019). Ecosystems say good management pays off. *Fish and Fisheries*, 20(1):66–96. 22

Fulton, E. A., Smith, A. D., and Punt, A. E. (2005). Which ecological indicators can robustly detect effects of fishing? *ICES Journal of Marine Science*, 62(3):540–551. 16

Fulton, E. A., Smith, A. D., Smith, D. C., and Johnson, P. (2014). An integrated approach is needed for ecosystem based fisheries management: insights from ecosystem-level management strategy evaluation. *PloS one*, 9(1):e84242. 18, 26, 27

Gaines, S. D., Costello, C., Owashi, B., Mangin, T., Bone, J., Molinos, J. G., Burden, M., Dennis, H., Halpern, B. S., Kappel, C. V., et al. (2018). Improved fisheries management could offset many negative effects of climate change. *Science advances*, 4(8):eaao1378. 122

Garcia-Suarez, L., Fennel, K., and John, J. G. (2023). Physical drivers and biogeochemical effects of the projected decline of the shelfbreak jet in the northwest north atlantic ocean. *Authorea Preprints*. 2, 57, 59, 82

Geary, W. L., Bode, M., Doherty, T. S., Fulton, E. A., Nimmo, D. G., Tulloch, A. I., Tulloch, V. J., and Ritchie, E. G. (2020). A guide to ecosystem models and their environmental applications. *Nature Ecology & Evolution*, 4(11):1459–1471. 7, 18, 25, 27

Gjøsæter, H., Bogstad, B., and Tjelmeland, S. (2009). Ecosystem effects of the three capelin stock collapses in the barents sea. *Marine biology research*, 5(1):40–53. 86

Gonçalves Neto, A., Langan, J. A., and Palter, J. B. (2021). Changes in the gulf stream preceded rapid warming of the northwest atlantic shelf. *Communications Earth & Environment*, 2(1):74. 2, 49, 50, 118

Gonzalez, C., Paz, X., Roman, E., and Hermida, M. (2006). Feeding habits of fish species distributed on the Grand Banks (NAFO Divisions 3NO, 2002-2005. Technical report, Northwest Atlantic Fisheries Organization. 88, 95, 109, 111

Grüss, A., Rose, K. A., Simons, J., Ainsworth, C. H., Babcock, E. A., Chagaris, D. D., De Mutsert, K., Froeschke, J., Himchak, P., Kaplan, I. C., et al. (2017). Recommendations on the use of ecosystem modeling for informing ecosystem-based fisheries management and restoration outcomes in the gulf of mexico. *Marine and Coastal Fisheries*, 9(1):281–295. 17

Grüss, A. and Thorson, J. T. (2019). Developing spatio-temporal models using multiple data types for evaluating population trends and habitat usage. *ICES Journal of Marine Science*, 76(6):1748–1761. 31, 53

Haggarty, D., Huynh, Q., Forrest, R., Anderson, S.C.and Bresch, M., and Keppel, E. (2021). Evaluation of potential rebuilding strategies for Inside Yelloweye Rockfish (Sebastes ruberrimus) in British Columbia. Technical report, Fisheries and Oceans Canada. 48, 119

Haidvogel, D. B., Arango, H., Budgell, W. P., Cornuelle, B. D., Curchitser, E., Di Lorenzo, E., Fennel, K., Geyer, W. R., Hermann, A. J., Lanerolle, L., et al. (2008). Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the regional ocean modeling system. *Journal of computational physics*, 227(7):3595–3624. 61

Hall, S. J. and Mainprize, B. (2004). Towards ecosystem-based fisheries management. *Fish and Fisheries*, 5(1):1–20. 15

Han, G., Lu, Z., Wang, Z., Helbig, J., Chen, N., and De Young, B. (2008). Seasonal variability of the labrador current and shelf circulation off newfoundland. *Journal of Geophysical Research: Oceans*, 113(C10). 1, 31

Han, G., Ma, Z., deYoung, B., Foreman, M., and Chen, N. (2011). Simulation of three-dimensional circulation and hydrography over the grand banks of newfoundland. *Ocean Modelling*, 40(3-4):199–210. 31

Hartvig, M., Andersen, K. H., and Beyer, J. E. (2011). Food web framework for size-structured populations. *Journal of theoretical Biology*, 272(1):113–122. 91, 95

Harvey, E., Gounand, I., Ward, C. L., and Altermatt, F. (2017). Bridging ecology and conservation: from ecological networks to ecosystem function. *Journal of Applied Ecology*, 54(2):371–379. 21

Hilborn, R. (2011). Future directions in ecosystem based fisheries management: A personal perspective. *Fisheries Research*, 108(2-3):235–239. 7, 13

Hilborn, R., Amoroso, R. O., Anderson, C. M., Baum, J. K., Branch, T. A., Costello, C., De Moor, C. L., Faraj, A., Hively, D., Jensen, O. P., et al. (2020). Effective fisheries management instrumental in improving fish stock status. *Proceedings of the National Academy of Sciences*, 117(4):2218–2224. 7, 121

Hilborn, R. and Walters, C. J. (2013). *Quantitative fisheries stock assessment: choice, dynamics and uncertainty.* Springer Science & Business Media. 12

Hill, K. T., Crone, P. R., and Zwolinski, J. P. (2017). Assessment of the pacific sardine resource in 2017 for usa management in 2017-18. Technical report, National Oceanic and Atmospheric Administration. 23, 27

Hollowed, A. (1992). Spatial and temporal distributions of pacific hake, merluccius productus, larvae and estimates of survival during early life stages. *Calif. Coop. Oceanic Fish. Invest. Rep 33: 100–123.* 39

Hollowed, A. B., Barange, M., Beamish, R. J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M. G., Hare, J. A., Holt, J., Ito, S.-i., et al. (2013). Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science*, 70(5):1023–1037. 7

Hollowed, A. B., Holsman, K. K., Haynie, A. C., Hermann, A. J., Punt, A. E., Aydin, K., Ianelli, J. N., Kasperski, S., Cheng, W., Faig, A., et al. (2020). Integrated modeling to evaluate climate change impacts on coupled social-ecological systems in alaska. *Frontiers in Marine Science*, 6:775. 123

Holsman, K., Haynie, A., Hollowed, A., Reum, J., Aydin, K., Hermann, A., Cheng, W., Faig, A., Ianelli, J., Kearney, K., et al. (2020). Ecosystem-based fisheries management forestalls climate-driven collapse. *Nature communications*, 11:4579. 17

Holsman, K. K., Hazen, E. L., Haynie, A., Gourguet, S., Hollowed, A., Bograd, S. J., Samhouri, J. F., and Aydin, K. (2019). Towards climate resiliency in fisheries management. *ICES Journal of Marine Science*, 76(5):1368–1378. 119

Holt, R. E., Hvingel, C., Agnalt, A.-L., Dolgov, A. V., Hjelset, A. M., and Bogstad, B. (2021). Snow crab (chionoecetes opilio), a new food item for north-east arctic cod (gadus morhua) in the barents sea. *ICES Journal of Marine Science*, 78(2):491–501. 52, 110, 119

Hornborg, S., van Putten, I., Novaglio, C., Fulton, E. A., Blanchard, J. L., Plagányi, É., Bulman, C., and Sainsbury, K. (2019). Ecosystem-based fisheries management requires broader performance indicators for the human dimension. *Marine Policy*, 108:103639. 26

Hoskins, A. J., Harwood, T. D., Ware, C., Williams, K. J., Perry, J. J., Ota, N., Croft, J. R., Yeates, D. K., Jetz, W., Golebiewski, M., et al. (2020). Bilbi: Supporting global biodiversity assessment through high-resolution macroecological modelling. *Environmental Modelling & Software*, 132:104806. 21

Howell, D., Schueller, A. M., Bentley, J. W., Buchheister, A., Chagaris, D., Cieri, M., Drew, K., Lundy, M. G., Pedreschi, D., Reid, D. G., et al. (2021). Combining ecosystem and single-species modeling to provide ecosystem-based fisheries management advice within current management systems. *Frontiers in Marine Science*, 7:607831. 18, 22, 23, 27, 123

Hutchings, J. A. and Myers, R. A. (1994). What can be learned from the collapse of a renewable resource? atlantic cod, gadus morhua, of newfoundland and labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(9):2126–2146. 118

Hutchings, J. A. and Rangeley, R. W. (2011). Correlates of recovery for canadian atlantic cod (gadus morhua). *Canadian Journal of Zoology*, 89(5):386–400. 121

Hutchings, J. A. and Reynolds, J. D. (2004). Marine fish population collapses: consequences for recovery and extinction risk. *BioScience*, 54(4):297–309. 114

ICES (2021). Technical guidelines-ices ecosystem overviews. Technical report, ICES Advice 2021, Section 16.2. 13, 15, 21

IPCC (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, volume In Press. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 56, 57

Iwamoto, M., Dorton, J., Newton, J., Yerta, M., Gibeaut, J., Shyka, T., Kirkpatrick, B., and Currier, R. (2019). Meeting regional, coastal and ocean user needs with tailored data products: A stakeholder-driven process. *Frontiers in Marine Science*, 6:290. 24

Izquierdo, F., Paradinas, I., Cerviño, S., Conesa, D., Alonso-Fernández, A., Velasco, F., Preciado, I., Punzón, A., Saborido-Rey, F., and Pennino, M. G. (2021). Spatio-temporal assessment of the european hake (merluccius merluccius) recruits in the northern iberian peninsula. *Frontiers in Marine Science*, 8:614675. 47

Jacobsen, N. S., Burgess, M. G., and Andersen, K. H. (2017). Efficiency of fisheries is increasing at the ecosystem level. *Fish and Fisheries*, 18(2):199–211. 95

Jutras, M., Dufour, C., Mucci, A., Cyr, F., and Gilbert, D. (2020). Temporal changes in the causes of the observed oxygen decline in the st. lawrence estuary. *Journal of Geophysical Research: Oceans*, 125(12):e2020JC016577. 2, 57

Kaiser, M., Williams, P. l., Jennings, S., Thomas, D., and Barnes, D. (2011). *Marine Ecology: Processes, Systems, and Impacts*. OUP Oxford. 1, 51

Kaplan, I. C., Francis, T. B., Punt, A. E., Koehn, L. E., Curchitser, E., Hurtado-Ferro, F., Johnson, K. F., Lluch-Cota, S. E., Sydeman, W. J., Essington, T. E., et al. (2019). A multi-model approach to understanding the role of pacific sardine in the california current food web. *Marine Ecology Progress Series*, 617:307–321. 21, 25

Kaplan, I. C., Gaichas, S. K., Stawitz, C. C., Lynch, P. D., Marshall, K. N., Deroba, J. J., Masi, M., Brodziak, J. K., Aydin, K. Y., Holsman, K., et al. (2021). Management strategy evaluation: allowing the light on the hill to illuminate more than one species. *Frontiers in Marine Science*, 8:624355. 26

Karnauskas, M., Walter III, J. F., Kelble, C. R., McPherson, M., Sagarese, S. R., Craig, J. K., Rios, A., Harford, W. J., Regan, S., Giordano, S. D., et al. (2021). To ebfm or not to ebfm? that is not the question. *Fish and Fisheries*, 22(3):646–651. 12

Kasperski, S., DePiper, G. S., Haynie, A. C., Blake, S., Colburn, L. L., Freitag, A., Jepson, M., Karnauskas, M., Leong, K. M., Lipton, D., et al. (2021). Assessing the state of coupled social-ecological modeling in support of ecosystem based fisheries management in the united states. *Frontiers in Marine Science*, 8:631400. 18, 25, 27

Kearney, K. A., Bograd, S. J., Drenkard, E., Gomez, F. A., Haltuch, M., Hermann, A. J., Jacox, M. G., Kaplan, I. C., Koenigstein, S., Luo, J. Y., et al. (2021). Using global-scale earth system models for regional fisheries applications. *Frontiers in Marine Science*, 8:622206. 56

Kerr, L. A., Cadrin, S. X., and Kovach, A. I. (2014). Consequences of a mismatch between biological and management units on our perception of atlantic cod off new england. *ICES Journal of Marine Science*, 71(6):1366–1381. 50

Kiørboe, T., Visser, A., and Andersen, K. H. (2018). A trait-based approach to ocean ecology. *ICES Journal of Marine Science*, 75(6):1849–1863. 20

Kirk, E. A., Reeves, A. D., and Blackstock, K. L. (2007). Path dependency and the implementation of environmental regulation. *Environment and Planning C: Government and Policy*, 25(2):250–268. 23

Knapman, P., Cook, R., and Blyth-Skyrme, R. (2020). OCI Grand Bank Yellowtail Flounder Trawl: Public Comment Draft Report June 2020. Technical report, Marine Stewardship Council. 32, 58

Koen-Alonso, M. and Cuff, A. (2018). Status and trends of the fish community in the Newfoundland Shelf (NAFO Div. 2J3K), Grand Bank (NAFO Div. 3LNO) and Southern Newfoundland Shelf (NAFO Div. 3Ps) Ecosystem Production Units. Technical report, Northwest Atlantic Fisheries Organization. 2, 31, 32, 89, 112, 118, 121

Koen-Alonso, M., Lindstrøm, U., and Cuff, A. (2021). Comparative modeling of cod-capelin dynamics in the newfoundland-labrador shelves and barents sea ecosystems. *Frontiers in Marine Science*, 8:579946. 109, 110

Koen-Alonso, M., Pepin, P., Fogarty, M. J., Kenny, A., and Kenchington, E. (2019). The northwest atlantic fisheries organization roadmap for the development and implementation of an ecosystem approach to fisheries: structure, state of development, and challenges. *Marine Policy*, 100:342–352. 21, 57

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. (2015). Tmb: automatic differentiation and laplace approximation. *arXiv preprint arXiv:1509.00660*. 63

Laman, E. A., Rooper, C. N., Turner, K., Rooney, S., Cooper, D. W., and Zimmermann, M. (2018). Using species distribution models to describe essential fish habitat in alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(8):1230–1255. 53

Laurent, A., Fennel, K., and Kuhn, A. (2021). An observation-based evaluation and ranking of historical earth system model simulations in the northwest north atlantic ocean. *Biogeosciences*, 18(5):1803–1822. 59, 61, 63

Lawler, J. J., Wiersma, Y. F., and Huettmann, F. (2010). Using species distribution models for conservation planning and ecological forecasting. In *Predictive species and habitat modeling in landscape ecology: Concepts and applications*, pages 271–290. Springer. 53

Laxton, M. R., Rodríguez de Rivera, Ó., Soriano-Redondo, A., and Illian, J. B. (2023). Balancing structural complexity with ecological insight in spatio-temporal species distribution models. *Methods in Ecology and Evolution*, 14(1):162–172. 83

Leach, K., Montgomery, W. I., and Reid, N. (2016). Modelling the influence of biotic factors on species distribution patterns. *Ecological Modelling*, 337:96–106. 17

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H., Chaudhary, A., De Palma, A., DeClerck, F. A., Di Marco, M., Doelman, J. C., Dürauer, M., et al. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, 585(7826):551–556. 12

Levin, P. S., Essington, T. E., Marshall, K. N., Koehn, L. E., Anderson, L. G., Bundy, A., Carothers, C., Coleman, F., Gerber, L. R., Grabowski, J. H., et al. (2018). Building effective fishery ecosystem plans. *Marine Policy*, 92:48–57. 21

Lewis, K., Rose, K., de Mutsert, K., Sable, S., Ainsworth, C., Brady, D., and Townsend, H. (2021). Using multiple ecological models to inform environmental decision-making. *Frontiers in Marine Science*, 8:625790. 25

Lewis, K. P., Buren, A. D., Regular, P. M., Mowbray, F. K., and Murphy, H. M. (2019). Forecasting capelin mallotus villosus biomass on the newfoundland shelf. *Marine Ecology Progress Series*, 616:171–183. 86, 89, 113

Libralato, S., Pranovi, F., Zucchetta, M., Monti, M. A., and Link, J. S. (2019). Global thresholds in properties emerging from cumulative curves of marine ecosystems. *Ecological indicators*, 103:554–562. 17, 27

Lidström, S. and Johnson, A. F. (2020). Ecosystem-based fisheries management: A perspective on the critique and development of the concept. *Fish and Fisheries*, 21(1):216–222. 13

Lindegren, M., Dakos, V., Gröger, J. P., Gårdmark, A., Kornilovs, G., Otto, S. A., and Möllmann, C. (2012). Early detection of ecosystem regime shifts: a multiple method evaluation for management application. *PLoS One*, 7(7):e38410. 17

Lindgren, F. and Rue, H. (2015). Bayesian spatial modelling with r-inla. *Journal of statistical software*, 63(19). 37, 63, 64

Link, J. S., Bogstad, B., Sparholt, H., and Lilly, G. R. (2009). Trophic role of atlantic cod in the ecosystem. *Fish and Fisheries*, 10(1):58–87. 88, 110

Link, J. S., Ihde, T. F., Townsend, H., Osgood, K. E., Schirripa, M. J., Kobayashi, D. R., Gaichas, S. K., Field, J. C., Levin, P. S., Aydin, K. Y., et al. (2010). Report of the 2nd national ecosystem modeling workshop (nemow ii): bridging the credibility gap dealing with uncertainty in ecosystem models. Technical report, National Oceanic and Atmospheric Administration. 25

Link, J. S. and Marshak, A. R. (2021). *Ecosystem-based fisheries management: progress, importance, and impacts in the United States*. Oxford University Press. 14, 113

Link, J. S. and Watson, R. A. (2019). Global ecosystem overfishing: Clear delineation within real limits to production. *Science Advances*, 5(6):eaav0474. 17, 27

Linner, R. M. and Chen, Y. (2022). Implications of stock structure in understanding juvenile atlantic cod (gadus morhua) habitat suitability in the gulf of maine. *Regional Studies in Marine Science*, 54:102473. 76

Litzow, M. A., Ciannelli, L., Cunningham, C. J., Johnson, B., and Puerta, P. (2019). Nonstationary effects of ocean temperature on pacific salmon productivity. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(11):1923–1928. 15

Liu, O. R., Ward, E. J., Anderson, S. C., Andrews, K. S., Barnett, L. A., Brodie, S., Carroll, G., Fiechter, J., Haltuch, M. A., Harvey, C. J., et al. (2023). Species redistribution creates unequal outcomes for multispecies fisheries under projected climate change. *Science Advances*, 9(33):eadg5468. 66

Lloret-Lloret, E., Navarro, J., Giménez, J., López, N., Albo-Puigserver, M., Pennino, M. G., and Coll, M. (2020). The seasonal distribution of a highly commercial fish is related to ontogenetic changes in its feeding strategy. *Frontiers in Marine Science*, 7:566686. 51

Lloret-Lloret, E., Pennino, M. G., Vilas, D., Bellido, J. M., Navarro, J., and Coll, M. (2021). Main drivers of spatial change in the biomass of commercial species between summer and winter in the nw mediterranean sea. *Marine Environmental Research*, 164:105227. 31

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W., Galbraith, E. D., Barange, M., Barrier, N., Bianchi, D., Blanchard, J. L., et al. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences*, 116(26):12907–12912. 15

Luan, J., Zhang, C., Xu, B., Xue, Y., and Ren, Y. (2020). The predictive performances of random forest models with limited sample size and different species traits. *Fisheries Research*, 227:105534. 56

Lucey, S. M., Aydin, K. Y., Gaichas, S. K., Cadrin, S. X., Fay, G., Fogarty, M. J., and Punt, A. (2021). Evaluating fishery management strategies using an ecosystem model as an operating model. *Fisheries Research*, 234:105780. 21

Lynam, C. P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G. A., and Stenseth, N. C. (2017). Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences*, 114(8):1952–1957. 86

Marcello, L. A., Mueter, F. J., Dawe, E. G., and Moriyasu, M. (2012). Effects of temperature and gadid predation on snow crab recruitment: comparisons between the bering sea and atlantic canada. *Marine Ecology Progress Series*, 469:249–261. 49

Mariani, P., Křivan, V., MacKenzie, B. R., and Mullon, C. (2016). The migration game in habitat network: the case of tuna. *Theoretical Ecology*, 9:219–232. 20

Marshak, A. R., Link, J. S., Shuford, R., Monaco, M. E., Johannesen, E., Bianchi, G., Anderson, M. R., Olsen, E., Smith, D. C., Schmidt, J. O., et al. (2017). International perceptions of an integrated, multi-sectoral, ecosystem approach to management. *ICES Journal of Marine Science*, 74(1):414–420. 23

Marshall, K. N., Koehn, L. E., Levin, P. S., Essington, T. E., and Jensen, O. P. (2019). Inclusion of ecosystem information in us fish stock assessments suggests progress toward ecosystem-based fisheries management. *ICES Journal of Marine Science*, 76(1):1–9. 7, 14

Martell, S. (2008). Fisheries management. In Jørgensen, S. E. and Fath, B. D., editors, *Encyclopedia of Ecology*, pages 1572–1582. Academic Press, Oxford. 30

Martínez-Minaya, J., Cameletti, M., Conesa, D., and Pennino, M. G. (2018). Species distribution modeling: a statistical review with focus in spatio-temporal issues. *Stochastic environmental research and risk assessment*, 32:3227–3244. 31

Mather, C. (2013). From cod to shellfish and back again? the new resource geography and newfoundland's fish economy. *Applied Geography*, 45:402–409. 58, 59

McGilliard, C. R., Punt, A. E., Methot Jr, R. D., and Hilborn, R. (2015). Accounting for marine reserves using spatial stock assessments. *Canadian Journal of Fisheries and Aquatic Sciences*, 72(2):262–280. 30

McKendrick, A. (1926). Applications of mathematics to medical problems. *Edimburgh Mathematical Society*. 92

Melbourne-Thomas, J., Audzijonyte, A., Brasier, M. J., Cresswell, K. A., Fogarty, H. E., Haward, M., Hobday, A. J., Hunt, H. L., Ling, S. D., McCormack, P. C., et al. (2021). Poleward bound: adapting to climate-driven species redistribution. *Reviews in Fish Biology and Fisheries*, pages 1–21. 122

Méndez, P. F., Amezaga, J. M., and Santamaría, L. (2019). Explaining path-dependent rigidity traps: increasing returns, power, discourses, and entrepreneurship intertwined in social-ecological systems. *Ecology and Society*. 23

Merrifield, A. L., Brunner, L., Lorenz, R., Humphrey, V., and Knutti, R. (2023). Climate model selection by independence, performance, and spread (climsips v1. 0.1) for regional applications. *Geoscientific Model Development*, 16(16):4715–4747. 56

Mildenberger, T. K., Berg, C. W., Kokkalis, A., Hordyk, A. R., Wetzel, C., Jacobsen, N. S., Punt, A. E., and Nielsen, J. R. (2022). Implementing the precautionary approach into fisheries management: Biomass reference points and uncertainty buffers. *Fish and Fisheries*, 23(1):73–92. 122

Morin, P. (2011). *Community ecology.* 2nd ed. Chichester, West Sussex; Hoboken, NJ: Wiley. 30

Morley, J. W., Frölicher, T. L., and Pinsky, M. L. (2020). Characterizing uncertainty in climate impact projections: a case study with seven marine species on the north american continental shelf. *ICES Journal of Marine Science*, 77(6):2118–2133. 68

Morrison, S. M. and Davoren, G. K. (2024). Habitat characteristics and diel patterns of sand lance (ammodytes spp) in coastal newfoundland. *Environmental Biology of Fishes*, 107(4):443–457. 88

Mullowney, D., Coffey, W., Baker, K., Evans, G., Fiander, D., and Colbourne, E., e. a. (2017). An Assessment of Newfoundland and Labrador Snow Crab (Chionoecetes opilio) in 2016. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2017/081. 39

Mullowney, D., Dawe, E., Coffey, W., Skanes, K., Hynick, E., and Fiander, D. e. a. (2014a). An Assessment of Newfoundland and Labrador Snow Crab (Chionoecetes opilio) in 2013. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/114. vi + 206 p. 48

Mullowney, D., Morris, C., Dawe, E., Zagorsky, I., and Goryanina, S. (2018). Dynamics of snow crab (chionoecetes opilio) movement and migration along the newfoundland and labrador and eastern barents sea continental shelves. *Reviews in Fish Biology and Fisheries*, 28:435–459. 47, 48, 52

Mullowney, D. R., Baker, K. D., Szuwalski, C. S., Boudreau, S. A., Cyr, F., and Kaiser, B. A. (2023). Sub-arctic no more: Short-and long-term global-scale prospects for snow crab (chionoecetes opilio) under global warming. *PLOS Climate*, 2(10):e0000294. 59, 79

Mullowney, D. R., Dawe, E. G., Colbourne, E. B., and Rose, G. A. (2014b). A review of factors contributing to the decline of newfoundland and labrador snow crab (chionoecetes opilio). *Reviews in Fish Biology and Fisheries*, 24:639–657. 51

Mullowney, D. R. and Rose, G. A. (2014). Is recovery of northern cod limited by poor feeding? the capelin hypothesis revisited. *ICES Journal of Marine Science*, 71(4):784–793. 110

Murawski, S. A. (2007). Ten myths concerning ecosystem approaches to marine resource management. *Marine Policy*, 31(6):681–690. 13

Murphy, H., Adamack, A., Mowbray, F., Lewis, K., and Bourne, C. (2024). Assessment of Capelin (Mallotus villosus) in NAFO Divisions 2J + 3KL to 2022. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2024/027. iv + 48 p. 89

Murphy, H. M., Adamack, A. T., and Cyr, F. (2021). Identifying possible drivers of the abrupt and persistent delay in capelin spawning timing following the 1991 stock collapse in newfoundland, canada. *ICES Journal of Marine Science*, 78(8):2709–2723. 89, 121

Myers, R., Mertz, G., and Bishop, C. (1993). Cod spawning in relation to physical and biological cycles of the northern Northwest Atlantic. Technical report, Northwest Atlantic Fisheries Organization. 88

NAFO (2004). NAFO Precautionary approach framework. Technical report, Northwest Atlantic Fisheries Organization. Serial No.N5062. 2004 NAFO/FC Doc. 04/18. 50

NAFO (2021a). Capelin in divisions 3no. Technical report, Northwest Atlantic Fisheries Organization. Advice June 2021 for 2022-2024. SC 27 May-11 Jun 2021. 6

NAFO (2021b). Northern shrimp in divisions 3lno. Technical report, Northwest Atlantic Fisheries Organization. Advice September 2021 for 2022-2023. SC/ NIPAG, 9 September, 2021. 6

Nicholson, E., Watermeyer, K. E., Rowland, J. A., Sato, C. F., Stevenson, S. L., Andrade, A., Brooks, T. M., Burgess, N. D., Cheng, S.-T., Grantham, H. S., et al. (2021). Scientific foundations for an ecosystem goal, milestones and indicators for the post-2020 global biodiversity framework. *Nature ecology & evolution*, 5(10):1338–1349. 12

Nilsen, I., Hansen, C., Kaplan, I., Holmes, E., and Langangen, Ø. (2022). Exploring the role of northeast atlantic cod in the barents sea food web using a multi-model approach. *Fish and Fisheries*, 23(5):1083–1098. 123

NL Government (2020). Sand Lance (Ammodytes dubius). Emerging species profile sheets. Technical report, Government of Newfoundland and Labrador. Department of Fisheries and Aquaculture. 88

NL Government (2023). Seafood industry year in review 2022. Fisheries, forestry and agriculture. Technical report, Government of Newfoundland and Labrador. 59

Norström, A. V., Cvitanovic, C., Löf, M. F., West, S., Wyborn, C., Balvanera, P., Bednarek, A. T., Bennett, E. M., Biggs, R., de Bremond, A., et al. (2020). Principles for knowledge co-production in sustainability research. *Nature sustainability*, 3(3):182–190. 24

Ojea, E., Lester, S. E., and Salgueiro-Otero, D. (2020). Adaptation of fishing communities to climate-driven shifts in target species. *One Earth*, 2(6):544–556. 49

Ostrom, E. (2009). A general framework for analyzing sustainability of social-ecological systems. *Science*, 325(5939):419–422. 25

O'Farrell, H., Grüss, A., Sagarese, S. R., Babcock, E. A., and Rose, K. A. (2017). Ecosystem modeling in the gulf of mexico: current status and future needs to address ecosystem-based fisheries management and restoration activities. *Reviews in fish biology and fisheries*, 27:587–614. 18

O'Leary, C. A., Thorson, J. T., Miller, T. J., and Nye, J. A. (2020). Comparison of multiple approaches to calculate time-varying biological reference points in climate-linked population-dynamics models. *ICES Journal of Marine Science*, 77(3):930–941. 13

Pace, M. L., Cole, J. J., Carpenter, S. R., and Kitchell, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in ecology & evolution*, 14(12):483–488. 87

Palacios-Abrantes, J., Frölicher, T. L., Reygondeau, G., Sumaila, U. R., Tagliabue, A., Wabnitz, C. C., and Cheung, W. W. (2022). Timing and magnitude of climate-driven range shifts in transboundary fish stocks challenge their management. *Global change biology*, 28(7):2312–2326. 20

Pante, E. and Simon-Bouhet, B. (2013). marmap: a package for importing, plotting and analyzing bathymetric and topographic data in r. *PLoS one*, 8(9):e73051. 35

Paradinas, I., Conesa, D., López-Quílez, A., Esteban, A., López, L. M. M., Bellido, J. M., and Pennino, M. G. (2020). Assessing the spatiotemporal persistence of fish distributions: a case study on two red mullet species (mullus surmuletus and m. barbatus) in the western mediterranean. *Marine Ecology Progress Series*, 644:173–185. 36

Parsons, D., Rideout, R., and Rogers, R. (2021). Assessment of Yellowtail Flounder in NAFO Divisions 3LNO using a Stock Production Model in a Bayesian framework. Technical report, Northwest Atlantic Fisheries Organization. 36, 39

Parsons, D., Rogers, B., and Rideout, R. (2020). An assessment of the witch flounder resource in nafo division 3no. Technical report, Northwest Atlantic Fisheries Organization. NAFO SRC Doc. 20/046. 6

Parsons, D., Skaner, K., and Rideou, R. (2023). Assessment of yellowtail flounder in nafo divisions 3lno. Technical report, Northwest Atlantic Fisheries Organization. NAFO SRC Doc. 23/016. 6

Patrick, W. S. and Link, J. S. (2015). Myths that continue to impede progress in ecosystem-based fisheries management. *Fisheries*, 40(4):155–160. 13

Pauly, D. et al. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends in ecology and evolution*, 10(10):430. 14

Pedersen, E. J., Thompson, P. L., Ball, R. A., Fortin, M.-J., Gouhier, T. C., Link, H., Moritz, C., Nenzen, H., Stanley, R. R., Taranu, Z. E., et al. (2017). Signatures of the collapse and incipient recovery of an overexploited marine ecosystem. *Royal Society Open Science*, 4(7):170215. 5, 58, 118

Pennino, M. G., Izquierdo, F., Paradinas, I., Cousido, M., Velasco, F., and Cerviño, S. (2022). Identifying persistent biomass areas: The case study of the common sole in the northern iberian waters. *Fisheries Research*, 248:106196. 36

Pepin, P., Higdon, J., Koen-Alonso, M., Fogarty, M., and Ollerhead, N. (2014). Application of ecoregion analysis to the identification of Ecosystem Production Units (EPUs) in the NAFO Convention Area. Technical report, Northwest Atlantic Fisheries Organization. NAFO SCR 2014 Doc. 14/069. 2, 32, 57

Pepin, P., King, J., Holt, C., Gurney-Smith, H., Shackell, N., Hedges, K., and Bundy, A. (2022). Incorporating knowledge of changes in climatic, oceanographic and ecological conditions in canadian stock assessments. *Fish and Fisheries*, 23(6):1332–1346. 7, 14, 113

Perry, R. I. and Smith, S. J. (1994). Identifying habitat associations of marine fishes using survey data: an application to the northwest atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 51(3):589–602. 49

Perryman, H. A., Hansen, C., Howell, D., and Olsen, E. (2021). A review of applications evaluating fisheries management scenarios through marine ecosystem models. *Reviews in Fisheries Science & Aquaculture*, 29(4):800–835. 22

Pershing, A. J., Alexander, M. A., Brady, D. C., Brickman, D., Curchitser, E. N., Diamond, A. W., McClenachan, L., Mills, K. E., Nichols, O. C., Pendleton, D. E., et al. (2021). Climate impacts on the gulf of maine ecosystem: a review of observed and expected changes in 2050 from rising temperatures. *Elem Sci Anth*, 9(1):00076. 66

Pershing, A. J., Alexander, M. A., Hernandez, C. M., Kerr, L. A., Le Bris, A., Mills, K. E., Nye, J. A., Record, N. R., Scannell, H. A., Scott, J. D., et al. (2015). Slow adaptation in the face of rapid warming leads to collapse of the gulf of maine cod fishery. *Science*, 350(6262):809–812. 80

Peterman, R. M. (2019). Continuous learning, teamwork, and lessons for young scientists. *ICES Journal of Marine Science*, 76(1):28–40. 25

Petrie, B., Frank, K. T., and Leggett, W. C. (2022). Temporal evolution of critical traits and their relationship to cod stock collapse and recovery. *Canadian Journal of Fisheries and Aquatic Sciences*, 79(11):1765–1779. 52

Petrie, B., Frank, K. T., Shackell, N. L., and Leggett, W. C. (2009). Structure and stability in exploited marine fish communities: quantifying critical transitions. *Fisheries Oceanography*, 18(2):83–101. 112, 121

Pikitch, E., Boersma, P., Boyd, I., Conover, D., Cury, P., Essington, T., Heppell, S., Houde, E., Mangel, M., Pauly, D., Plaganyi, E., Sainsbury, K., and Steneck, R. (2012). Little fish, big impact: Managing a crucial link in ocean food webs. Technical report, Lenfest Ocean Program. Washington, DC. 108 pp. 7, 86

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., et al. (2004). Ecosystem-based fishery management. *Science*, 305(5682):346–347. 7, 13

Pinsky, M. L., Fenichel, E., Fogarty, M., Levin, S., McCay, B., St. Martin, K., Selden, R. L., and Young, T. (2021). Fish and fisheries in hot water: What is happening and how do we adapt? *Population Ecology*, 63(1):17–26. 83

Pinsky, M. L. and Mantua, N. J. (2014). Emerging adaptation approaches for climate-ready fisheries management. *Oceanography*, 27(4):146–159. 56, 119, 122

Pinsky, M. L., Reygondeau, G., Caddell, R., Palacios-Abrantes, J., Spijkers, J., and Cheung, W. W. (2018). Preparing ocean governance for species on the move. *Science*, 360(6394):1189–1191. 20

Pinsky, M. L., Selden, R. L., and Kitchel, Z. J. (2020). Climate-driven shifts in marine species ranges: scaling from organisms to communities. *Annual review of marine science*, 12(1):153–179. 78, 80

Plagányi, É. E. (2007). Models for an ecosystem approach to fisheries. Technical report, Food & Agriculture Org. 18

Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani, S. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79(3-4):403–417. 121

Pollock, L. J., O'connor, L. M., Mokany, K., Rosauer, D. F., Talluto, M. V., and Thuiller, W. (2020). Protecting biodiversity (in all its complexity): new models and methods. *Trends in Ecology & Evolution*, 35(12):1119–1128. 21, 28

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., and McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a joint species distribution model (jsdm). *Methods in Ecology and Evolution*, 5(5):397–406. 53

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., et al. (2013). Global imprint of climate change on marine life. *Nature climate change*, 3(10):919–925. 15, 79

Punt, A. E. (2023). Those who fail to learn from history are condemned to repeat it: A perspective on current stock assessment good practices and the consequences of not following them. *Fisheries Research*, 261:106642. 30

Punt, A. E., A'mar, T., Bond, N. A., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A., Haltuch, M. A., Hollowed, A. B., and Szuwalski, C. (2014). Fisheries management under climate and environmental uncertainty: control rules and performance simulation. *ICES Journal of Marine Science*, 71(8):2208–2220. 17

Punt, A. E., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A., and Haddon, M. (2016a). Management strategy evaluation: best practices. *Fish and fisheries*, 17(2):303–334. 22

Punt, A. E., Dalton, M. G., Daly, B., Jackson, T., Long, W. C., Stockhausen, W. T., Szuwalski, C., and Zheng, J. (2022). A framework for assessing harvest strategy choice when considering multiple interacting fisheries and a changing environment: The example of eastern bering sea crab stocks. *Fisheries Research*, 252:106338. 22, 27

Punt, A. E., MacCall, A. D., Essington, T. E., Francis, T. B., Hurtado-Ferro, F., Johnson, K. F., Kaplan, I. C., Koehn, L. E., Levin, P. S., and Sydeman, W. J. (2016b). Exploring the implications of the harvest control rule for pacific sardine, accounting for predator dynamics: A mice model. *Ecological Modelling*, 337:79–95. 22

Razzaque, J., Visseren-Hamakers, I., Gautam, A. P., Gerber, L., Islar, M., Karim, M. S., Kelemen, E., Liu, J., Lui, G., McElwee, P., et al. (2019). Options for decision makers. *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. 14

Redding, D. W., Lucas, T. C., Blackburn, T. M., and Jones, K. E. (2017). Evaluating bayesian spatial methods for modelling species distributions with clumped and restricted occurrence data. *PloS one*, 12(11):e0187602. 31

Regular, P., . (2023). Data proposed for use in operating models for the 2023 management strategy evaluation review for greenland halibut in nafo subarea 2 and divisions 3klmno. Technical report, Northwest Atlantic Fisheries Organization. NAFO SCR Doc. 23/007. 6

Regular, P. M., Buren, A. D., Dwyer, K. S., Cadigan, N. G., Gregory, R. S., Koen-Alonso, M., Rideout, R. M., Robertson, G. J., Robertson, M. D., Stenson, G. B., et al. (2022). Indexing starvation mortality to assess its role in the population regulation of northern cod. *Fisheries Research*, 247:106180. 52, 109, 110

Regular, P. M., Robertson, G. J., Rogers, R., and Lewis, K. P. (2020). Improving the communication and accessibility of stock assessment using interactive visualization tools. *Canadian Journal of Fisheries and Aquatic Sciences*, 77(9):1592–1600. 94

Rendall, A. R., Sutherland, D. R., Baker, C. M., Raymond, B., Cooke, R., and White, J. G. (2021). Managing ecosystems in a sea of uncertainty: invasive species management and assisted colonizations. *Ecological Applications*, 31(4):e02306. 17

Reum, J., Woodworth-Jefcoats, P., Novaglio, C., Forestier, R., Audzijonyte, A., Gårdmark, A., Lindmark, M., and Blanchard, J. (2024). Temperature-dependence assumptions drive projected responses of diverse size-based food webs to warming. *Earth's Future*, 12(3):e2023EF003852. 99, 123

Reum, J. C., Blanchard, J. L., Holsman, K. K., Aydin, K., Hollowed, A. B., Hermann, A. J., Cheng, W., Faig, A., Haynie, A. C., and Punt, A. E. (2020). Ensemble projections of future climate change impacts on the eastern bering sea food web using a multispecies size spectrum model. *Frontiers in Marine Science*, 7:124. 81, 115, 124

Rice, J. C. and Rochet, M.-J. (2005). A framework for selecting a suite of indicators for fisheries management. *ICES Journal of Marine Science*, 62(3):516–527. 16

Richardson, D. E., Palmer, M. C., and Smith, B. E. (2014). The influence of forage fish abundance on the aggregation of gulf of maine atlantic cod (gadus morhua) and their catchability in the fishery. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(9):1349–1362. 52

Rideout, R. M. and Ings, D. (2019). Temporal And Spatial Coverage Of Canadian (Newfoundland And Labrador Region) Spring And Autumn Multi-Species RV Bottom Trawl Surveys, With An Emphasis On Surveys Conducted In 2018. Technical report, Northwest Atlantic Fisheries Organization. NAFO SCR 2019 Doc. 19/15. 33, 47, 81

Rideout, R. M., Rogers, R., and Ings, D. (2021). An Updated Assessment of the Cod Stock in NAFO Divisions 3NO. Technical report, Northwest Atlantic Fisheries Organization. NAFO SCR 2021 Doc. 21/031. 33, 36, 39, 58, 89

Roberts, K., Stepanuk, J., Kim, H., Thorne, L., Chong-Montenegro, C., and Nye, J. (2023). Developing a subseasonal ecological forecast to reduce fisheries bycatch in the northeast us. *Progress in Oceanography*, 213:103021. 123

Robertson, M. D., Koen-Alonso, M., Regular, P. M., Cadigan, N., and Zhang, F. (2022). Accounting for a nonlinear functional response when estimating prey dynamics using predator diet data. *Methods in Ecology and Evolution*, 13(4):880–893. 88, 90

Robinson, L., Hobday, A., Possingham, H., and Richardson, A. J. (2015). Trailing edges projected to move faster than leading edges for large pelagic fish habitats under climate change. *Deep Sea Research Part II: Topical Studies in Oceanography*, 113:225–234. 79

Robinson, N. M., Nelson, W. A., Costello, M. J., Sutherland, J. E., and Lundquist, C. J. (2017). A systematic review of marine-based species distribution models (sdms) with recommendations for best practice. *Frontiers in Marine Science*, 4:421. 49

Rochet, M.-J. and Rice, J. C. (2005). Do explicit criteria help in selecting indicators for ecosystem-based fisheries management? *ICES Journal of Marine Science*, 62(3):528–539. 16

Rodrigues, A. S., Monsarrat, S., Charpentier, A., Brooks, T. M., Hoffmann, M., Reeves, R., Palomares, M. L., and Turvey, S. T. (2019). Unshifting the baseline: a framework for documenting historical population changes and assessing long-term anthropogenic impacts. *Philosophical Transactions of the Royal Society B*, 374(1788):20190220. 14

Rogers, B., Perreault, A., Simpson, M., and Varkey, D. (2022). Assessment of 3ln redfish using aspic model in 2022 (sebastes mentella and s. fasciatus). Technical report, Northwest Atlantic Fisheries Organization. NAFO SRC Doc. 22/013. 6

Rose, G. A. (2005). Capelin (mallotus villosus) distribution and climate: a sea “canary” for marine ecosystem change. *ICES Journal of Marine Science*, 62(7):1524–1530. 87

Rose, G. A. and Kulka, D. W. (1999). Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (gadus morhua) declined. *Canadian Journal of Fisheries and Aquatic Sciences*, 56(S1):118–127. 50

Rose, K. A., Holsman, K., Nye, J. A., Markowitz, E. H., Banha, T. N., Bueno-Pardo, J., Deslauriers, D., Fulton, E. A., Huebert, K. B., Huret, M., et al. (2024). Advancing bioenergetics-based modeling to improve climate change projections of marine ecosystems. *Marine Ecology Progress Series*, 732:193–221. 124

Rounsevell, M. D., Arneth, A., Brown, C., Cheung, W. W., Gimenez, O., Holman, I., Leadley, P., Luján, C., Mahevas, S., Maréchaux, I., et al. (2021). Identifying uncertainties in scenarios and models of socio-ecological systems in support of decision-making. *One Earth*, 4(7):967–985. 25

Rue, H., Martino, S., and Chopin, N. (2009). Approximate bayesian inference for latent gaussian models by using integrated nested laplace approximations. *Journal of the Royal Statistical Society Series B: Statistical Methodology*, 71(2):319–392. 64

Ruiz-Díaz, R. (2023). Using an ebfm lens to guide the management of marine biological resources under changing conditions. *Fish and Fisheries*, 24(2):199–211. 83, 113

Ruiz-Diaz, R., Pennino, M. G., Fisher, J. A., and Eddy, T. D. (2024). Decadal changes in biomass and distribution of key fisheries species on newfoundland’s grand banks. *Plos one*, 19(4):e0300311. 58, 79, 80, 88

Rutherford, K., Fennel, K., Garcia Suarez, L., and John, J. G. (2024). Uncertainty in the evolution of northwestern north atlantic circulation leads to diverging biogeochemical projections. *Biogeosciences*, 21(1):301–314. 57, 59, 63, 82, 119

Rutterford, L. A., Simpson, S. D., Bogstad, B., Devine, J. A., and Genner, M. J. (2023). Sea temperature is the primary driver of recent and predicted fish community structure across northeast atlantic shelf seas. *Global Change Biology*, 29(9):2510–2521. 53

Saba, V. S., Griffies, S. M., Anderson, W. G., Winton, M., Alexander, M. A., Delworth, T. L., Hare, J. A., Harrison, M. J., Rosati, A., Vecchi, G. A., et al. (2016). Enhanced warming of the n orthwest a tlantic o cean under climate change. *Journal of Geophysical Research: Oceans*, 121(1):118–132. 2, 49, 118

Sadykova, D., Scott, B. E., De Dominicis, M., Wakelin, S. L., Sadykov, A., and Wolf, J. (2017). Bayesian joint models with inla exploring marine mobile predator–prey and competitor species habitat overlap. *Ecology and Evolution*, 7(14):5212–5226. 17

Sala, E. and Knowlton, N. (2006). Global marine biodiversity trends. *Annu. Rev. Environ. Resour.*, 31(1):93–122. 12, 21

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., and Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465(7298):609–612. 109

Scott, F., Blanchard, J. L., and Andersen, K. H. (2014). mizer: an r package for multispecies, trait-based and community size spectrum ecological modelling. *Methods in Ecology and Evolution*, 5(10):1121–1125. 90, 91, 92, 93, 97

Selden, R. L., Batt, R. D., Saba, V. S., and Pinsky, M. L. (2018). Diversity in thermal affinity among key piscivores buffers impacts of ocean warming on predator–prey interactions. *Global Change Biology*, 24(1):117–131. 52, 83

Shelton, A. O., Thorson, J. T., Ward, E. J., and Feist, B. E. (2014). Spatial semiparametric models improve estimates of species abundance and distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(11):1655–1666. 31, 48

Shelton, P. A., Sinclair, A. F., Chouinard, G. A., Mohn, R., and Duplisea, D. E. (2006). Fishing under low productivity conditions is further delaying recovery of northwest atlantic cod (gadus morhua). *Canadian Journal of fisheries and aquatic sciences*, 63(2):235–238. 112

Simpson, M. R. and Walsh, S. J. (2004). Changes in the spatial structure of grand bank yellowtail flounder: testing maccall's basin hypothesis. *Journal of Sea Research*, 51(3-4):199–210. 49, 76, 79

Skern-Mauritzen, M., Ottersen, G., Handegard, N. O., Huse, G., Dingsør, G. E., Stenseth, N. C., and Kjesbu, O. S. (2016). Ecosystem processes are rarely included in tactical fisheries management. *Fish and Fisheries*, 17(1):165–175. 7, 12, 13

Skogen, M. D., Hjøllo, S. S., Sandø, A. B., and Tjiputra, J. (2018). Future ecosystem changes in the northeast atlantic: a comparison between a global and a regional model system. *ICES Journal of Marine Science*, 75(7):2355–2369. 56

Smedbol, R., Shelton, P., Swain, D., Frechet, A., and GA, C. (2002). Review of population structure, distribution and abundance of cod (Gadus morhua) in Atlantic Canada in a species-at-risk context. Technical report, Fisheries and Oceans Canada. DFO 2002 Can. Sci. Adv. Sec. Doc. 2002/082. 50

Smith, S. J. (1990). Use of statistical models for the estimation of abundance from groundfish trawl survey data. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(5):894–903. 30

Sobie, S., Zwiers, F., and Curry, C. (2021). Climate model projections for canada: a comparison of cmip5 and cmip6. *Atmosphere-Ocean*, 59(4-5):269–284. 66

Sosebee, K., Simpson, M., and Miri, C. (2022). Assessment of thorny skate (amblyraja radiata donovan, 1808) in nafo divisions 3lno and subdivision 3ps. Technical report, Northwest Atlantic Fisheries Organization. NAFO SRC Doc. 22/026. 6

Staudinger, M. D., Goyert, H., Suca, J. J., Coleman, K., Welch, L., Llopiz, J. K., Wiley, D., Altman, I., Applegate, A., Auster, P., et al. (2020). The role of sand lances (ammodytes sp.) in the northwest atlantic ecosystem: A synthesis of current knowledge with implications for conservation and management. *Fish and Fisheries*, 21(3):522–556. 88, 89

Stenson, G. (2013). Estimating consumption of prey by Harp Seals, (Pagophilus groenlandicus) in NAFO Divisions 2J3KL. Technical report, Fisheries and Oceans Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/156. iii + 26 p. (Errata: October 2015). 88, 115

Stephenson, R. L., Wiber, M., Paul, S., Angel, E., Benson, A., Charles, A., Chouinard, O., Edwards, D., Foley, P., Lane, D., et al. (2019). Integrating diverse objectives for sustainable fisheries in canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(3):480–496. 21

Stock, C. A., Alexander, M. A., Bond, N. A., Brander, K. M., Cheung, W. W., Curchitser, E. N., Delworth, T. L., Dunne, J. P., Griffies, S. M., Haltuch, M. A., et al. (2011). On the use of ipcc-class models to assess the impact of climate on living marine resources. *Progress in Oceanography*, 88(1-4):1–27. 56, 57, 63, 119

Strong, D. R. (1992). Are trophic cascades all wet? differentiation and donor-control in speciose ecosystems. *Ecology*, 73(3):747–754. 112

Sumaila, U. R., Palacios-Abrantes, J., and Cheung, W. W. (2020). Climate change, shifting threat points, and the management of transboundary fish stocks. *Ecology & Society*, 25(4). 49

Sunday, J. M., Bates, A. E., and Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2(9):686–690. 79

Sydeman, W. J., Poloczanska, E., Reed, T. E., and Thompson, S. A. (2015). Climate change and marine vertebrates. *Science*, 350(6262):772–777. 52

Szuwalski, C. S., Aydin, K., Fedewa, E. J., Garber-Yonts, B., and Litzow, M. A. (2023). The collapse of eastern bering sea snow crab. *Science*, 382(6668):306–310. 82, 117

Szuwalski, C. S., Burgess, M. G., Costello, C., and Gaines, S. D. (2017). High fishery catches through trophic cascades in china. *Proceedings of the National Academy of Sciences*, 114(4):717–721. 95

Tam, J. and Bundy, A. (2019). Mass-balance models of the Newfoundland and Labrador Shelf ecosystem for 1985-1987 and 2013-2015. Technical report, Fisheries and Oceans Canada. Can. Tech. Rep. Fish. Aquat. Sci. 3328: vii + 78 p. 88, 109, 111

Tam, J. C., Link, J. S., Large, S. I., Andrews, K., Friedland, K. D., Gove, J., Hazen, E., Holsman, K., Karnauskas, M., Samhouri, J. F., et al. (2017). Comparing apples to oranges: common trends and thresholds in anthropogenic and environmental pressures across multiple marine ecosystems. *Frontiers in Marine Science*, 4:282. 16

Tanaka, K. R., Chang, J.-H., Xue, Y., Li, Z., Jacobson, L., and Chen, Y. (2019). Mesoscale climatic impacts on the distribution of homarus americanus in the us inshore gulf of maine. *Canadian Journal of Fisheries and Aquatic Sciences*, 76(4):608–625. 52

Therriault, J., Petrie, B., Pepin, P., Gagnon, J., Gregory, D., Helbig, J., Herman, A., Lefaivre, D., Mitchell, M., Pelchat, B., Runge, J., and Sameoto, D. (1998). Proposal for a northwest atlantic zonal monitoring program. Technical report, Canadian Technical Report of Hydrography and Ocean Sciences 194: vii+57p. Fisheries and Oceans Canada. 117

Thompson, P. L., Rooper, C. N., Nephin, J., Park, A. E., Christian, J. R., Davies, S. C., Hunter, K., Lyons, D. A., Peña, M. A., Proudfoot, B., et al. (2023). Response of pacific halibut (hippoglossus stenolepis) to future climate scenarios in the northeast pacific ocean. *Fisheries Research*, 258:106540. 53, 67, 81, 83

Thorson, J. T., Munch, S. B., Cope, J. M., and Gao, J. (2017). Predicting life history parameters for all fishes worldwide. *Ecological Applications*, 27(8):2262–2276. 93

Thorson, J. T., Pinsky, M. L., and Ward, E. J. (2016). Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. *Methods in Ecology and Evolution*, 7(8):990–1002. 31

Thorson, J. T., Shelton, A. O., Ward, E. J., and Skaug, H. J. (2015). Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for west coast groundfishes. *ICES Journal of Marine Science*, 72(5):1297–1310. 31, 36

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., and Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. *Nature Communications*, 10(1):1446. 81

Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., de Jonge, M. M., Oksanen, J., and Ovaskainen, O. (2020). Joint species distribution modelling with the r-package hmsc. *Methods in ecology and evolution*, 11(3):442–447. 17

Tobler, W. R. (1970). A computer movie simulating urban growth in the detroit region. *Economic geography*, 46(sup1):234–240. 30

Topping, C. J. and Lagisz, M. (2012). Spatial dynamic factors affecting population-level risk assessment for a terrestrial arthropod: an agent-based modeling approach. *Human and Ecological Risk Assessment: An International Journal*, 18(1):168–180. 17

Townsend, H., Harvey, C. J., DeReynier, Y., Davis, D., Zador, S. G., Gaichas, S., Weijerman, M., Hazen, E. L., and Kaplan, I. C. (2019). Progress on implementing ecosystem-based fisheries management in the united states through the use of ecosystem models and analysis. *Frontiers in Marine Science*, 6:641. 22, 24, 123

Tretyakov, I. (2015). Capelin stock assessment in NAFO Divisions 3NO Based on data from trawl surveys. Technical report, Northwest Atlantic Fisheries Organization. NAFO SCR Doc. 15/027. 87, 89, 113

Trochta, J. T., Pons, M., Rudd, M. B., Krigbaum, M., Tanz, A., and Hilborn, R. (2018). Ecosystem-based fisheries management: perception on definitions, implementations, and aspirations. *PloS one*, 13(1):e0190467. 13

Trzcinski, M. K., Mohn, R., and Bowen, W. D. (2006). Continued decline of an atlantic cod population: how important is gray seal predation? *Ecological Applications*, 16(6):2276–2292. 115

Tulk, F. J., Cadigan, N. G., Brattey, J., and Robert, D. (2017). Spatial synchronicity in recruitment of atlantic cod (gadus morhua) stocks off newfoundland and labrador and the flemish cap. *Fisheries Research*, 191:49–59. 50

Vehtari, A., Gelman, A., and Gabry, J. (2017). Practical bayesian model evaluation using leave-one-out cross-validation and waic. *Statistics and computing*, 27:1413–1432. 38

Vert-Pre, K. A., Amoroso, R. O., Jensen, O. P., and Hilborn, R. (2013). Frequency and intensity of productivity regime shifts in marine fish stocks. *Proceedings of the National Academy of Sciences*, 110(5):1779–1784. 13

Von Foerster, H. and Stohlman, F. (1959). The kinetics of cellular proliferation. *Grune & Stratton, 3(9)*. 92

Walsh, S. (1992). Factors influencing distribution of juvenile yellowtail flounder (limanda ferruginea) on the grand bank of newfoundland. *Netherlands Journal of Sea Research*, 29(1-3):193–203. 49

Ward, D., Melbourne-Thomas, J., Pecl, G. T., Evans, K., Green, M., McCormack, P. C., Novaglio, C., Trebilco, R., Bax, N., Brasier, M. J., et al. (2022). Safeguarding marine life: conservation of biodiversity and ecosystems. *Reviews in fish biology and fisheries*, 32(1):65–100. 14

Weiskopf, S. R., Myers, B. J., Arce-Plata, M. I., Blanchard, J. L., Ferrier, S., Fulton, E. A., Harfoot, M., Isbell, F., Johnson, J. A., Mori, A. S., et al. (2022). A conceptual framework to integrate biodiversity, ecosystem function, and ecosystem service models. *BioScience*, 72(11):1062–1073. 20

Wheeland, L., Dwyer, K., Kumar, R., Rideout, R., Perreault, A., and Rogers, B. (2021). Assessment of american plaice in div. 3lno. Technical report, Northwest Atlantic Fisheries Organization. NAFO SRC Soc. 21/035. 6

Wheeland, L., Novaczek, E., Regular, P., Rideout, R., and Rogers, B. (2022). An assessment of the status of redfish in nafo division 3o. Technical report, Northwest Atlantic Fisheries Organization. NAFO SRC Doc. 22/044. 6

Windle, M. J., Rose, G. A., Devillers, R., and Fortin, M.-J. (2012). Spatio-temporal variations in invertebrate- cod- environment relationships on the newfoundland–labrador shelf, 1995- 2009. *Marine Ecology Progress Series*, 469:263–278. 34, 76

Winters, G. (1983). Analysis of the biological and demographic parameters of northern sand lance, ammodytes dubius, from the newfoundland grand bank. *Canadian Journal of Fisheries and Aquatic Sciences*, 40(4):409–419. 87

Winters, G. and Dalley, E. (1988). Meristic composition of sand lance (ammodytes spp.) in newfoundland waters with a review of species designations in the northwest atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 45(3):516–529. 88

Woodworth-Jefcoats, P. A., Blanchard, J. L., and Drazen, J. C. (2019). Relative impacts of simultaneous stressors on a pelagic marine ecosystem. *Frontiers in Marine Science*, 6:383. 115, 123

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B., Lotze, H. K., Micheli, F., Palumbi, S. R., et al. (2006). Impacts of biodiversity loss on ocean ecosystem services. *science*, 314(5800):787–790. 12

Worm, B. and Lotze, H. K. (2021). Marine biodiversity and climate change. In *Climate change*, pages 445–464. Elsevier. 12

Worm, B. and Myers, R. A. (2003). Meta-analysis of cod–shrimp interactions reveals top-down control in oceanic food webs. *Ecology*, 84(1):162–173. 110, 120

Yu, H., Cooper, A. R., and Infante, D. M. (2020). Improving species distribution model predictive accuracy using species abundance: Application with boosted regression trees. *Ecological Modelling*, 432:109202. 56

Zhao, H., Han, G., and Wang, D. (2013). Timing and magnitude of spring bloom and effects of physical environments over the grand banks of newfoundland. *Journal of Geophysical Research: Biogeosciences*, 118(4):1385–1396. 1

Zhou, S., Smith, A. D., Punt, A. E., Richardson, A. J., Gibbs, M., Fulton, E. A., Pascoe, S., Bulman, C., Bayliss, P., and Sainsbury, K. (2010). Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proceedings of the National Academy of Sciences*, 107(21):9485–9489. 13

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, 1(1):3–14. 38

APPENDIX A

Supplementary material for Chapter 3

A.1 Mesh details and covariates

Delaunay triangulation mesh

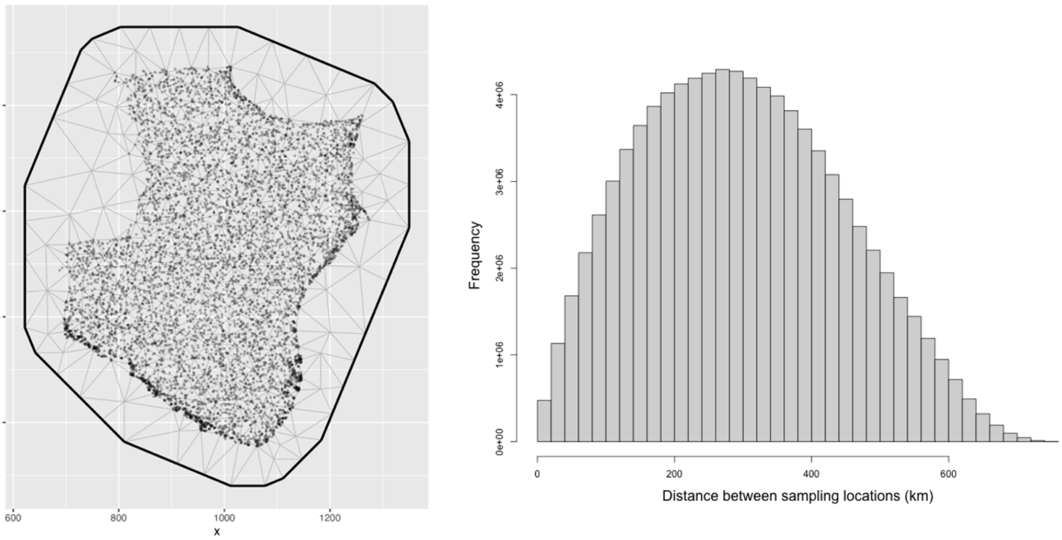


FIGURE A.1: Left graph displays the Delaunay triangulation mesh used in the models with a cutoff = 20 km. Grey dots indicate observations. Right graphs shows an histogram of the distance between sampling sites in Km.

Mesh description

fm_mesh_2d object:

Manifold: $\mathbb{R}^2$
V / E / T: 467 / 1359 / 893
Euler char.: 1
Constraints: 39 boundary edges (1 group: 0), 0 boundary edges
Bounding box: $(622.1104, 1350.0463) \times (4679.981, 5548.451) \times (0, 0)$
Basis d.o.f.: 467

Correlation between covariates observation and data used to predict

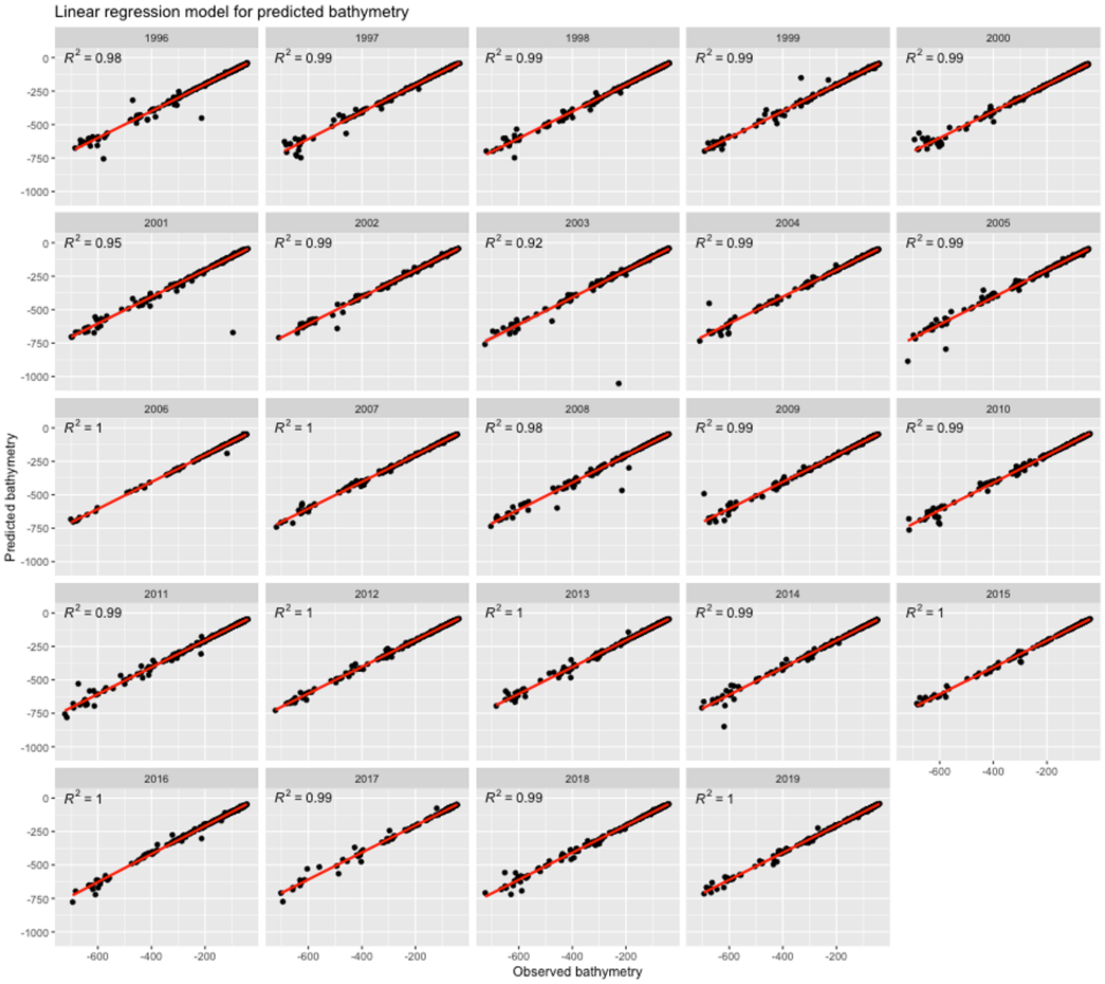


FIGURE A.2: Correlation between observed bathymetry (obtained from the bottom trawl survey) and GEBCO bathymetry used to predict. .

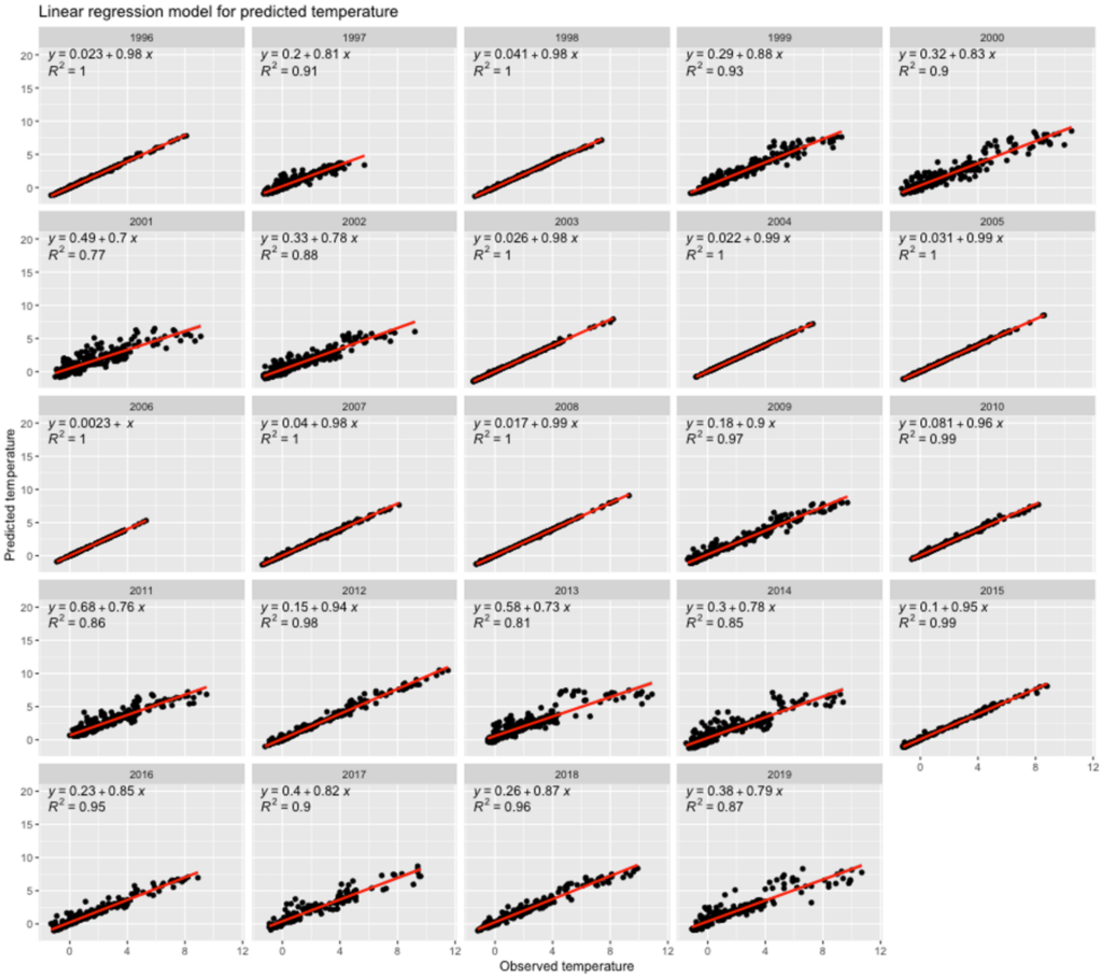
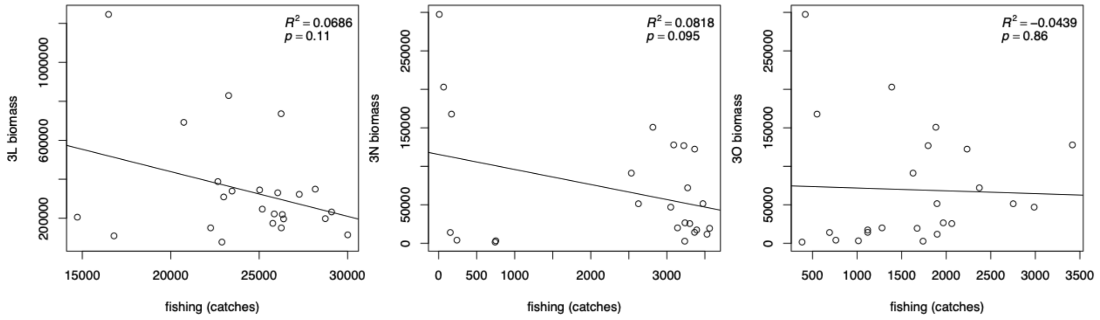


FIGURE A.3: Correlation between observed bottom temperature (obtained from the bottom trawl survey) and DFO interpolated bottom temperature data used to predict.

Relationship between species biomass and fishing effort at division level

a) Snow crab



b) Yellowtail flounder

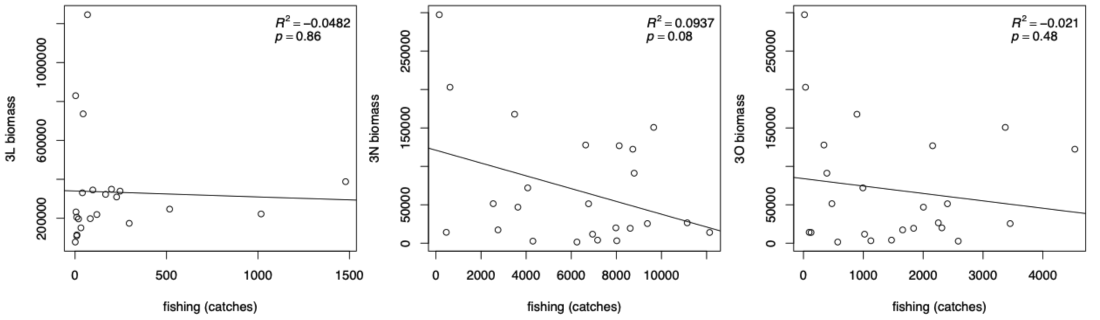


FIGURE A.4: Linear relationship between biomass and catches of snow crab (a) and yellowtail flounder (b) calculated at division level (3L, 3N and 3O).

Delta_gamma biomass prediction per year

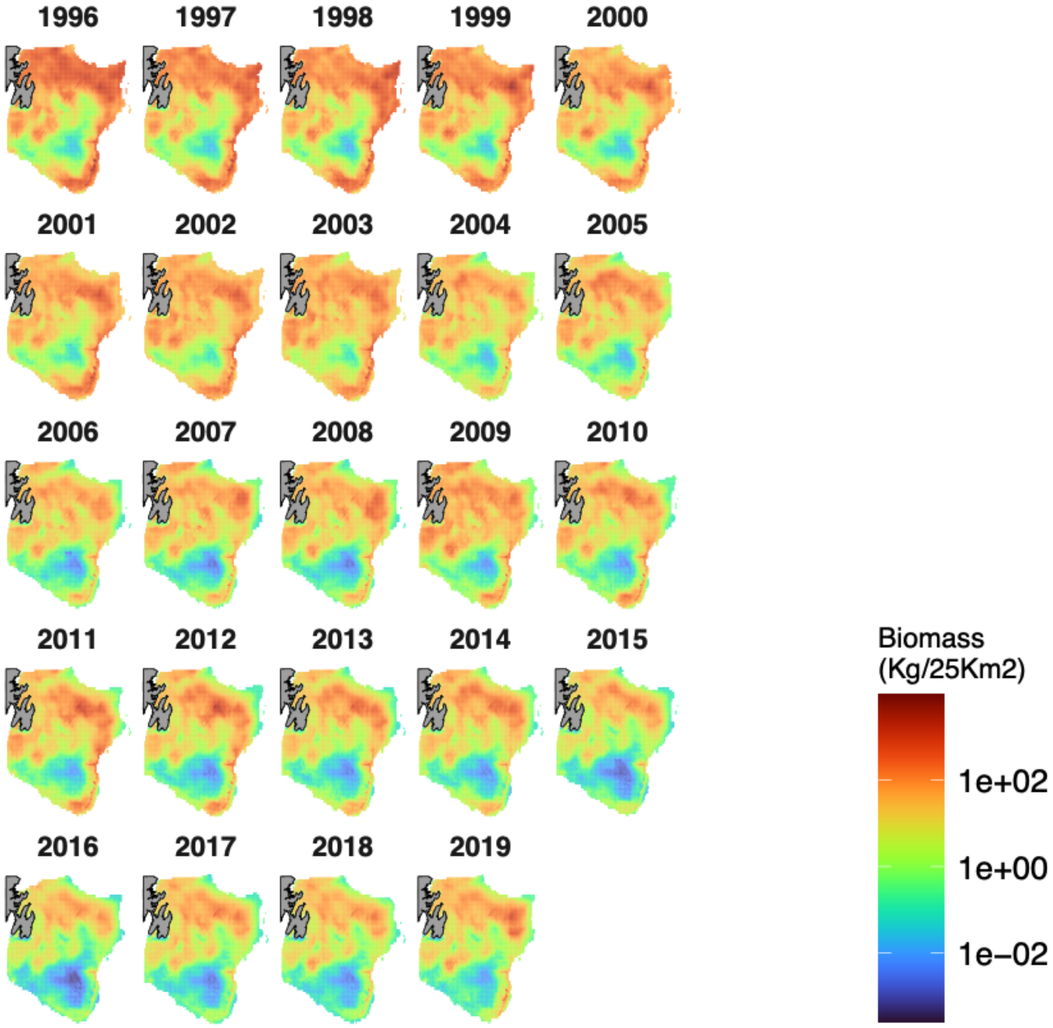


Figure A.5: Maps of snow crab biomass distribution over the Grand Banks obtained from the combined prediction of the delta_gamma model. Biomass is in log scale.

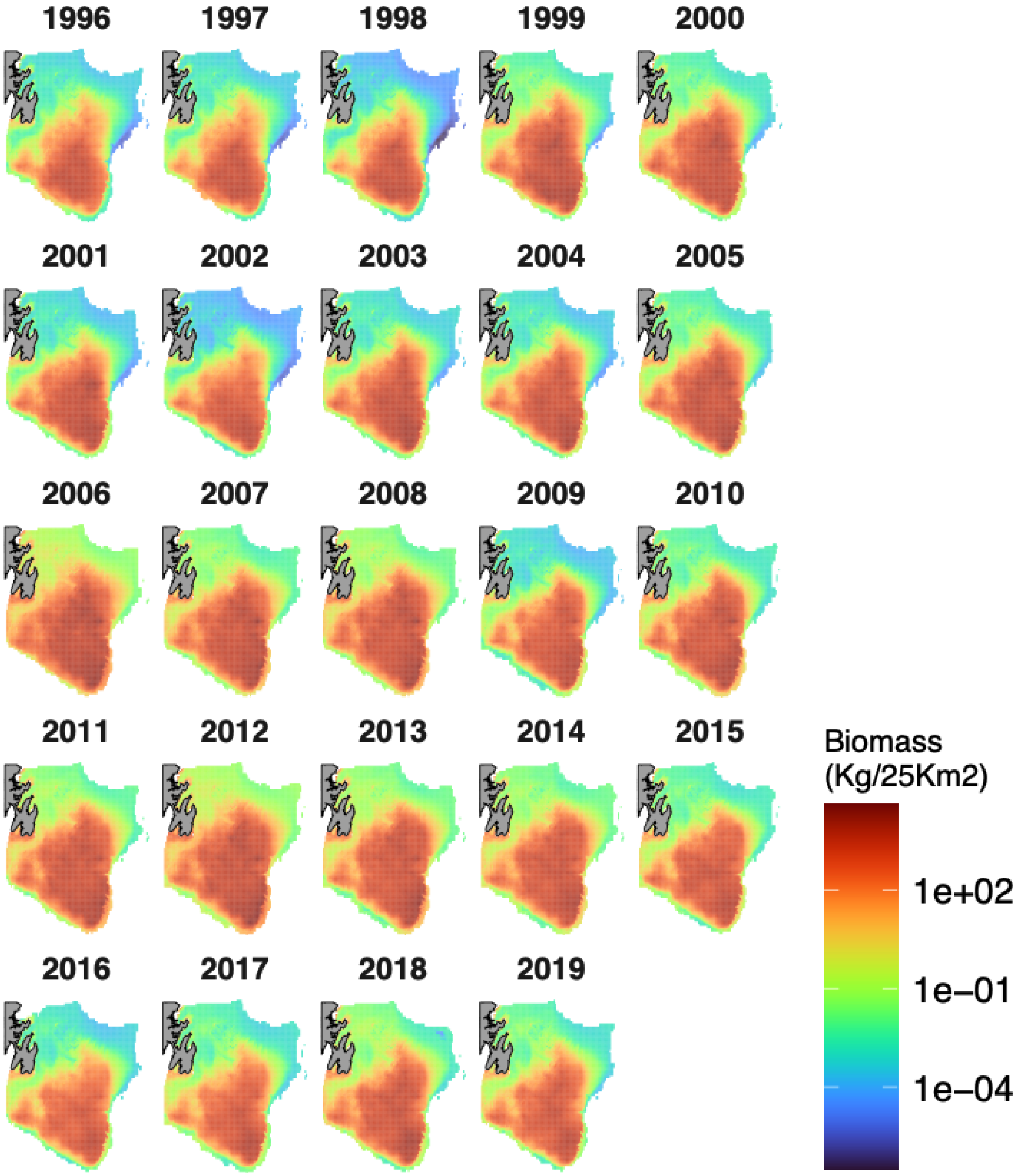


FIGURE A.6: Maps of yellowtail flounder biomass distribution over the Grand Banks obtained from the combined prediction of the delta_gamma model. Biomass is in log scale.

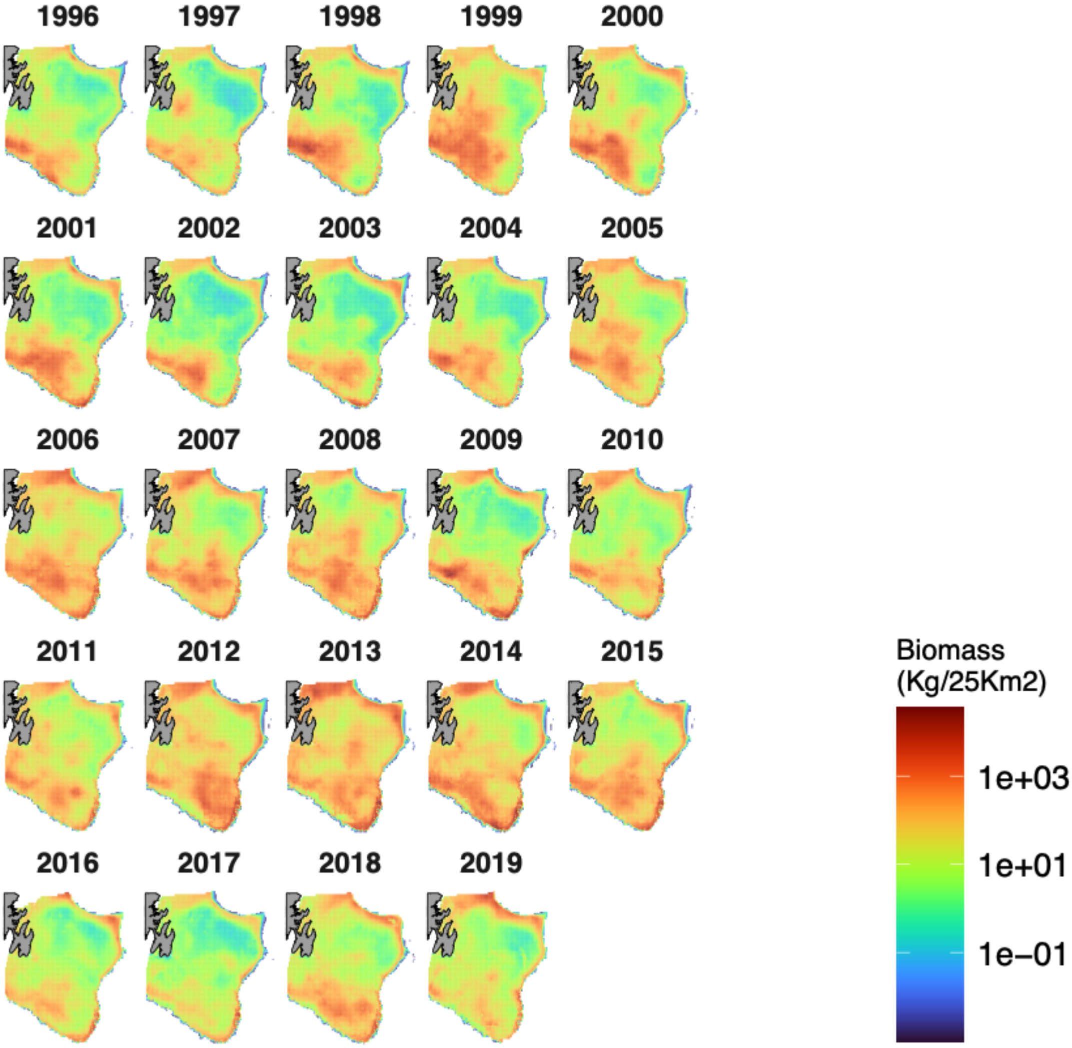


FIGURE A.7: Maps of Atlantic cod biomass distribution over the Grand Banks obtained from the combined prediction of the delta_gamma model. Biomass is in log scale.

Changes in the centre of gravity calculated from the dataset

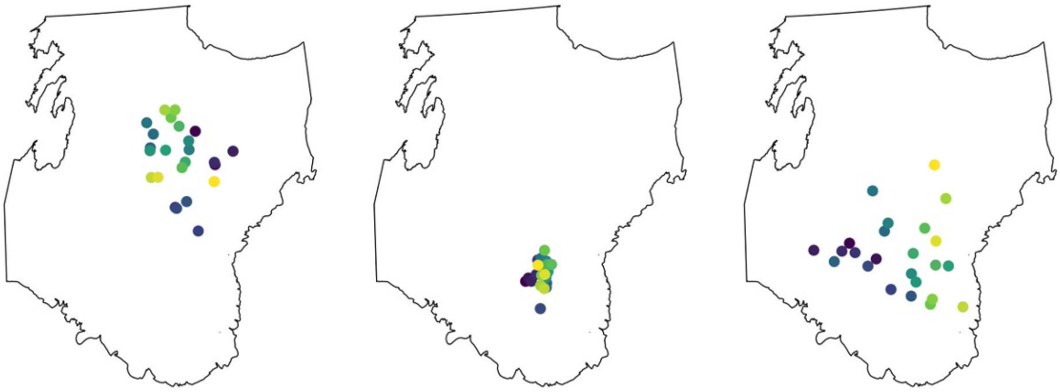


FIGURE A.8: Changes in the centre of gravity of snow crab (left), yellowtail flounder (center) and Atlantic cod (right).

A.2 Models validation

Snow crab model outputs

Spatiotemporal model fit by ML ['sdmTMB']

Formula: biomass ∼ 0 + as.factor(year) + s(depth_log) + s(tempatfishing)

Mesh: mesh
Time column: year
Data: data
Family: delta_gamma(link1 = 'logit', link2 = 'log')

- **Delta/hurdle model 1**

Family: binomial(link = 'logit')

	coef.est	coef.se
as.factor(year)1996	0.84	0.65
as.factor(year)1997	0.96	0.65
as.factor(year)1998	1.15	0.64
as.factor(year)1999	2.09	0.65
as.factor(year)2000	1.83	0.65
as.factor(year)2001	1.87	0.65
as.factor(year)2002	2.78	0.66
as.factor(year)2003	1.87	0.65
as.factor(year)2004	1.04	0.64
as.factor(year)2005	0.65	0.64

as.factor(year)2006	-0.34	0.66
as.factor(year)2007	-0.68	0.64
as.factor(year)2008	-0.56	0.64
as.factor(year)2009	0.45	0.64
as.factor(year)2010	0.56	0.64
as.factor(year)2011	0.75	0.65
as.factor(year)2012	0.07	0.65
as.factor(year)2013	-0.04	0.64
as.factor(year)2014	0.02	0.65
as.factor(year)2015	-0.50	0.67
as.factor(year)2016	-0.53	0.65
as.factor(year)2017	-0.38	0.67
as.factor(year)2018	-0.51	0.65
as.factor(year)2019	-0.22	0.64
sdepth_log	5.75	6.84
stempatfishing	-4.48	0.79

Smooth terms:

	Std. Dev.
sds(depth_log)	5
sds(tempatfishing)	0

Spatiotemporal AR1 correlation (rho): 0.86
Matern range: 145.52
Spatial SD: 1.82
Spatiotemporal SD: 1.22

- **Delta/hurdle model 2**

Family: Gamma(link = 'log')

	coef.est	coef.se
as.factor(year)1996	4.38	0.33
as.factor(year)1997	4.02	0.33
as.factor(year)1998	4.06	0.33
as.factor(year)1999	3.83	0.33
as.factor(year)2000	3.31	0.33
as.factor(year)2001	3.28	0.33
as.factor(year)2002	3.29	0.33
as.factor(year)2003	3.43	0.33
as.factor(year)2004	2.61	0.33
as.factor(year)2005	2.66	0.34
as.factor(year)2006	2.36	0.36
as.factor(year)2007	2.66	0.35

as.factor(year)2008	2.55	0.35
as.factor(year)2009	3.08	0.34
as.factor(year)2010	2.49	0.34
as.factor(year)2011	2.83	0.34
as.factor(year)2012	2.64	0.35
as.factor(year)2013	2.33	0.34
as.factor(year)2014	2.38	0.35
as.factor(year)2015	1.62	0.37
as.factor(year)2016	1.17	0.35
as.factor(year)2017	1.76	0.40
as.factor(year)2018	1.67	0.36
as.factor(year)2019	2.06	0.35
sdepth_log	8.43	4.60
stempatfishing	2.84	4.94

Smooth terms:

	Std. Dev.
sds(depth_log)	3.28
sds(tempatfishing)	1.57

Dispersion parameter: 0.93
Spatiotemporal AR1 correlation (rho): 0.71
Matern range: 97.00
Spatial SD: 1.15
Spatiotemporal SD: 1.22

ML criterion at convergence: 8017.538

Snow crab model diagnostic plots

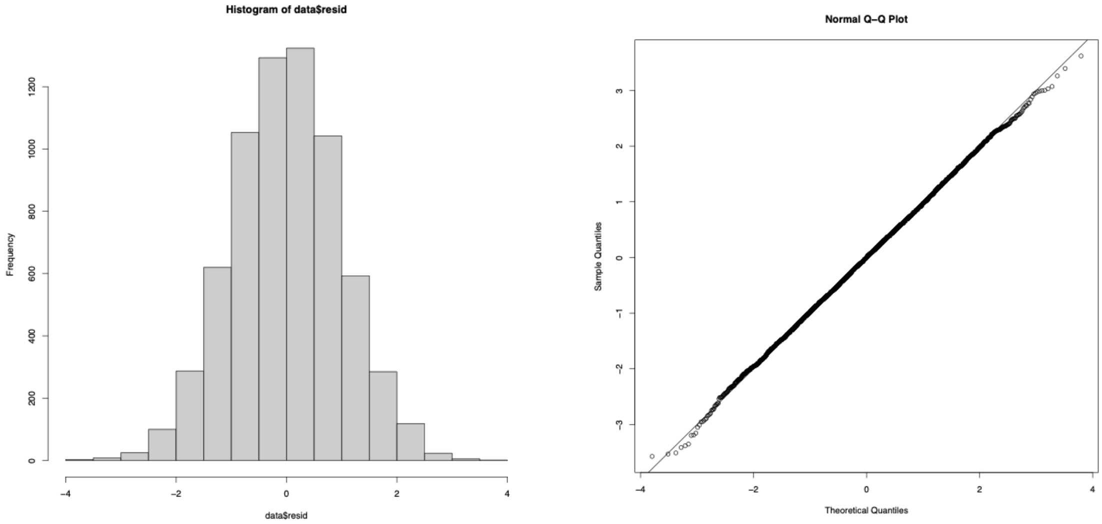


Figure A.9: Histogram (left) and quantile-quantile normality (QQ) plot for snow crab biomass model (right) with random effects estimated with MCMC while fixing fixed effects at their MLE values.

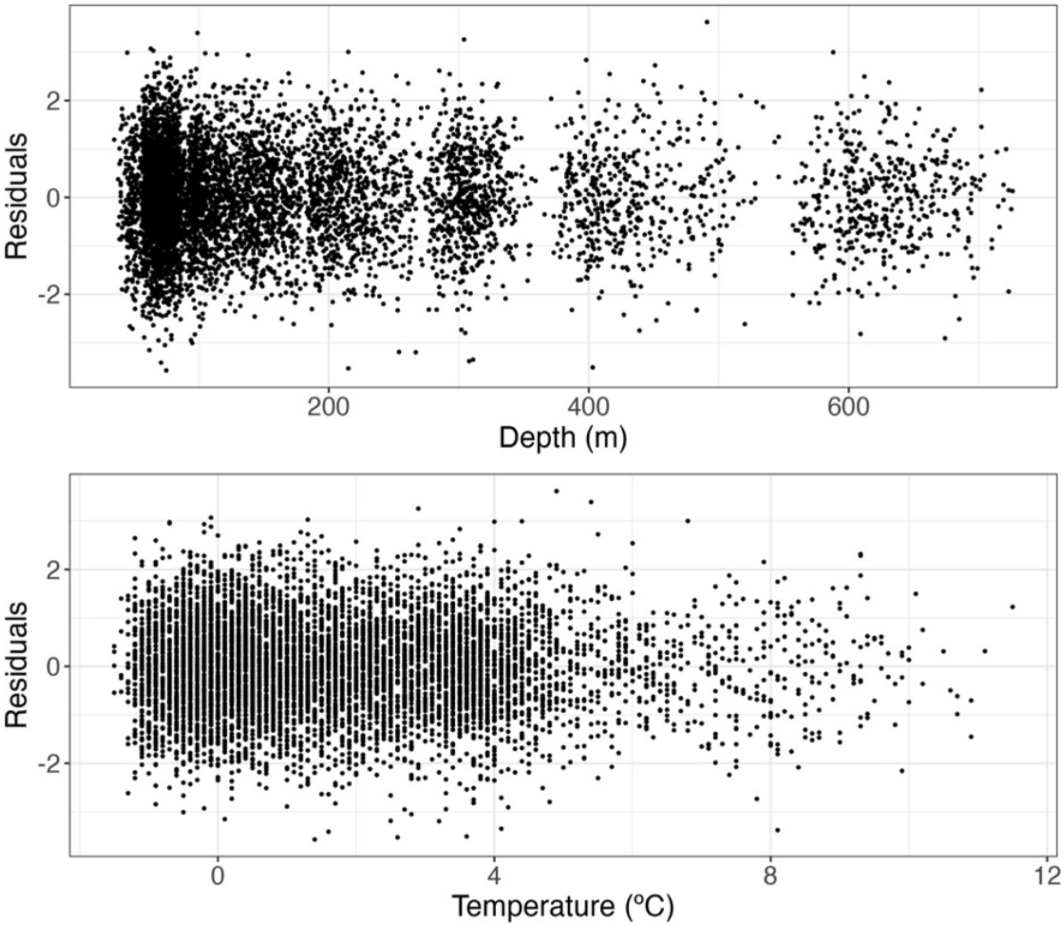


Figure A.10: Plot of snow crab biomass model residuals against each explanatory variable, depth (upper plot) and temperature (lower plot).

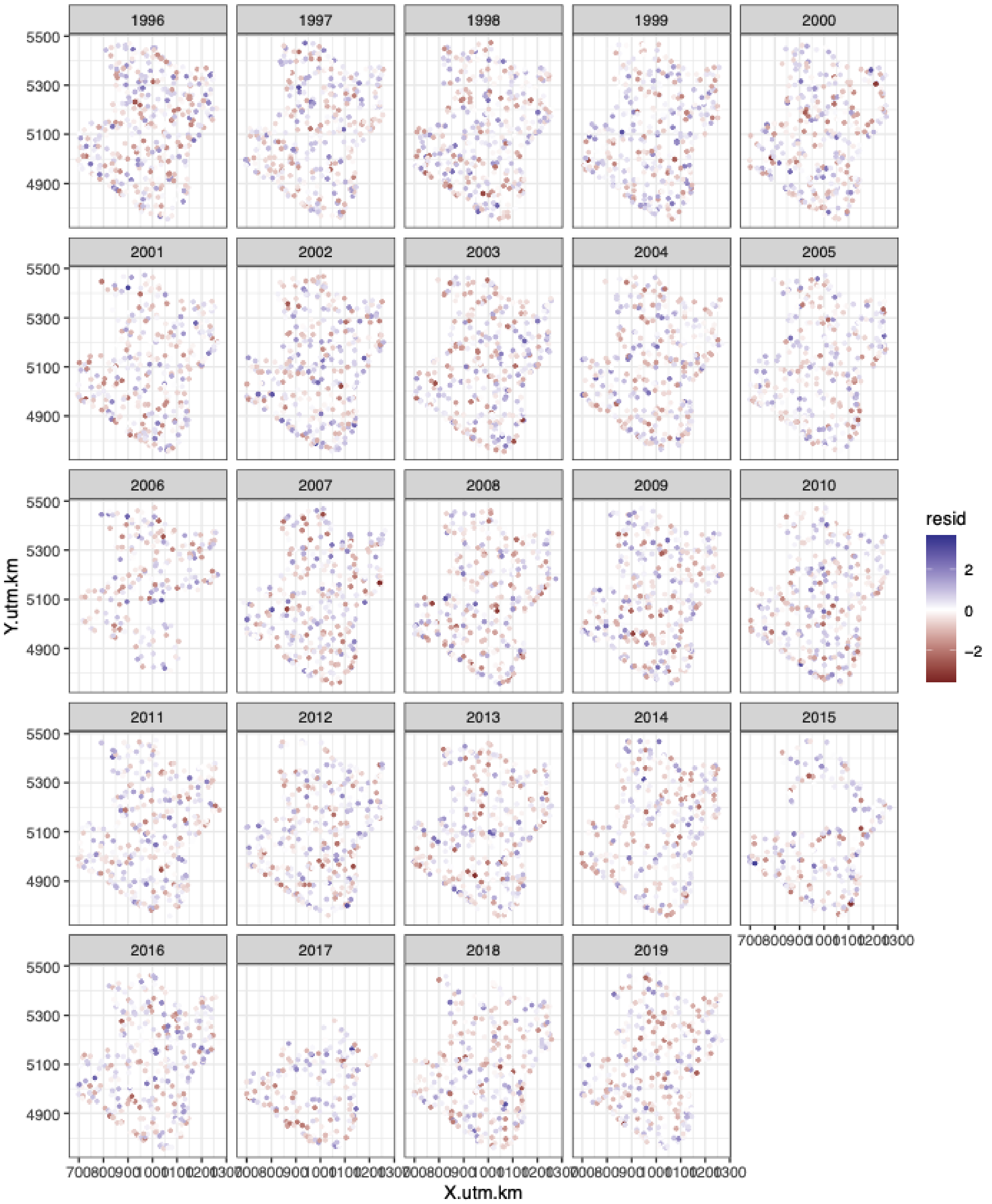


FIGURE A.11: Spatial and temporal distribution of residuals based on snow crab biomass model.

Yellowtail flounder model output

Spatiotemporal model fit by ML ['sdmTMB']

Formula: biomass ∼ 0 + as.factor(year) + s(depth_log) + s(tempatfishing)

Mesh: mesh
Time column: year
Data: data
Family: delta_gamma(link1 = 'logit', link2 = 'log')

- **Delta/hurdle model 1**

Family: binomial(link = 'logit')

	coef.est	coef.se
as.factor(year)1996	-4.85	1.47
as.factor(year)1997	-4.75	1.51
as.factor(year)1998	-6.53	1.47
as.factor(year)1999	-3.97	1.45
as.factor(year)2000	-3.45	1.45
as.factor(year)2001	-4.78	1.46
as.factor(year)2002	-5.44	1.46
as.factor(year)2003	-4.36	1.46
as.factor(year)2004	-4.61	1.44
as.factor(year)2005	-3.82	1.43
as.factor(year)2006	-0.65	1.44
as.factor(year)2007	-2.37	1.42
as.factor(year)2008	-1.88	1.41
as.factor(year)2009	-4.88	1.44
as.factor(year)2010	-3.33	1.42
as.factor(year)2011	-2.11	1.41
as.factor(year)2012	-1.11	1.41
as.factor(year)2013	-1.95	1.41
as.factor(year)2014	-1.87	1.42
as.factor(year)2015	-3.51	1.45
as.factor(year)2016	-4.05	1.43
as.factor(year)2017	-3.52	1.48
as.factor(year)2018	-3.05	1.43
as.factor(year)2019	-3.62	1.44
sdepth_log	-13.32	6.31
stempatfishing	-2.56	3.62

Smooth terms:

	Std. Dev.
sds(depth_log)	2.85
sds(tempatfishing)	1.61

Spatiotemporal AR1 correlation (rho): 0.82
Matern range: 231.86
Spatial SD: 2.69
Spatiotemporal SD: 1.55

- **Delta/hurdle model 2**

Family: Gamma(link = 'log')

	coef.est	coef.se
as.factor(year)1996	3.22	0.54
as.factor(year)1997	3.26	0.55
as.factor(year)1998	3.20	0.54
as.factor(year)1999	4.42	0.52
as.factor(year)2000	4.25	0.52
as.factor(year)2001	3.77	0.54
as.factor(year)2002	2.90	0.54
as.factor(year)2003	3.89	0.53
as.factor(year)2004	3.74	0.52
as.factor(year)2005	4.56	0.51
as.factor(year)2006	5.09	0.51
as.factor(year)2007	4.70	0.50
as.factor(year)2008	4.81	0.50
as.factor(year)2009	4.00	0.52
as.factor(year)2010	4.56	0.51
as.factor(year)2011	4.83	0.50
as.factor(year)2012	5.31	0.50
as.factor(year)2013	4.73	0.50
as.factor(year)2014	4.43	0.51
as.factor(year)2015	4.28	0.52
as.factor(year)2016	3.36	0.51
as.factor(year)2017	3.48	0.53
as.factor(year)2018	4.35	0.51
as.factor(year)2019	3.79	0.52
sdepth_log	0.58	4.92
stempatfishing	-0.78	1.94

Smooth terms:

	Std. Dev.
sds(depth_log)	2.42
sds(tempatfishing)	0.78

Dispersion parameter: 1.25
Spatiotemporal AR1 correlation (rho): 0.73
Matern range: 128.11

Spatial SD: 1.25
Spatiotemporal SD: 1.55

ML criterion at convergence: 12570.374

Yellowtail flounder diagnostic plots

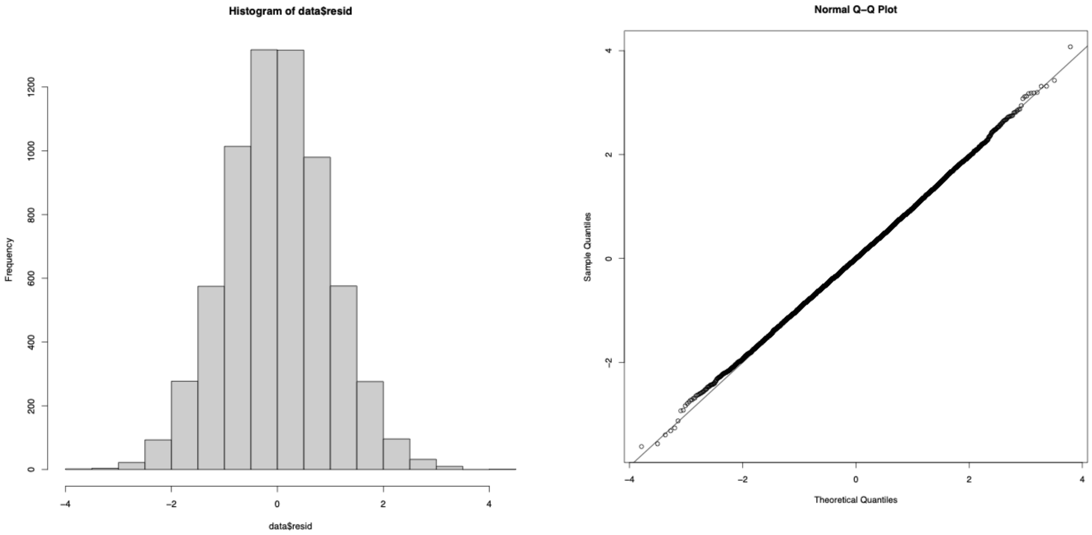


Figure A.12: Histogram (left) and quantile-quantile normality (QQ) plot for yellowtail flounder biomass model (right) with random effects estimated with MCMC while fixing fixed effects at their MLE values.

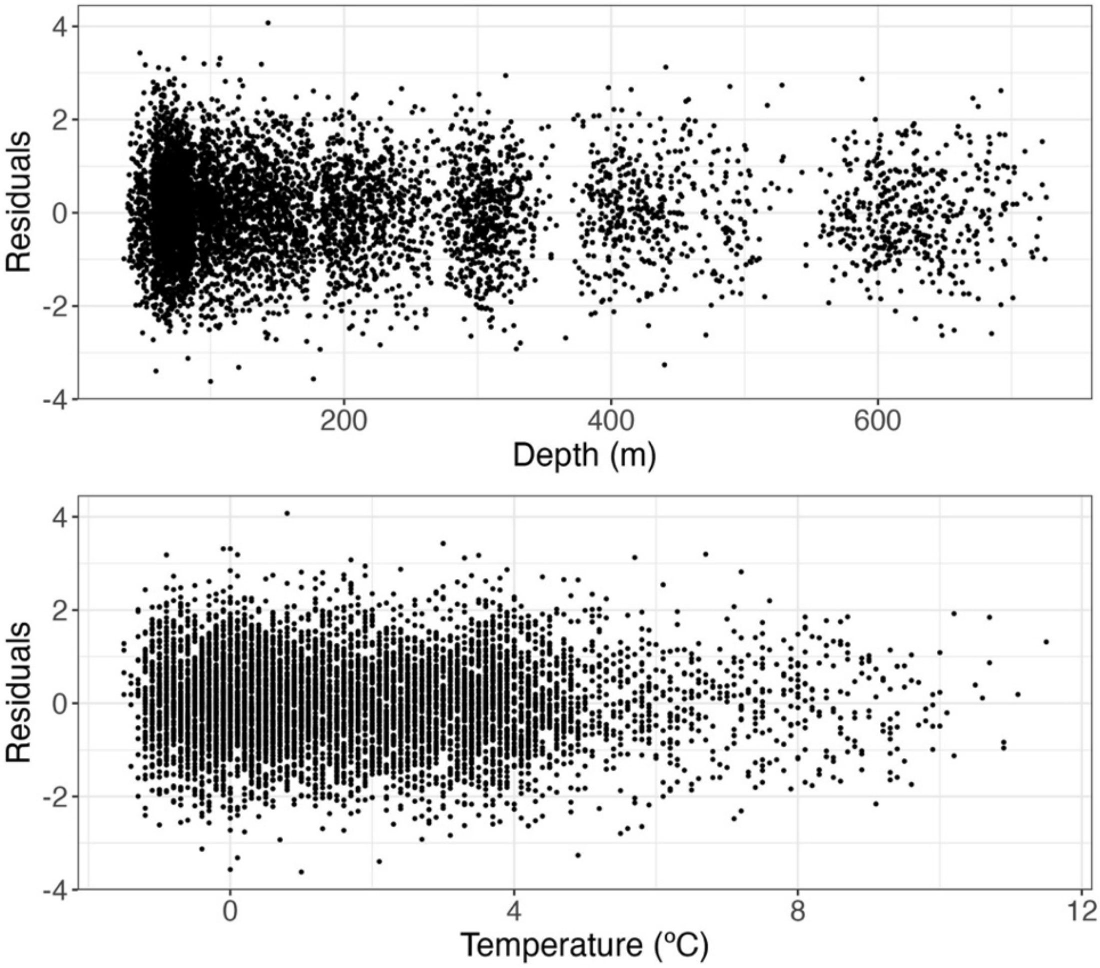


FIGURE A.13: Plot of yellowtail flounder biomass model residuals against each explanatory variable, depth (upper plot) and temperature (lower plot).

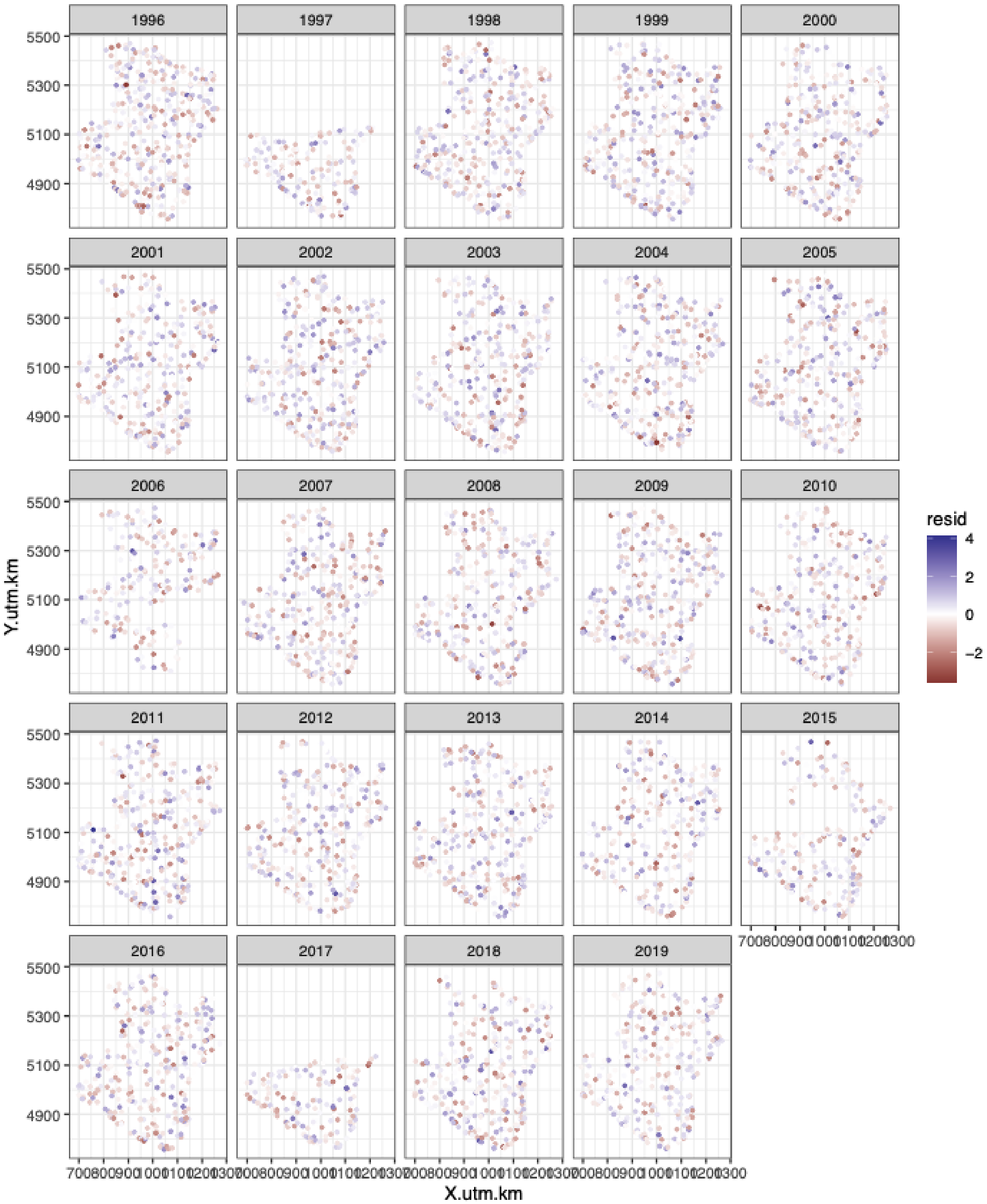


FIGURE A.14: Spatial and temporal distribution of residuals based on yellowtail flounder biomass model.

Atlantic cod model output

Spatiotemporal model fit by ML ['sdmTMB']

Formula: biomass $\sim$ 0 + as.factor(year) + s(depth_log) + s(tempatfishing)

Mesh: mesh
Time column: year
Data: data
Family: delta_gamma(link1 = 'logit', link2 = 'log')

- **Delta/hurdle model 1**

Family: binomial(link = 'logit')

	coef.est	coef.se
as.factor(year)1996	0.27	0.50
as.factor(year)1997	-0.35	0.51
as.factor(year)1998	-0.41	0.50
as.factor(year)1999	0.85	0.51
as.factor(year)2000	0.73	0.51
as.factor(year)2001	0.93	0.51
as.factor(year)2002	0.14	0.51
as.factor(year)2003	0.10	0.51
as.factor(year)2004	-0.55	0.51
as.factor(year)2005	0.52	0.51
as.factor(year)2006	1.31	0.54
as.factor(year)2007	1.14	0.52
as.factor(year)2008	1.07	0.51
as.factor(year)2009	0.53	0.51
as.factor(year)2010	0.38	0.51
as.factor(year)2011	0.13	0.51
as.factor(year)2012	1.20	0.52
as.factor(year)2013	1.37	0.52
as.factor(year)2014	1.24	0.52
as.factor(year)2015	1.12	0.53
as.factor(year)2016	1.19	0.51
as.factor(year)2017	-0.18	0.56
as.factor(year)2018	0.66	0.51
as.factor(year)2019	0.82	0.51
sdepth_log	-7.72	7.90
stempatfishing	2.21	4.73

Smooth terms:

	Std. Dev.
sds(depth_log)	8.94
sds(tempatfishing)	3.04

Matern range: 189.74
Spatial SD: 1.04
Spatiotemporal SD: 0.85

- **Delta/hurdle model 2**

Family: Gamma(link = 'log')

	coef.est	coef.se
as.factor(year)1996	4.01	0.33
as.factor(year)1997	4.37	0.35
as.factor(year)1998	4.51	0.34
as.factor(year)1999	4.71	0.33
as.factor(year)2000	4.57	0.33
as.factor(year)2001	4.49	0.33
as.factor(year)2002	3.89	0.34
as.factor(year)2003	4.22	0.34
as.factor(year)2004	4.00	0.34
as.factor(year)2005	4.73	0.33
as.factor(year)2006	5.07	0.35
as.factor(year)2007	4.83	0.33
as.factor(year)2008	4.97	0.33
as.factor(year)2009	4.61	0.34
as.factor(year)2010	4.31	0.33
as.factor(year)2011	4.46	0.33
as.factor(year)2012	5.33	0.33
as.factor(year)2013	5.55	0.33
as.factor(year)2014	5.60	0.34
as.factor(year)2015	5.03	0.35
as.factor(year)2016	4.12	0.33
as.factor(year)2017	3.71	0.41
as.factor(year)2018	4.60	0.34
as.factor(year)2019	4.19	0.33
sdepth_log	-5.21	4.98
stempatfishing	1.32	3.20

Smooth terms:

	Std. Dev.
sds(depth_log)	3.07
sds(tempatfishing)	1.68

Dispersion parameter: 0.75
Matern range: 95.97
Spatial SD: 0.98
Spatiotemporal SD: 0.85

ML criterion at convergence: 13000.057

Atlantic cod diagnostic plots

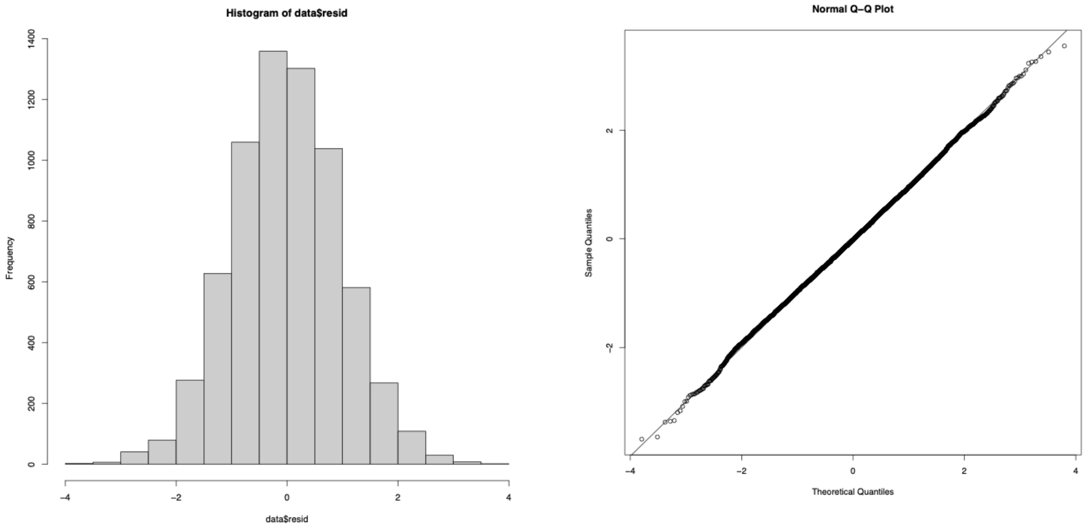


FIGURE A.15: Histogram (left) and quantile-quantile normality (QQ) plot for Atlantic cod biomass model (right) with random effects estimated with MCMC while fixing fixed effects at their MLE values.

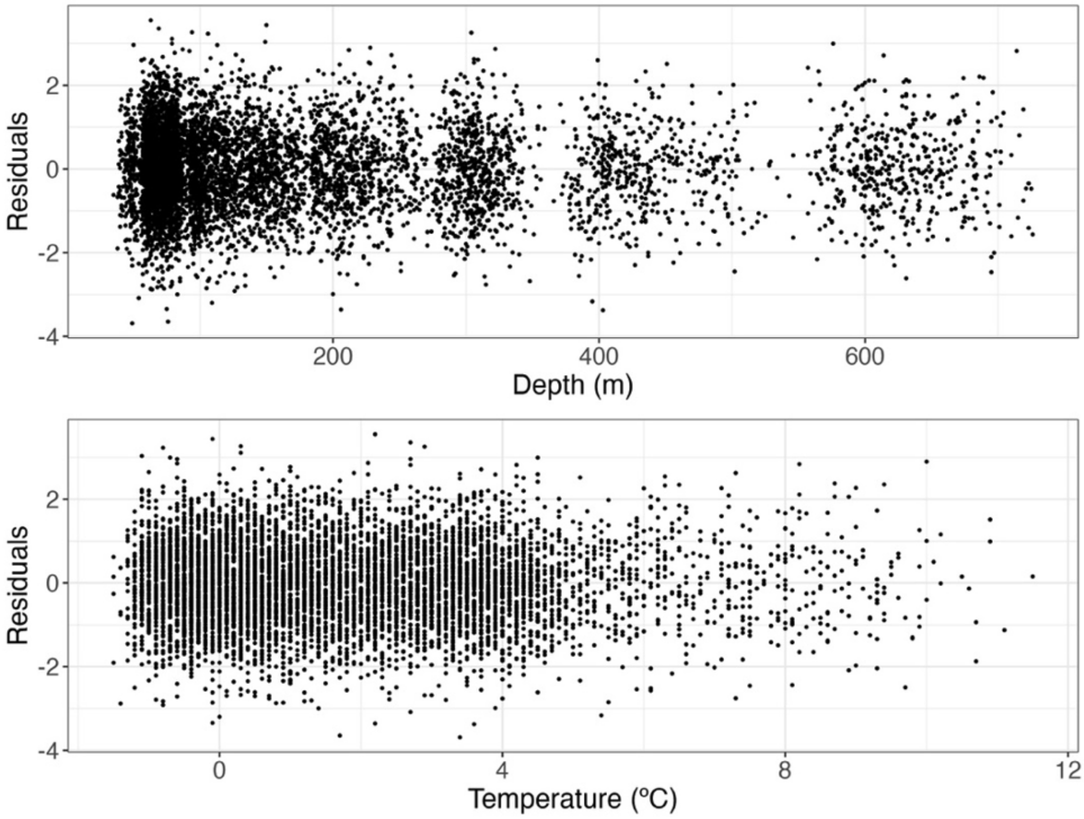


FIGURE A.16: Plot of Atlantic cod biomass model residuals against each explanatory variable, depth (upper plot) and temperature (lower plot).

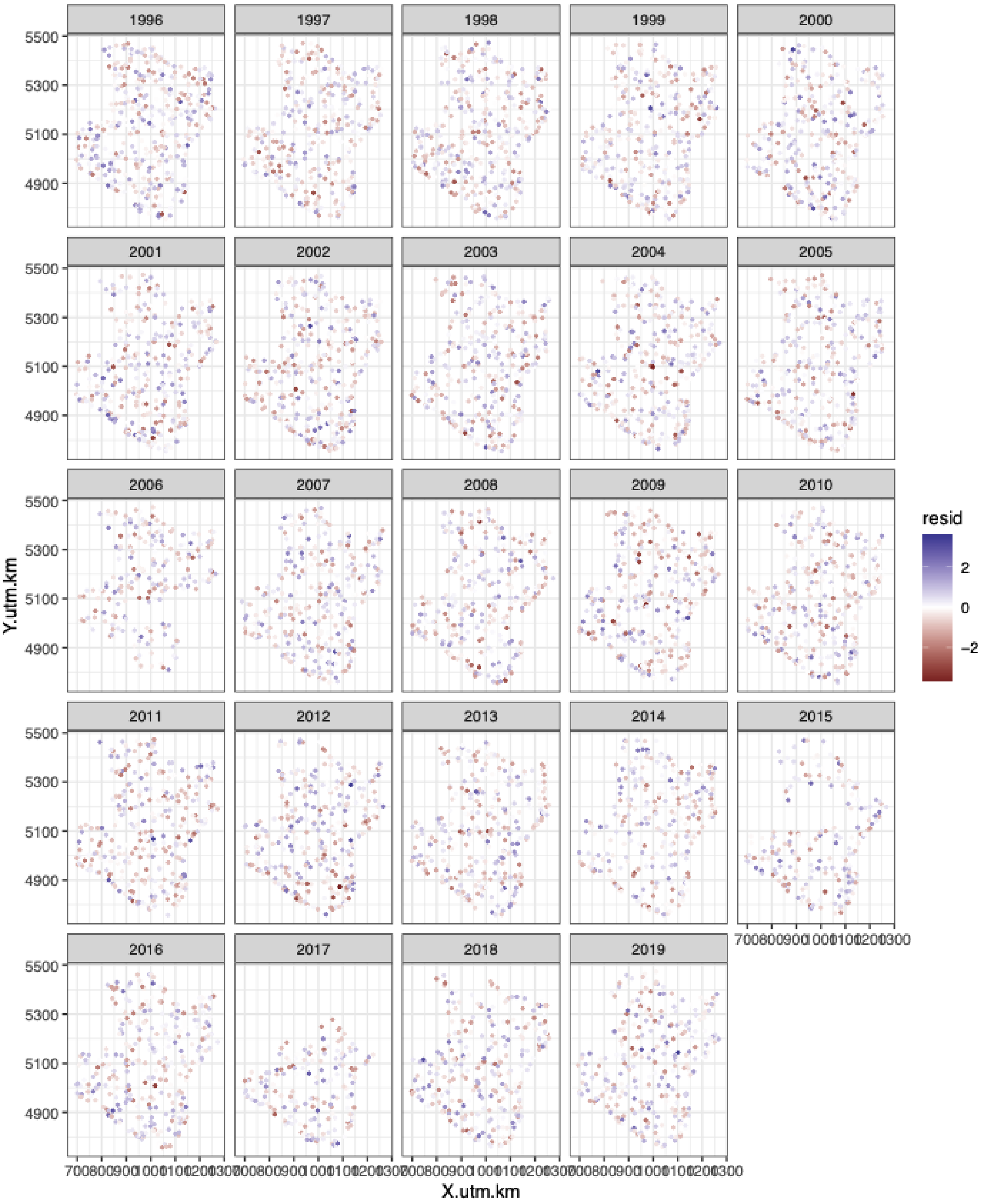


FIGURE A.17: Spatial and temporal distribution of residuals based on Atlantic cod biomass model.

APPENDIX B

Supplementary material for Chapter 4

B.1 Models diagnostics by species

Snow crab

Table B.1: Candidate species distribution models for snow crab that were evaluated for fit to observed data. Akaike information criteria (AIC), Akaike weights (Δ AIC) and out-of-sample log likelihood (Loglik) measures were used to identify the best model. Loglik are displayed as negative loglikelihood values for easier interpretation, with lower values indicating the model with better predictability. Depth and temperature were represented as second order polynomials and depth was log transformed. Df indicates the degree of freedom. The best scoring models are indicated in bold. Deviance explained is the percent deviance explained when compared to an intercept-only null model.

Model	Family	Configuration	df	AIC	Neg. Log Likelihood	Deviance explained	ΔAIC	ΔNeg. Log Likelihood
4	delta_gamma	biomass ~ depth	7	21002	10494.03	55.60 %	2859	1437.537
3	delta_gamma	biomass ~ temp + depth	11	19941	9959.721	57.86 %	1798	903.228
2	delta_lognormal	biomass ~ temp + depth | spatial	15	18143	9056.493	61.69 %	0	0
1	delta_gamma	biomass ~ temp + depth | spatial	15	18204	9087.013	61.56 %	61	30.52

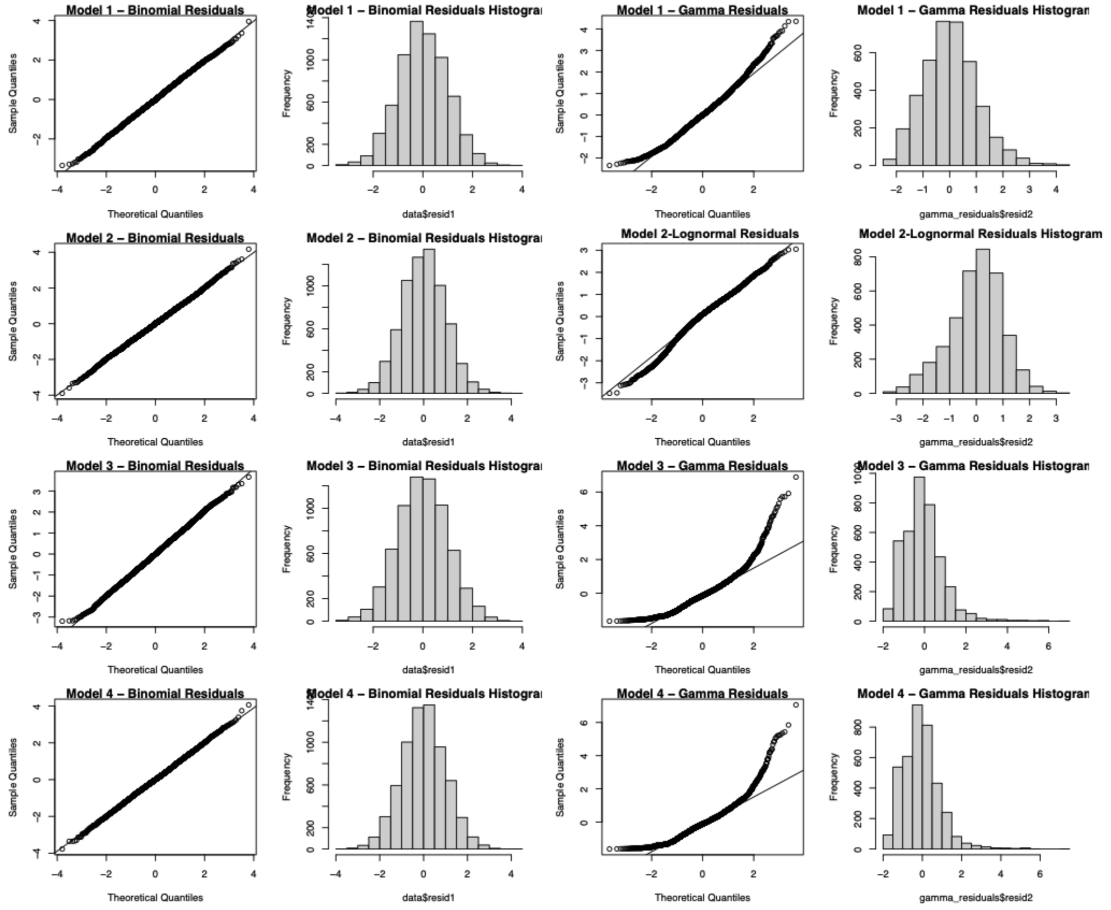


Figure B.1: Quantile residuals for the four model configurations described in Table 1.

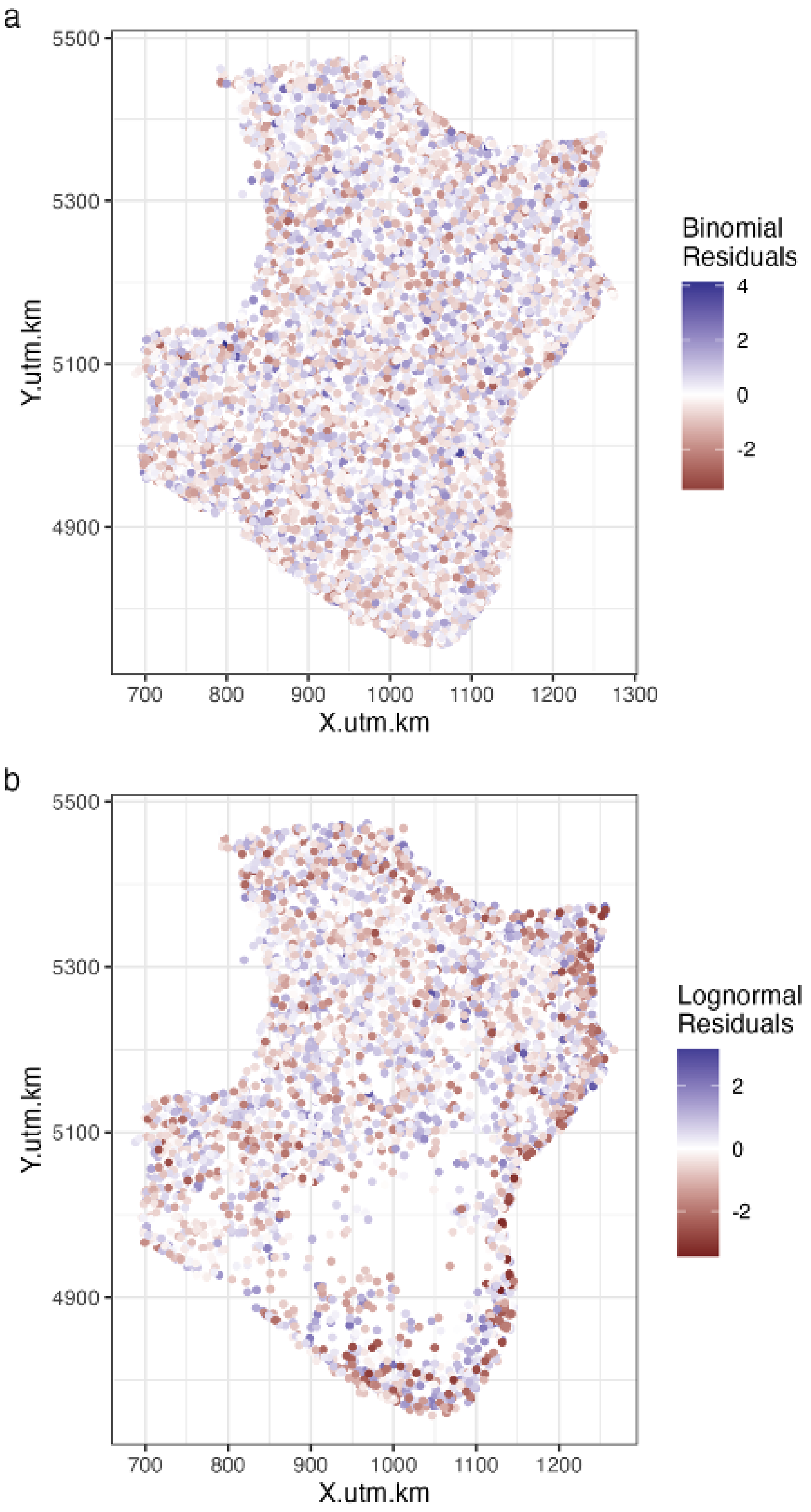


FIGURE B.2: Spatial patters of snow crab SDM residuals for the binomial (a) and lognormal (b) component.

Yellowtail flounder

Table B.2: Candidate species distribution models for yellowtail flounder that were evaluated for fit to observed data. Akaike information criteria (AIC), Akaike weights (Δ AIC) and out-of-sample log likelihood (Loglik) measures were used to identify the best model. Loglik are displayed as negative loglikelihood values for easier interpretation, with lower values indicating the model with better predictability. Depth and temperature were represented as second order polynomials and depth was log transformed. Df indicates the degree of freedom. The best scoring models are indicated in bold. Deviance explained is the percent deviance explained when compared to an intercept-only null model.

Model	Family	Configuration	df	AIC	Neg. Log Likelihood	Deviance explained	ΔAIC	ΔNeg. Log Likelihood
4	delta_gamma	biomass ∼ depth	7	28083	14034.51	62.25 %	1729	872.64
3	delta_gamma	biomass ∼ temp + depth	11	27713	13845.29	62.75 %	1359	683.42
2	delta_lognormal	biomass ∼ temp + depth | spatial	15	26578	13273.86	64.30 %	224	111.99
1	delta_gamma	biomass ∼ temp + depth | spatial	15	26354	13161.87	64.6 %	0	0

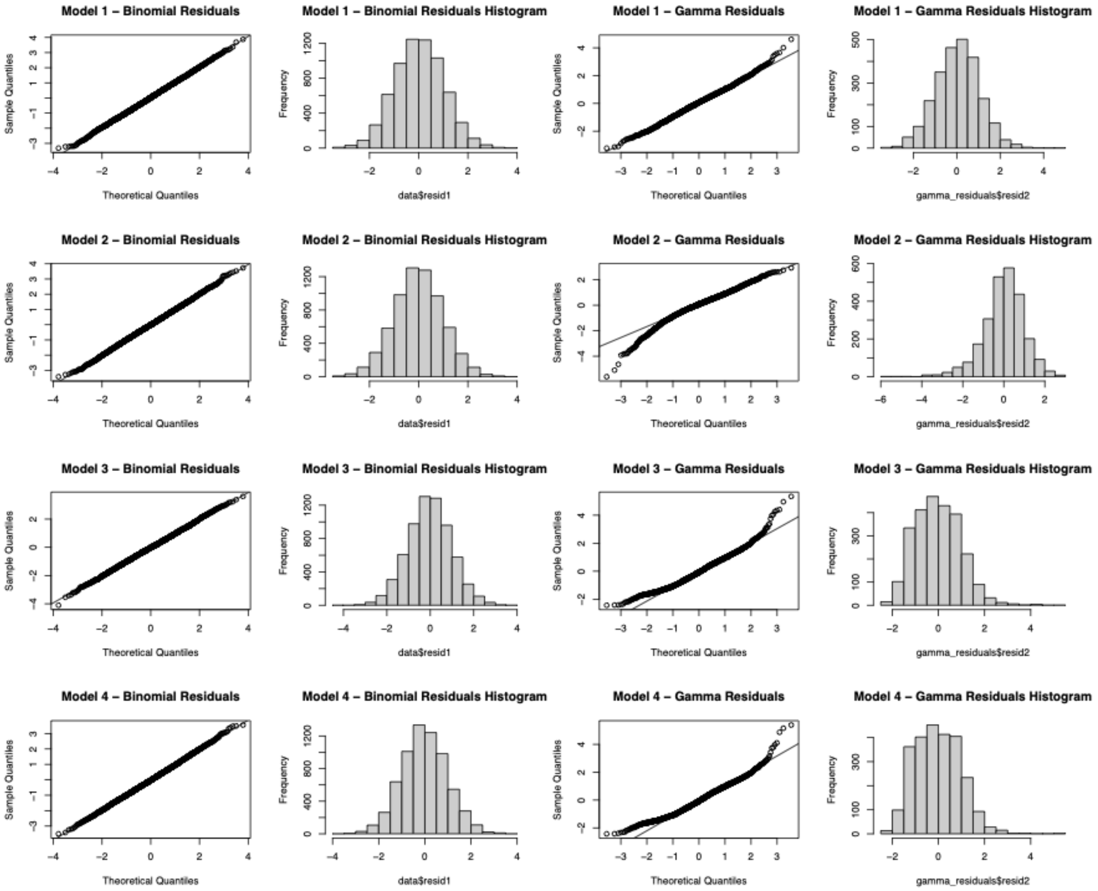


Figure B.3: Quantile residuals for the four model configurations described in Table 2.

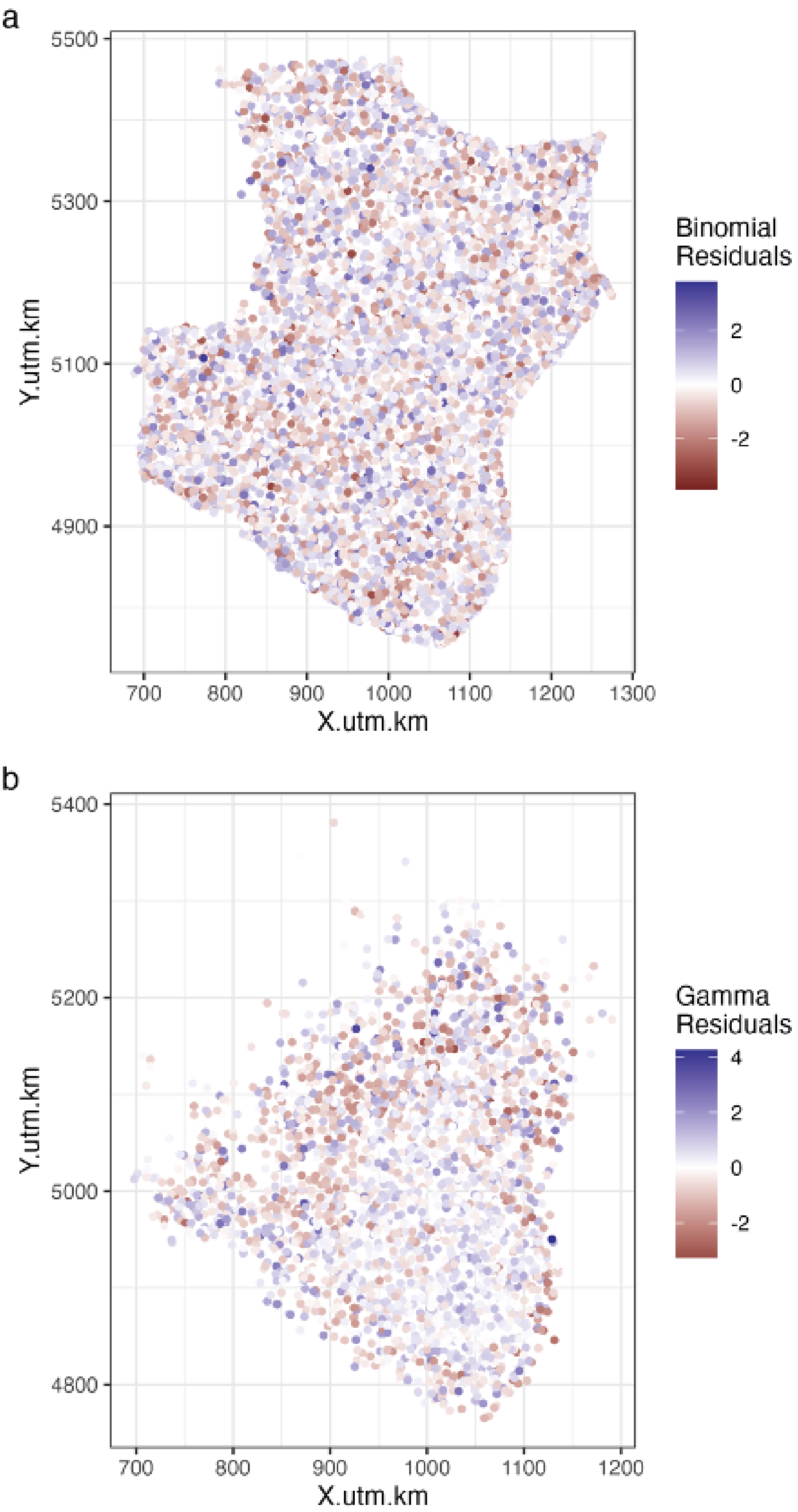


FIGURE B.4: Spatial patters of yellowtail flounder SDM residuals for the binomial (a) and gamma (b) component.

Atlantic cod

TABLE B.3: Candidate species distribution models for Atlantic cod that were evaluated for fit to observed data. Akaike information criteria (AIC), Akaike weights (Δ AIC) and out-of-sample log likelihood (Loglik) measures were used to identify the best model. Loglik are displayed as negative loglikelihood values for easier interpretation, with lower values indicating the model with better predictability. Depth and temperature were represented as second order polynomials and depth was log transformed. Df indicates the degree of freedom. The best scoring models are indicated in bold. Deviance explained is the percent deviance explained when compared to an intercept-only null model.

Model	Family	Configuration	df	AIC	Neg. Log Likelihood	Deviance explained	ΔAIC	ΔNeg. Log Likelihood
4	delta_gamma	biomass ~ depth	7	31406	15695.98	59.9 %	4419	2217.67
3	delta_gamma	biomass ~ temp + depth	11	30408	15193.14	61.25 %	3421	1714.83
2	delta_lognormal	biomass ~ temp + depth | spatial	15	26987	13478.31	65.63 %	0	0
1	delta_gamma	biomass ~ temp + depth | spatial	15	27845	13907.38	64.53 %	858	429.07

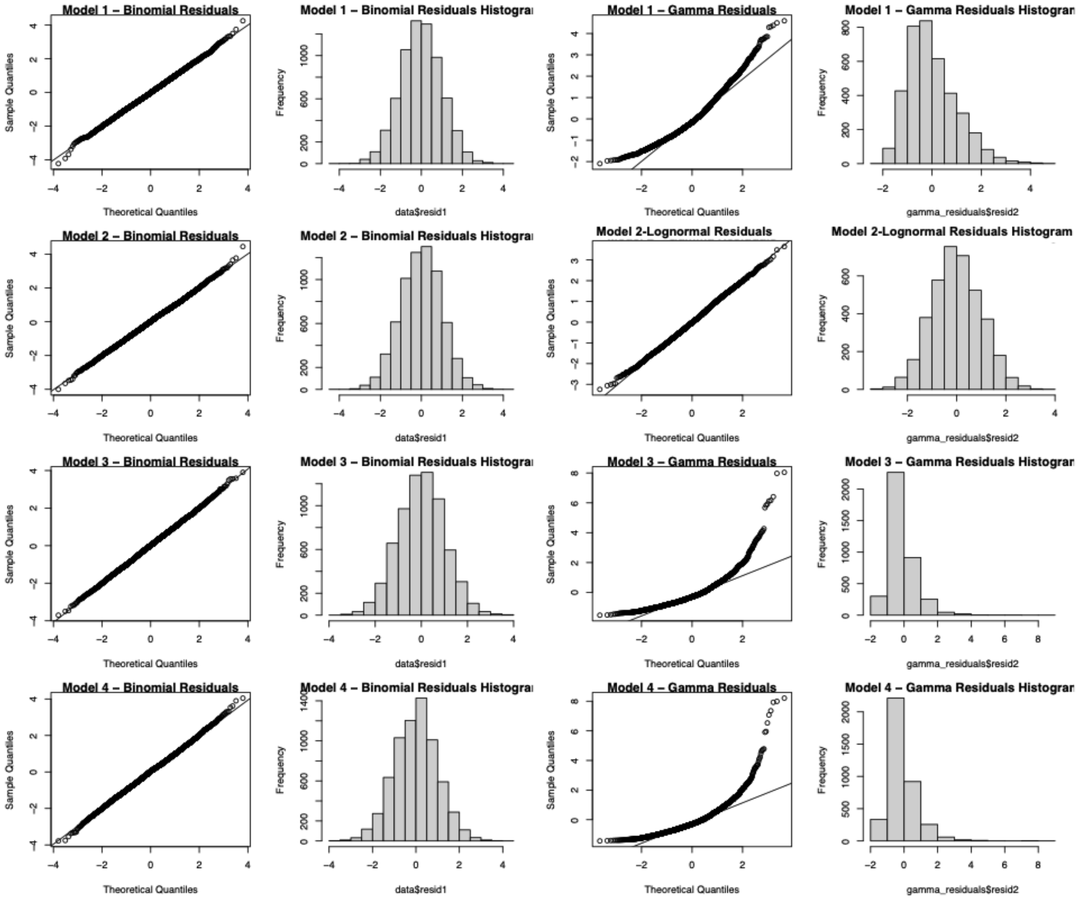


FIGURE B.5: Quantile residuals for the four model configurations described in Table 3.

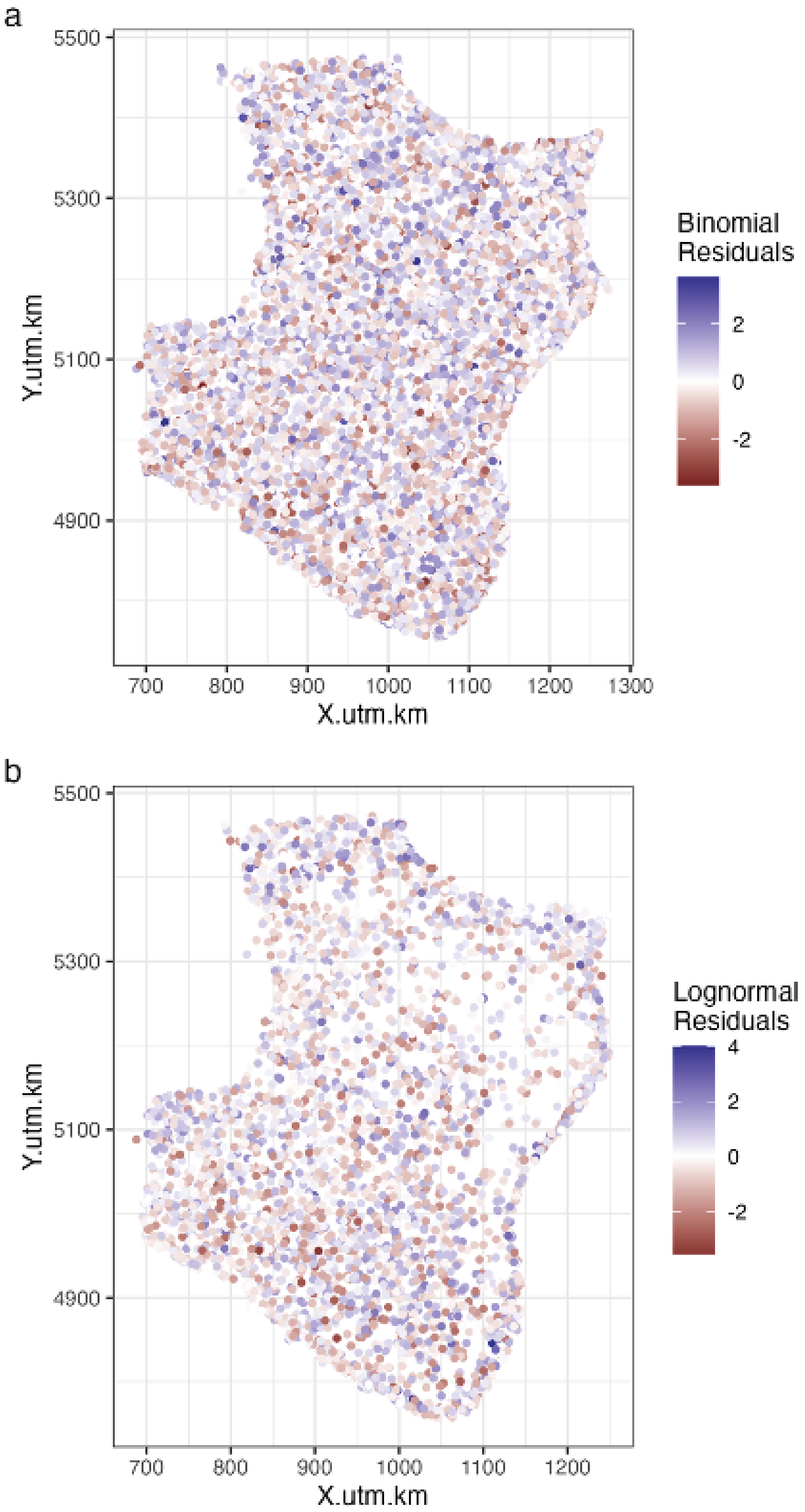


FIGURE B.6: Spatial patters of Atlantic cod SDM residuals for the binomial (a) and lognormal (b) component.

B.2 Model predictability

Historical period

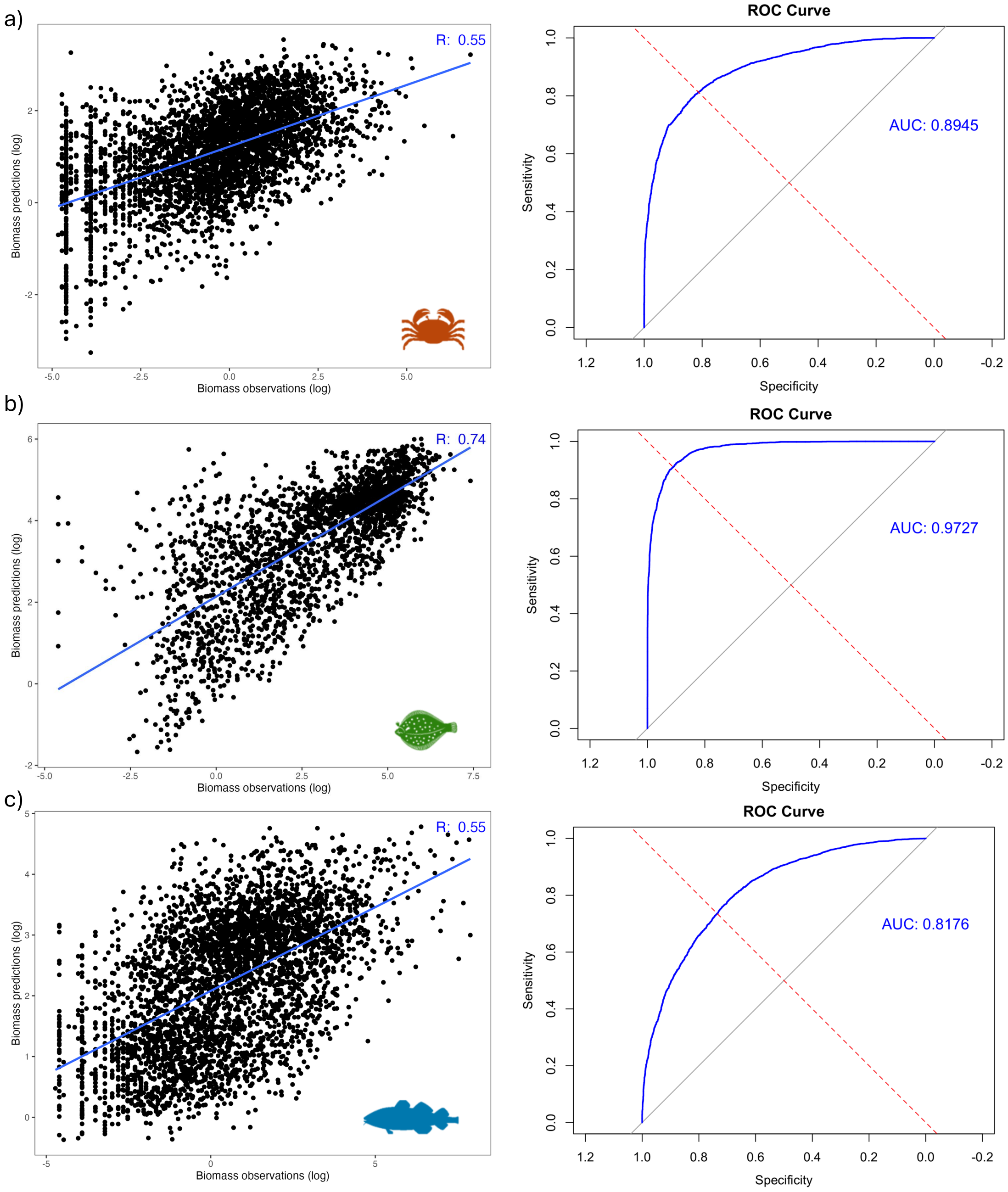


FIGURE B.7: Predictive performance of species distribution models for a) snow crab, b) yellowtail flounder, and c) Atlantic cod. The left panels display the Pearson correlation coefficients between predicted and observed values for the gamma component. The right panels present the area under the curve (AUC) for the binomial component.

Out-of-sample cross-validation

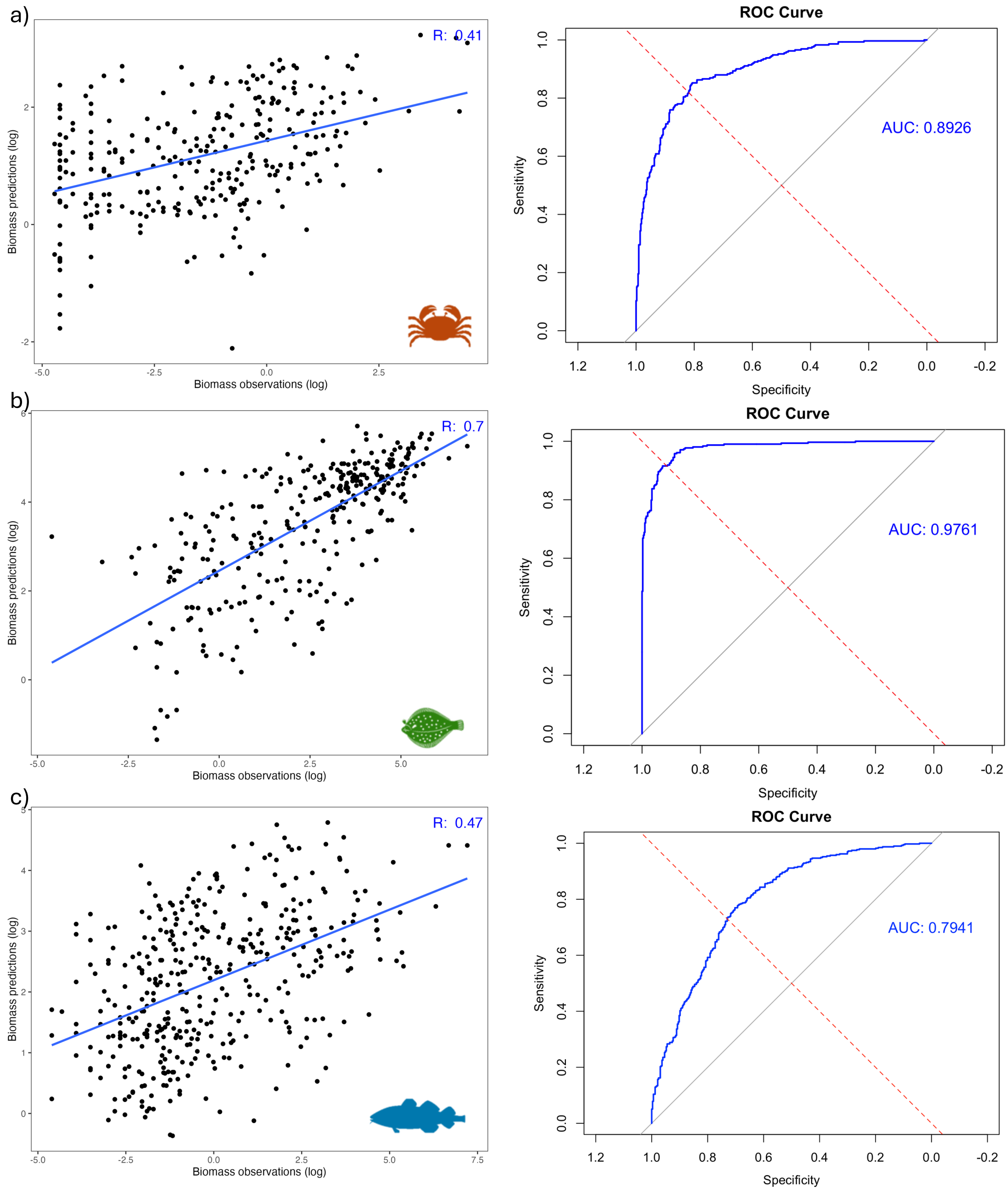


FIGURE B.8: Out-of-sample predictive performance of species distribution models for a) snow crab, b) yellowtail flounder, and c) Atlantic cod from 2017 to 2019. The left panels show the Pearson correlation between predicted and observed values for the gamma component, while the right panels display the area under the curve (AUC) for the binomial component.

B.3 SDMs outputs

Table B.4: Estimates and confidence intervals for snow crab, yellowtail flounder and Atlantic cod based on the fitted species distribution model

Effect	Term	Estimate	Std. Error	Conf. Low	Conf. High
Snow crab					
Fixed	Intercept	0.493	0.496	-0.478	1.47
Fixed	poly(depth, 2)1	35.7	9.42	17.2	54.1
Fixed	poly(depth, 2)2	-49.5	5.14	-59.6	-39.5
Fixed	poly(tempatfishing, 2)1	-38.7	5.54	-49.6	-27.8
Fixed	poly(tempatfishing, 2)2	0.525	3.9	-7.12	8.17
Random	Matern range	150	26.4	160	211
Random	Spatial sd	1.73	0.235	1.33	2.26
Yellowtail flounder					
Fixed	Intercept	-2.89	2.02	-6.84	1.06
Fixed	poly(depth, 2)1	-167	15.1	-196	-137
Fixed	poly(depth, 2)2	6.9	11	-14.7	28.5
Fixed	poly(tempatfishing, 2)1	4.59	7.2	-9.52	18.7
Fixed	poly(tempatfishing, 2)2	-28.8	5.51	-39.5	-18
Random	Matern range	399	122	220	726
Random	Spatial sd	2.77	0.736	1.65	4.67
Atlantic cod					
Fixed	Intercept	0.454	0.256	-0.0478	0.956
Fixed	poly(depth, 2)1	-20.2	7.86	-35.7	-4.83
Fixed	poly(depth, 2)2	-93.1	4.98	-103	-83.3
Fixed	poly(tempatfishing, 2)1	38.3	4.82	28.8	47.7
Fixed	poly(tempatfishing, 2)2	-50.8	3.47	-57.6	-44
Random	Matern range	117	20.4	82.8	164
Random	Spatial sd	1.10	0.115	0.898	1.35

B.4 Temperature bias correction

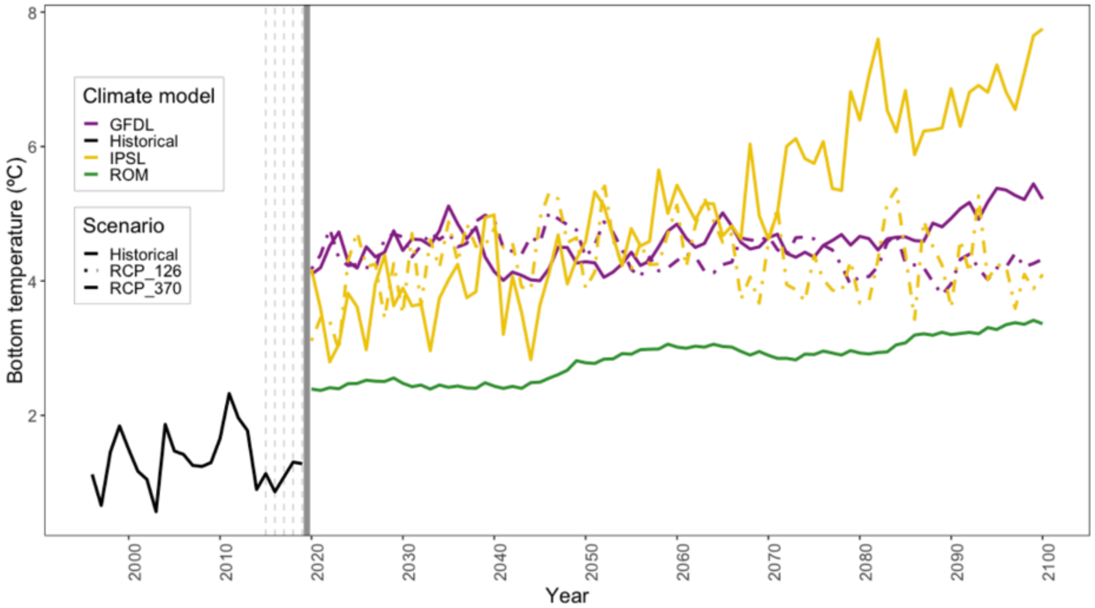


FIGURE B.9: Original temperature outputs derived from climate models

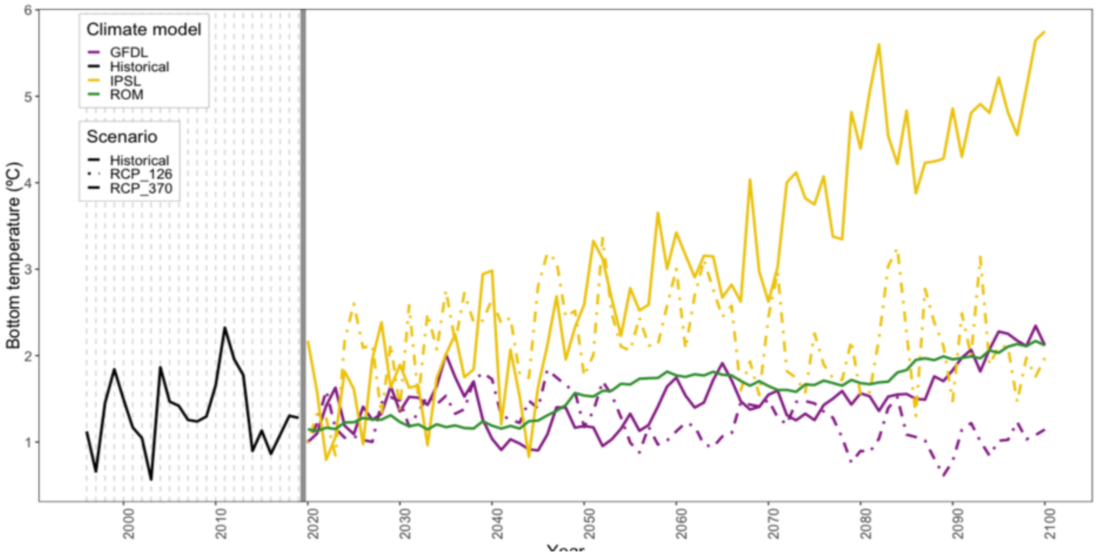


FIGURE B.10: Temperature outputs derived from climate models corrected to observations using years 2015-2019.

B.5 ESM bathymetry bias assessment

To calculate bathymetry bias among climate models (i.e., IPSL and GFDL) and observations (bathymetry values from the GEBCO project), we performed depth data interpolation or re-gridding from climate model outputs to align with the spatial grid resolution of observed data. This interpolation process ensured a consistent spatial alignment between model outputs and observational data. Subsequently, we extracted the depth values from both the observed dataset and the interpolated/regridded datasets for each climate model at each grid cell and calculated the relative error as:

$$\frac{Z_{\mathrm{CM},K}(i,j) - Z_{\mathrm{obs}}(i,j)}{Z_{\mathrm{obs}}(i,j)} \tag{B.1}$$

Where $Z_{\mathrm{CM},K}$ represents the bathymetry at the grid cell (i,j) of climate model K; $Z_{\mathrm{Hist}}(i,j)$ is the bathymetry at the same grid cell for the observations.

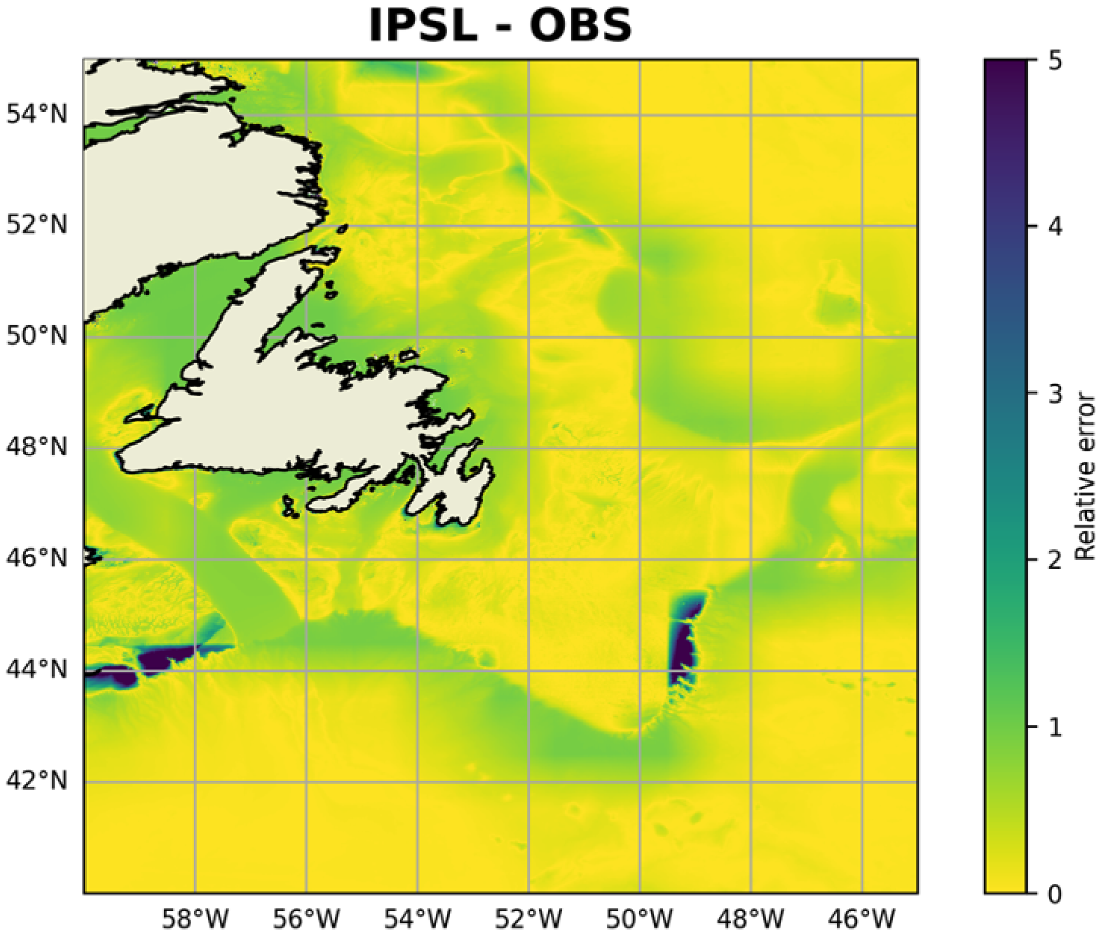


FIGURE B.11: Relative bathymetry error of the IPSL model relative to observations.

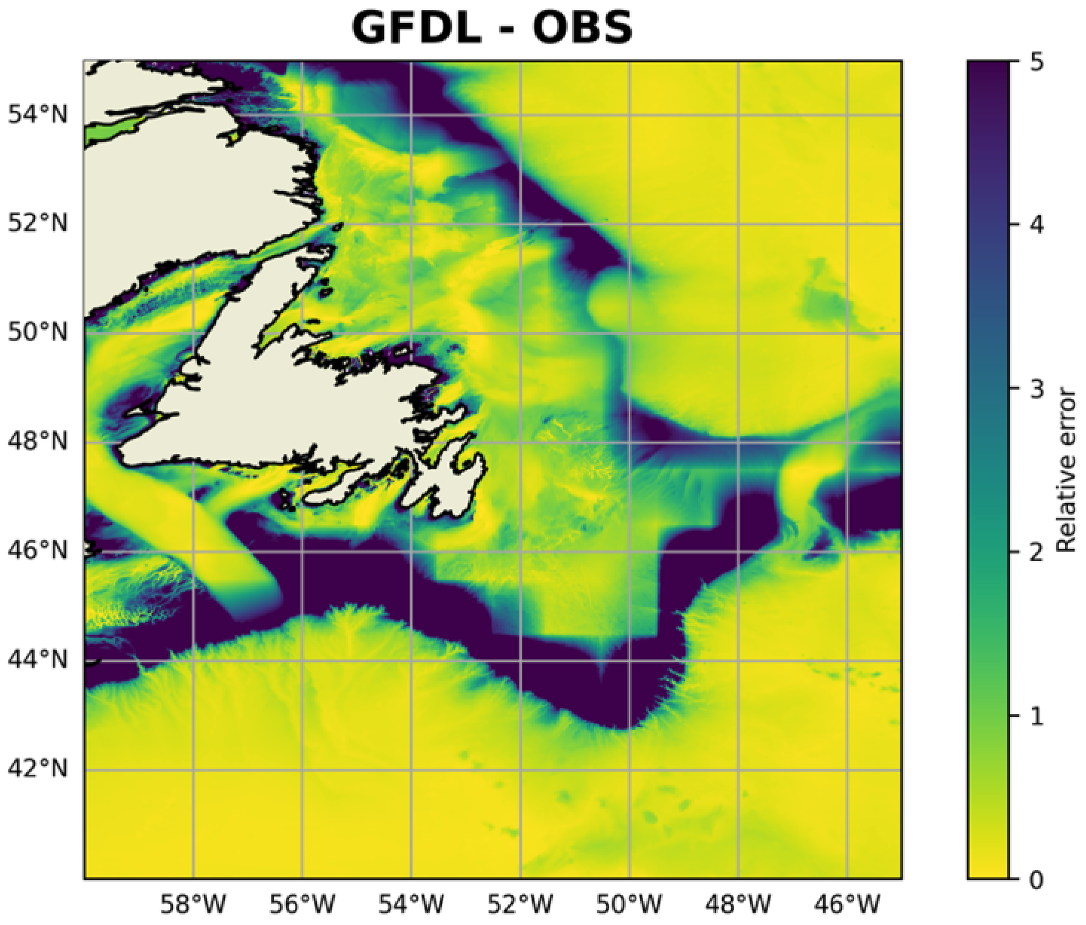


FIGURE B.12: Relative bathymetry error of the GFDL climate model relative to observations.

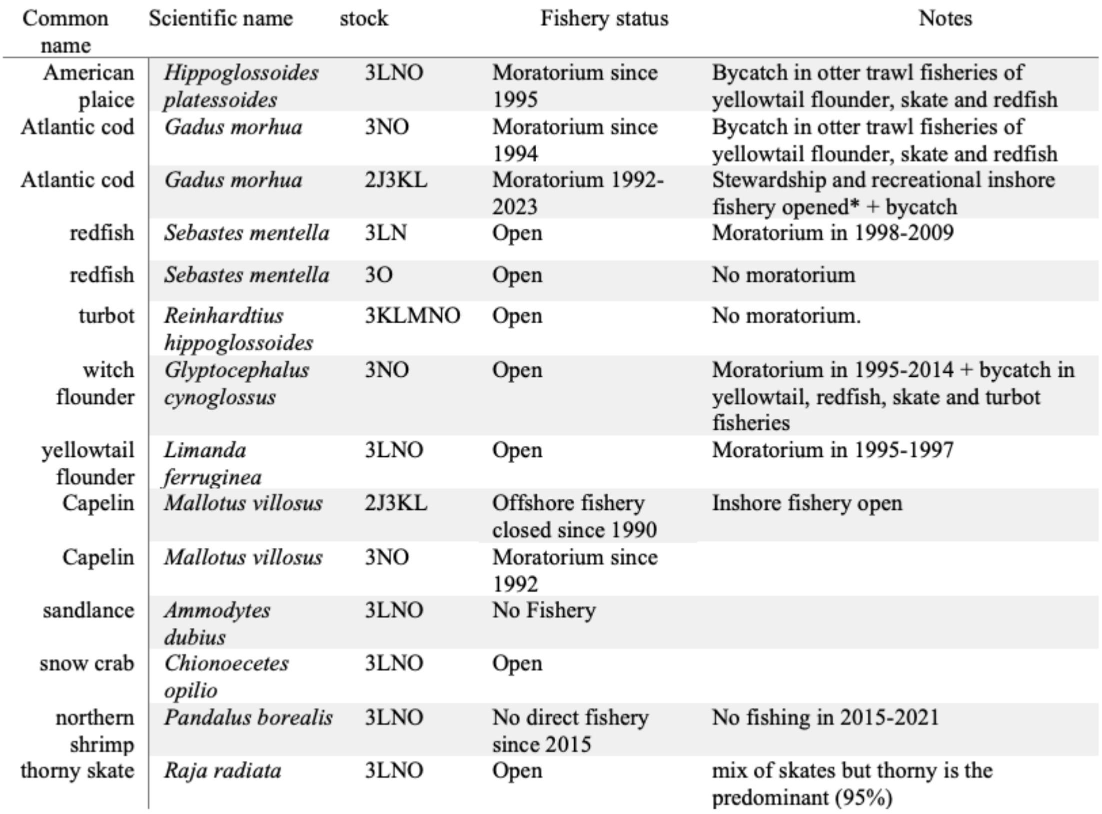
APPENDIX C

Supplementary material for Chapter 5

C.1 Supporting Tables

Grand Banks stocks and fisheries status

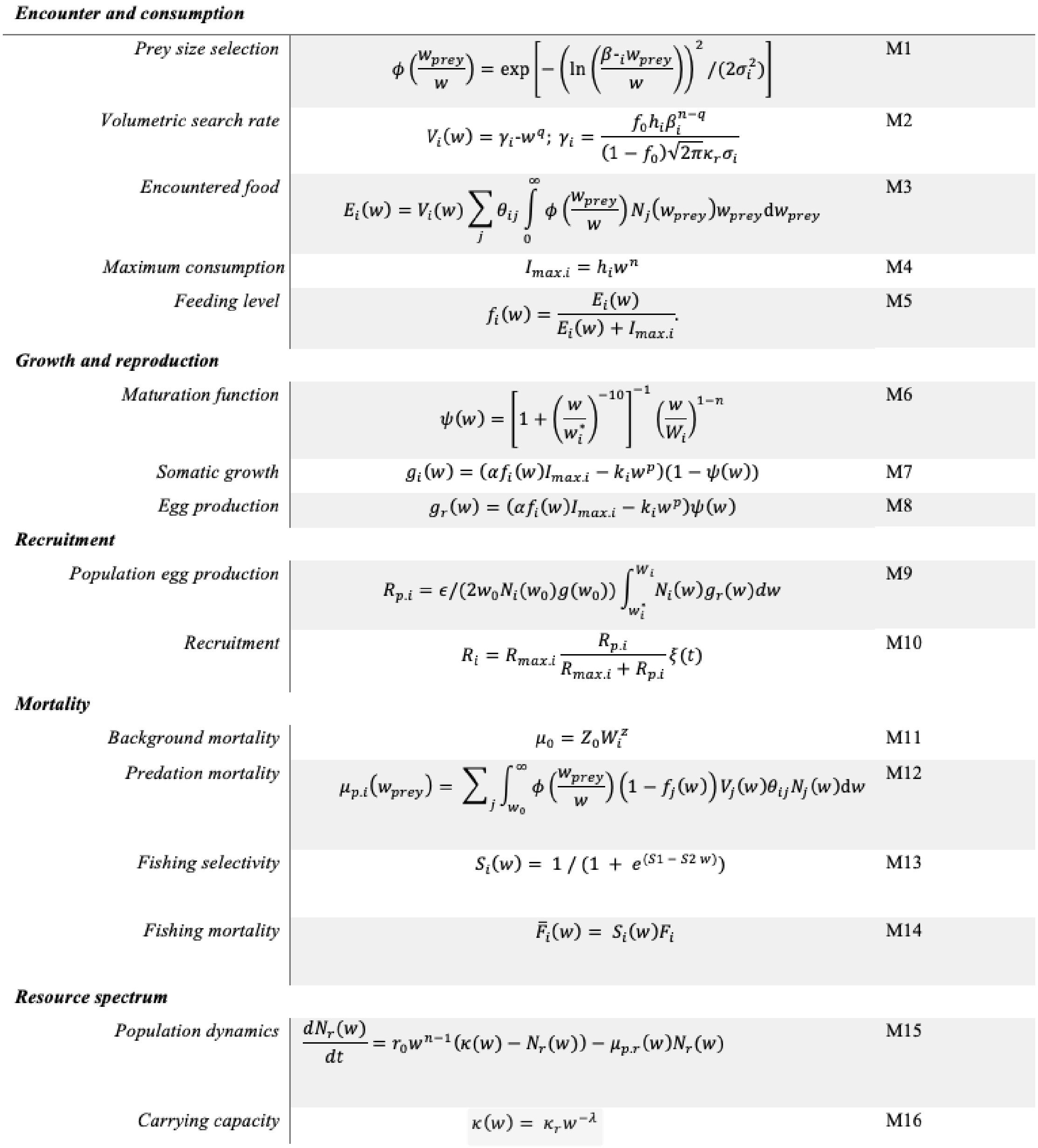
Table C.1: Information on the Grand Banks stocks and fisheries status



Common name	Scientific name	stock	Fishery status	Notes
American plaice	*Hippoglossoides platessoides*	3LNO	Moratorium since 1995	Bycatch in otter trawl fisheries of yellowtail flounder, skate and redfish
Atlantic cod	*Gadus morhua*	3NO	Moratorium since 1994	Bycatch in otter trawl fisheries of yellowtail flounder, skate and redfish
Atlantic cod	*Gadus morhua*	2J3KL	Moratorium 1992-2023	Stewardship and recreational inshore fishery opened* + bycatch
redfish	*Sebastes mentella*	3LN	Open	Moratorium in 1998-2009
redfish	*Sebastes mentella*	3O	Open	No moratorium
turbot	*Reinhardtius hippoglossoides*	3KLMNO	Open	No moratorium.
witch flounder	*Glyptocephalus cynoglossus*	3NO	Open	Moratorium in 1995-2014 + bycatch in yellowtail, redfish, skate and turbot fisheries
yellowtail flounder	*Limanda ferruginea*	3LNO	Open	Moratorium in 1995-1997
Capelin	*Mallotus villosus*	2J3KL	Offshore fishery closed since 1990	Inshore fishery open
Capelin	*Mallotus villosus*	3NO	Moratorium since 1992	
sandlance	*Ammodytes dubius*	3LNO	No Fishery	
snow crab	*Chionoecetes opilio*	3LNO	Open	
northern shrimp	*Pandalus borealis*	3LNO	No direct fishery since 2015	No fishing in 2015-2021
thorny skate	*Raja radiata*	3LNO	Open	mix of skates but thorny is the predominant (95%)

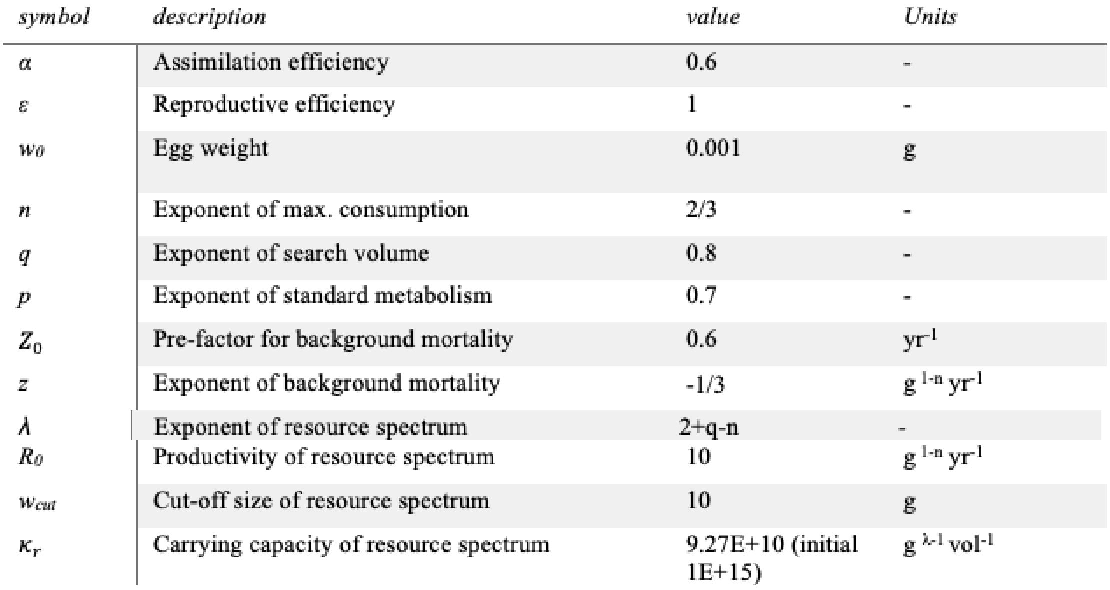
MIZER Size spectrum model equations and parameters

TABLE C.2: Multispecies size spectrum model equations



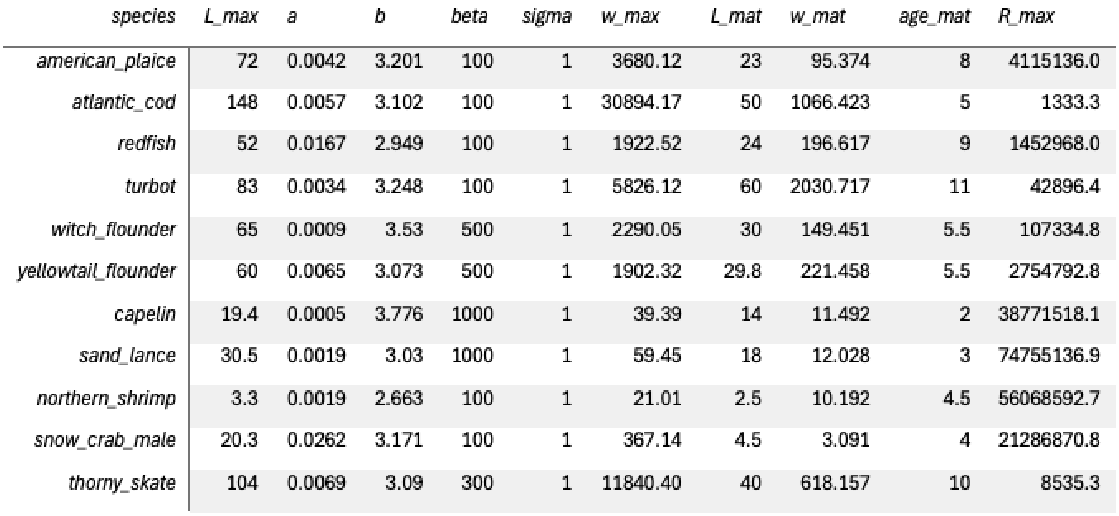
Encounter and consumption		
Prey size selection	$\phi\left(\frac{w_{prey}}{w}\right) = \exp\left[-\left(\ln\left(\frac{\beta_{-i} w_{prey}}{w}\right)\right)^2 / (2\sigma_i^2)\right]$	M1
Volumetric search rate	$V_i(w) = \gamma_i \text{-} w^q;\ \gamma_i = \frac{f_0 h_i \beta_i^{n-q}}{(1-f_0)\sqrt{2\pi}\kappa_r \sigma_i}$	M2
Encountered food	$E_i(w) = V_i(w) \sum_j \theta_{ij} \int_0^\infty \phi\left(\frac{w_{prey}}{w}\right) N_j(w_{prey}) w_{prey} \mathrm{d}w_{prey}$	M3
Maximum consumption	$I_{max.i} = h_i w^n$	M4
Feeding level	$f_i(w) = \frac{E_i(w)}{E_i(w) + I_{max.i}}.$	M5
Growth and reproduction		
Maturation function	$\psi(w) = \left[1 + \left(\frac{w}{w_i^*}\right)^{-10}\right]^{-1} \left(\frac{w}{W_i}\right)^{1-n}$	M6
Somatic growth	$g_i(w) = (\alpha f_i(w) I_{max.i} - k_i w^p)(1 - \psi(w))$	M7
Egg production	$g_r(w) = (\alpha f_i(w) I_{max.i} - k_i w^p)\psi(w)$	M8
Recruitment		
Population egg production	$R_{p.i} = \epsilon / (2 w_0 N_i(w_0) g(w_0)) \int_{w_i^*}^{W_i} N_i(w) g_r(w) dw$	M9
Recruitment	$R_i = R_{max.i} \frac{R_{p.i}}{R_{max.i} + R_{p.i}} \xi(t)$	M10
Mortality		
Background mortality	$\mu_0 = Z_0 W_i^z$	M11
Predation mortality	$\mu_{p.i}(w_{prey}) = \sum_j \int_{w_0}^\infty \phi\left(\frac{w_{prey}}{w}\right) \left(1 - f_j(w)\right) V_j(w) \theta_{ij} N_j(w) \mathrm{d}w$	M12
Fishing selectivity	$S_i(w) = 1 / (1 + e^{(S1 - S2\, w)})$	M13
Fishing mortality	$\bar{F}_i(w) = S_i(w) F_i$	M14
Resource spectrum		
Population dynamics	$\frac{dN_r(w)}{dt} = r_0 w^{n-1}(\kappa(w) - N_r(w)) - \mu_{p.r}(w) N_r(w)$	M15
Carrying capacity	$\kappa(w) = \kappa_r w^{-\lambda}$	M16

Table C.3: Fixed input parameters



symbol	*description*	*value*	*Units*
α	Assimilation efficiency	0.6	-
ε	Reproductive efficiency	1	-
w_0	Egg weight	0.001	g
n	Exponent of max. consumption	2/3	-
q	Exponent of search volume	0.8	-
p	Exponent of standard metabolism	0.7	-
Z_0	Pre-factor for background mortality	0.6	yr^{-1}
z	Exponent of background mortality	-1/3	$g^{1-n}\, yr^{-1}$
λ	Exponent of resource spectrum	2+q-n	-
R_0	Productivity of resource spectrum	10	$g^{1-n}\, yr^{-1}$
w_{cut}	Cut-off size of resource spectrum	10	g
κ_r	Carrying capacity of resource spectrum	9.27E+10 (initial 1E+15)	$g^{\lambda-1}\, vol^{-1}$

Table C.4: Species-specific input parameters

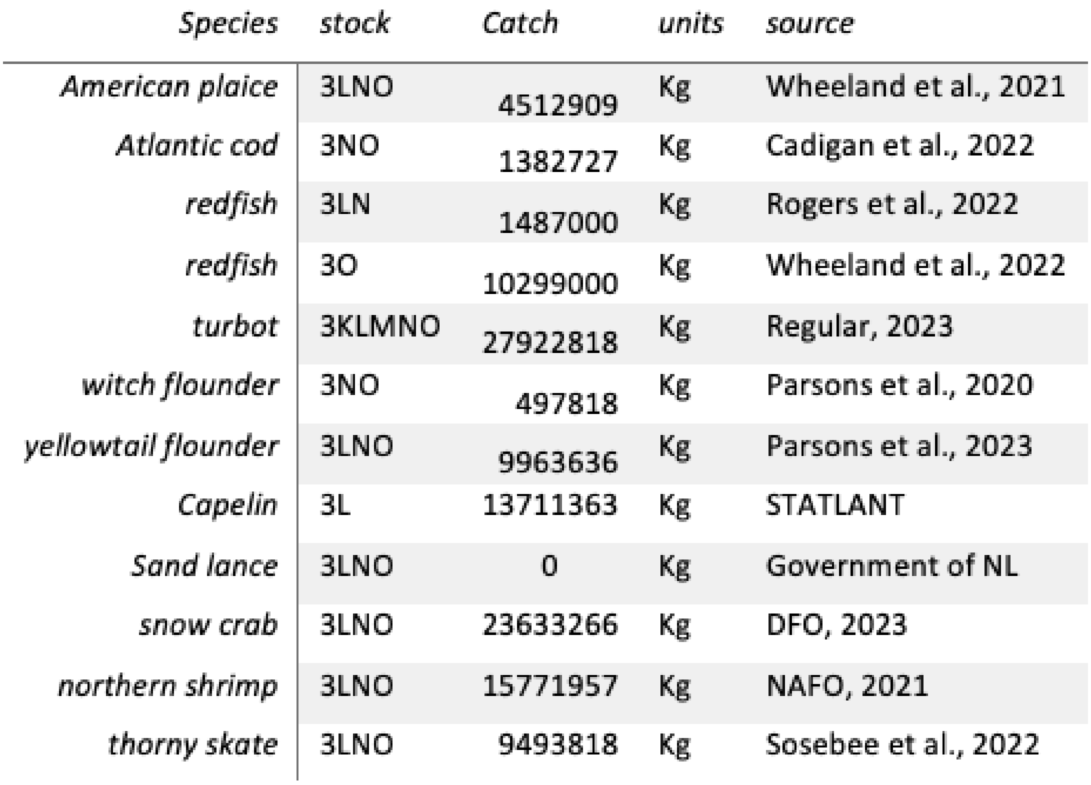


species	L_max	a	b	beta	sigma	w_max	L_mat	w_mat	age_mat	R_max
american_plaice	72	0.0042	3.201	100	1	3680.12	23	95.374	8	4115136.0
atlantic_cod	148	0.0057	3.102	100	1	30894.17	50	1066.423	5	1333.3
redfish	52	0.0167	2.949	100	1	1922.52	24	196.617	9	1452968.0
turbot	83	0.0034	3.248	100	1	5826.12	60	2030.717	11	42896.4
witch_flounder	65	0.0009	3.53	500	1	2290.05	30	149.451	5.5	107334.8
yellowtail_flounder	60	0.0065	3.073	500	1	1902.32	29.8	221.458	5.5	2754792.8
capelin	19.4	0.0005	3.776	1000	1	39.39	14	11.492	2	38771518.1
sand_lance	30.5	0.0019	3.03	1000	1	59.45	18	12.028	3	74755136.9
northern_shrimp	3.3	0.0019	2.663	100	1	21.01	2.5	10.192	4.5	56068592.7
snow_crab_male	20.3	0.0262	3.171	100	1	367.14	4.5	3.091	4	21286870.8
thorny_skate	104	0.0069	3.09	300	1	11840.40	40	618.157	10	8535.3

Table C.5: Species maturity information. *Lmat* is the length at maturity and $age - mat$ is the age at maturity

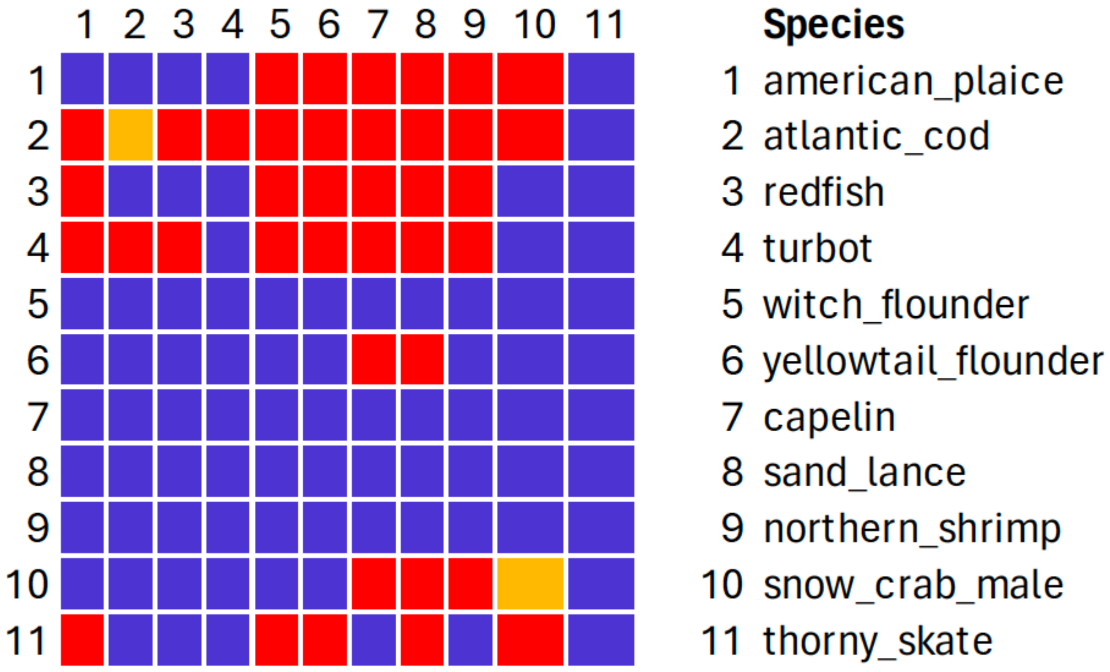
Species	*Lmat*	*age_mat*	*Source*
american_plaice	23	8	Wheeland et al., 2021
atlantic_cod	50	5	DFO, 2021
redfish	24	9	Rogers et al., 2022
turbot	60	11	Treble and Dwyer, 2008
witch_flounder	30	5.5	Swain et al., 2012
yellowtail_flounder	29.8	5.5	Robins and Ray, 1986
capelin	23	2	Mowbray et al., 2023
sand_lance	18	3	Government of Newfoundland and Labrador
northern_shrimp	2.5	4.5	Beita, 2021
snow_crab_male	4.5	4	DFO, 2019
thorny_skate	40	10	COSEWIC, 2012

TABLE C.6: 10 year average (1996-2006) species catch data.



Species	*stock*	*Catch*	*units*	*source*
American plaice	3LNO	4512909	Kg	Wheeland et al., 2021
Atlantic cod	3NO	1382727	Kg	Cadigan et al., 2022
redfish	3LN	1487000	Kg	Rogers et al., 2022
redfish	3O	10299000	Kg	Wheeland et al., 2022
turbot	3KLMNO	27922818	Kg	Regular, 2023
witch flounder	3NO	497818	Kg	Parsons et al., 2020
yellowtail flounder	3LNO	9963636	Kg	Parsons et al., 2023
Capelin	3L	13711363	Kg	STATLANT
Sand lance	3LNO	0	Kg	Government of NL
snow crab	3LNO	23633266	Kg	DFO, 2023
northern shrimp	3LNO	15771957	Kg	NAFO, 2021
thorny skate	3LNO	9493818	Kg	Sosebee et al., 2022

C.2 Supporting Figures



	1	2	3	4	5	6	7	8	9	10	11
1	🟦	🟦	🟦	🟦	🟥	🟥	🟥	🟥	🟥	🟥	🟦
2	🟥	🟧	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟦
3	🟥	🟦	🟦	🟦	🟥	🟥	🟥	🟥	🟥	🟦	🟦
4	🟥	🟥	🟥	🟦	🟥	🟥	🟥	🟥	🟥	🟦	🟦
5	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
6	🟦	🟦	🟦	🟦	🟦	🟦	🟥	🟥	🟦	🟦	🟦
7	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
8	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
9	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦
10	🟦	🟦	🟦	🟦	🟦	🟦	🟥	🟥	🟥	🟧	🟦
11	🟥	🟦	🟦	🟦	🟥	🟥	🟦	🟥	🟦	🟥	🟦

	Species
1	american_plaice
2	atlantic_cod
3	redfish
4	turbot
5	witch_flounder
6	yellowtail_flounder
7	capelin
8	sand_lance
9	northern_shrimp
10	snow_crab_male
11	thorny_skate

FIGURE C.1: Species interaction matrix. Blue indicates absence (value = 0); red indicates presence (values =1); Orange indicates cannibalism (value = 0.02).

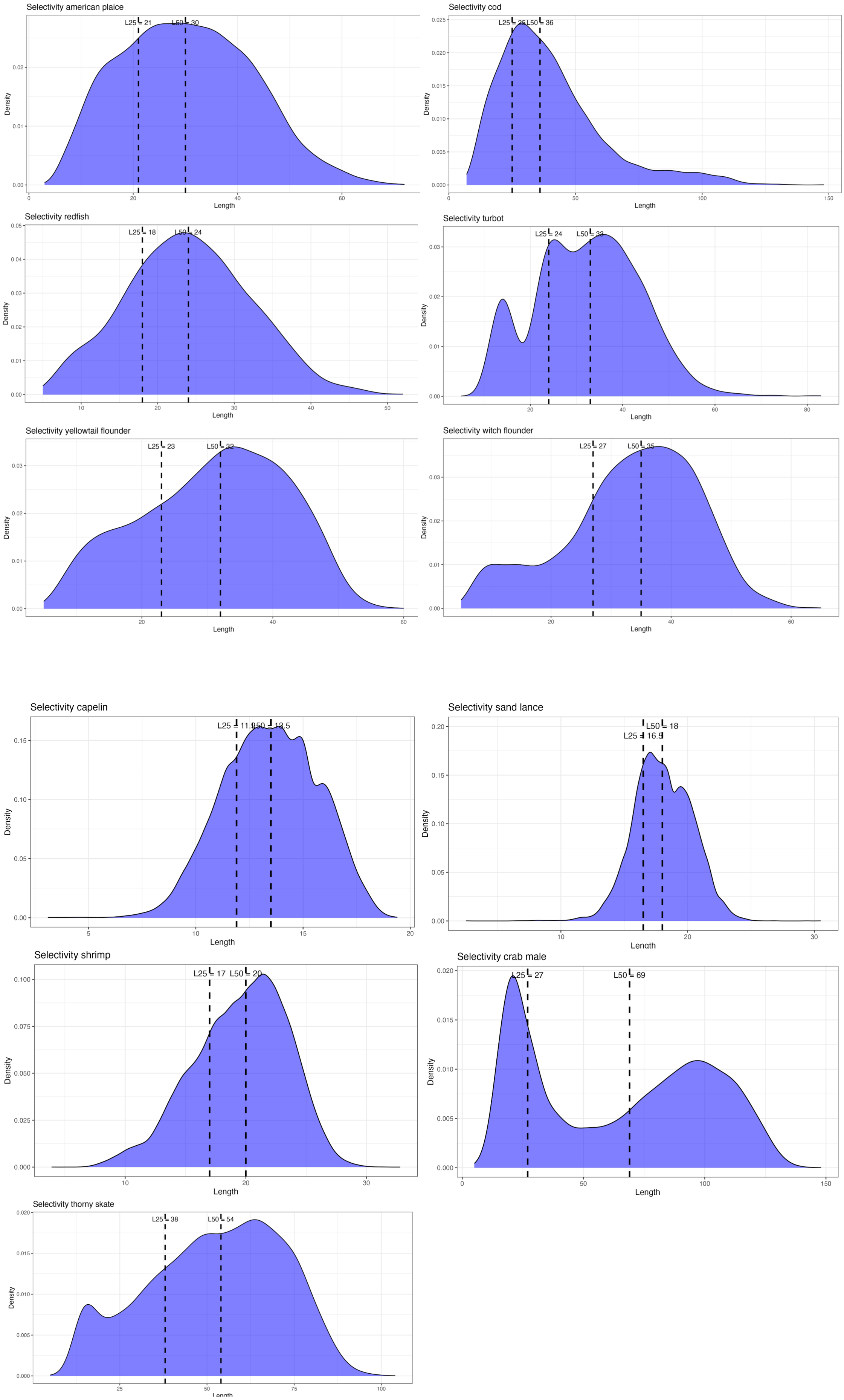


FIGURE C.2: Selectivity of the gear

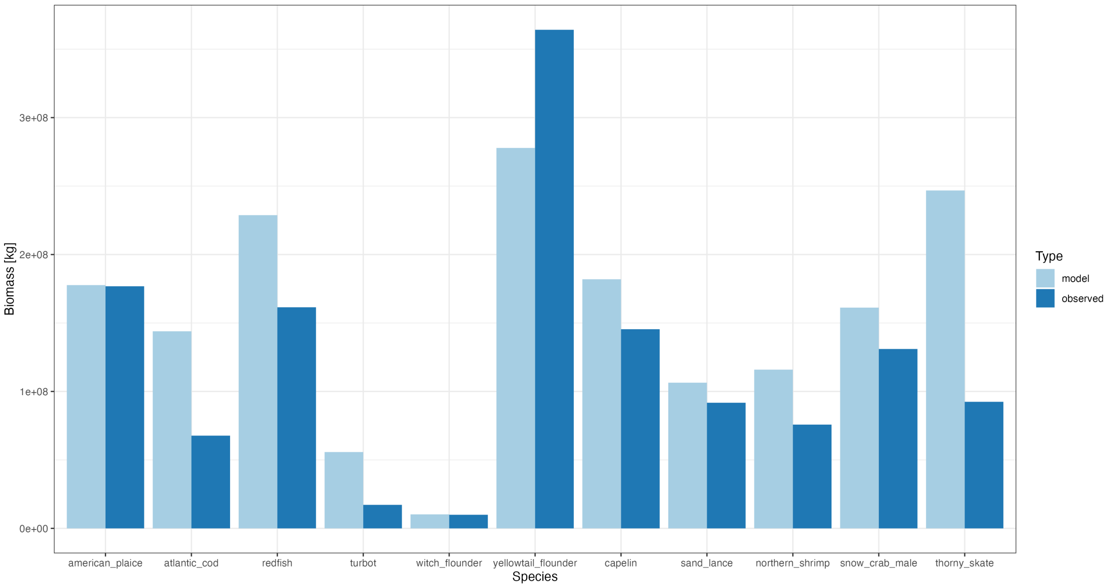


FIGURE C.3: Observed (blue) and modelled (red) equilibrium biomass of the 11 species included in the Grand Banks model.

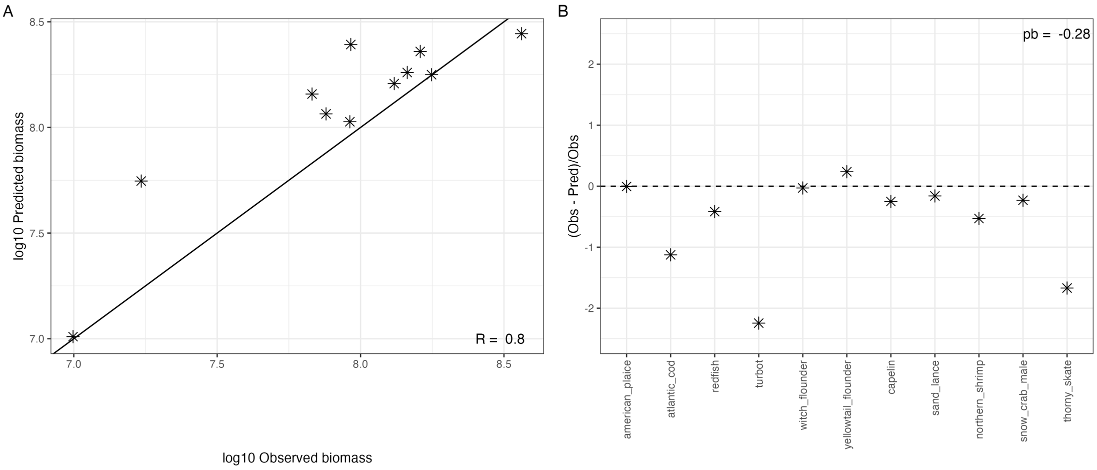


FIGURE C.4: Model calibration results. Log 10 predicted versus log 10 observed (time-averaged) biomass. Pearson's correlation coefficients (R) are shown in panel (A) and proportion of bias (pb) in panel (B).

Sensitivity to fishing

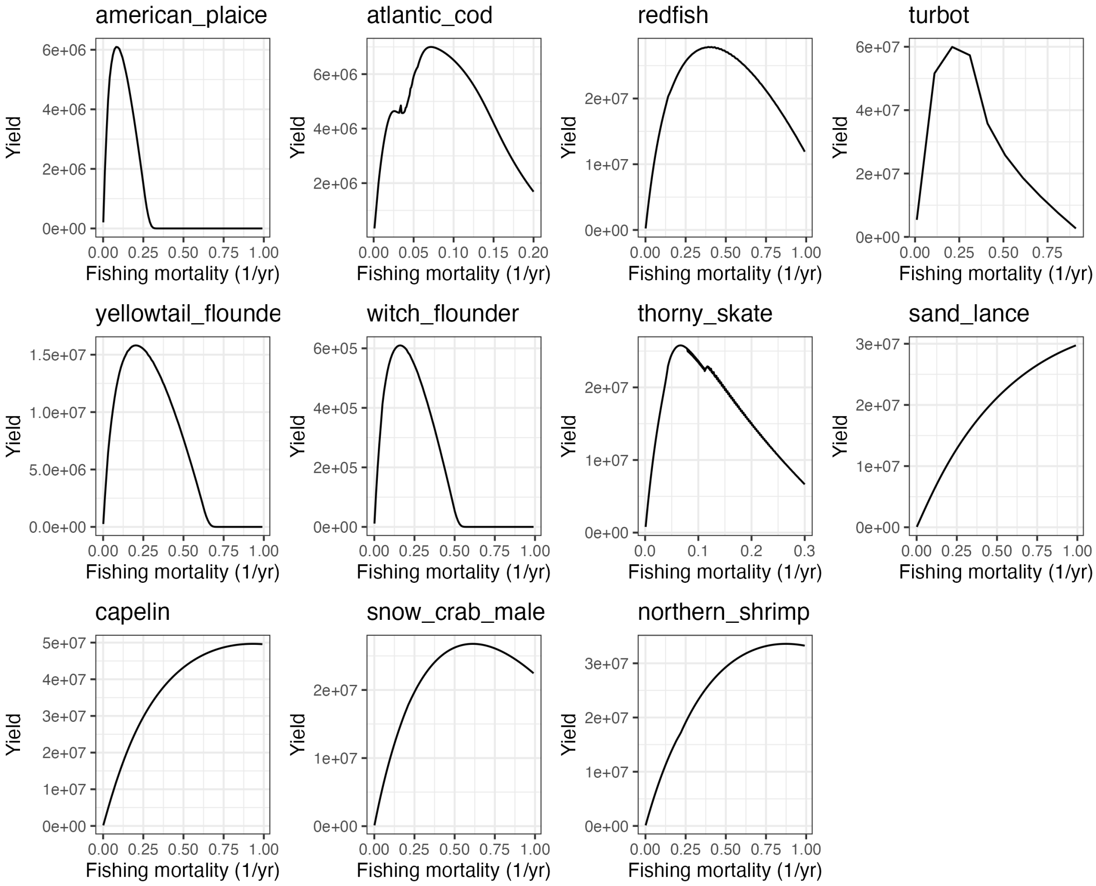


Figure C.5: Sensitivity to fishing. Yield versus Fishing mortality

Model outputs

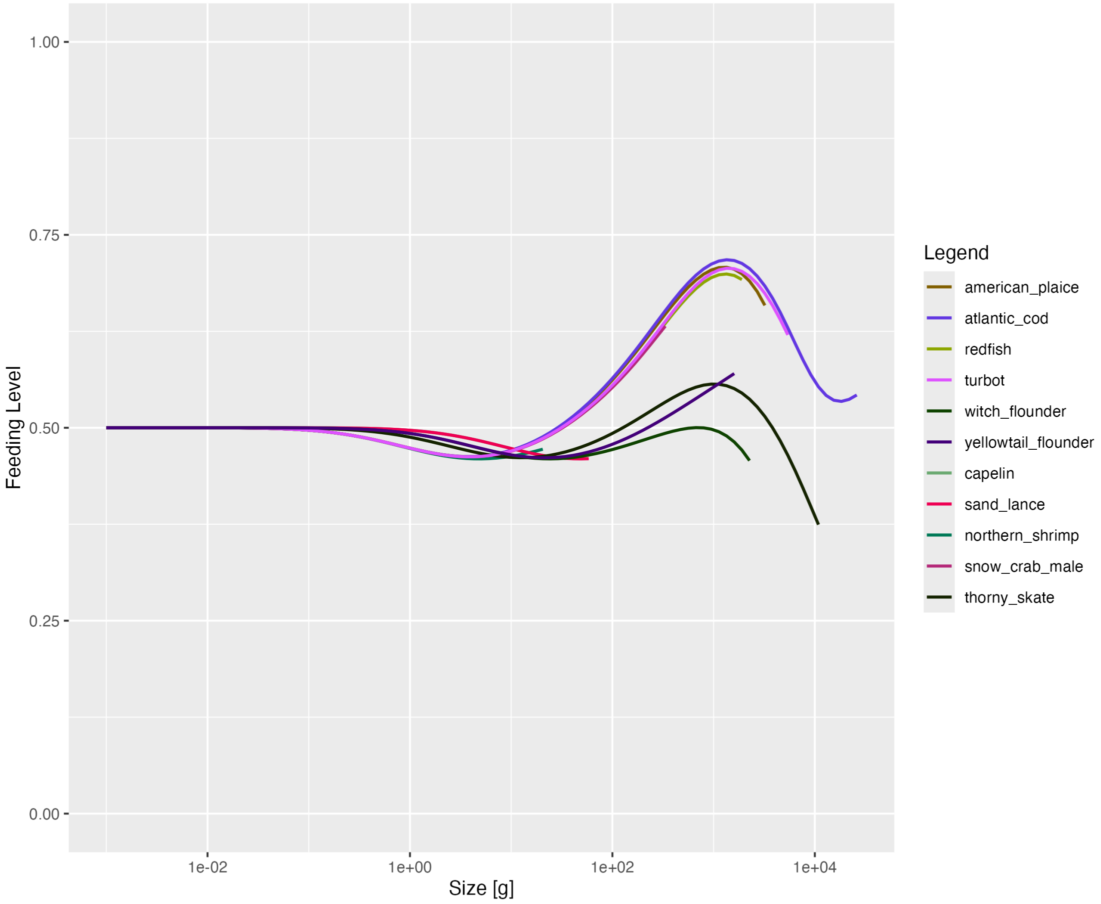


Figure C.6: Feeding levels

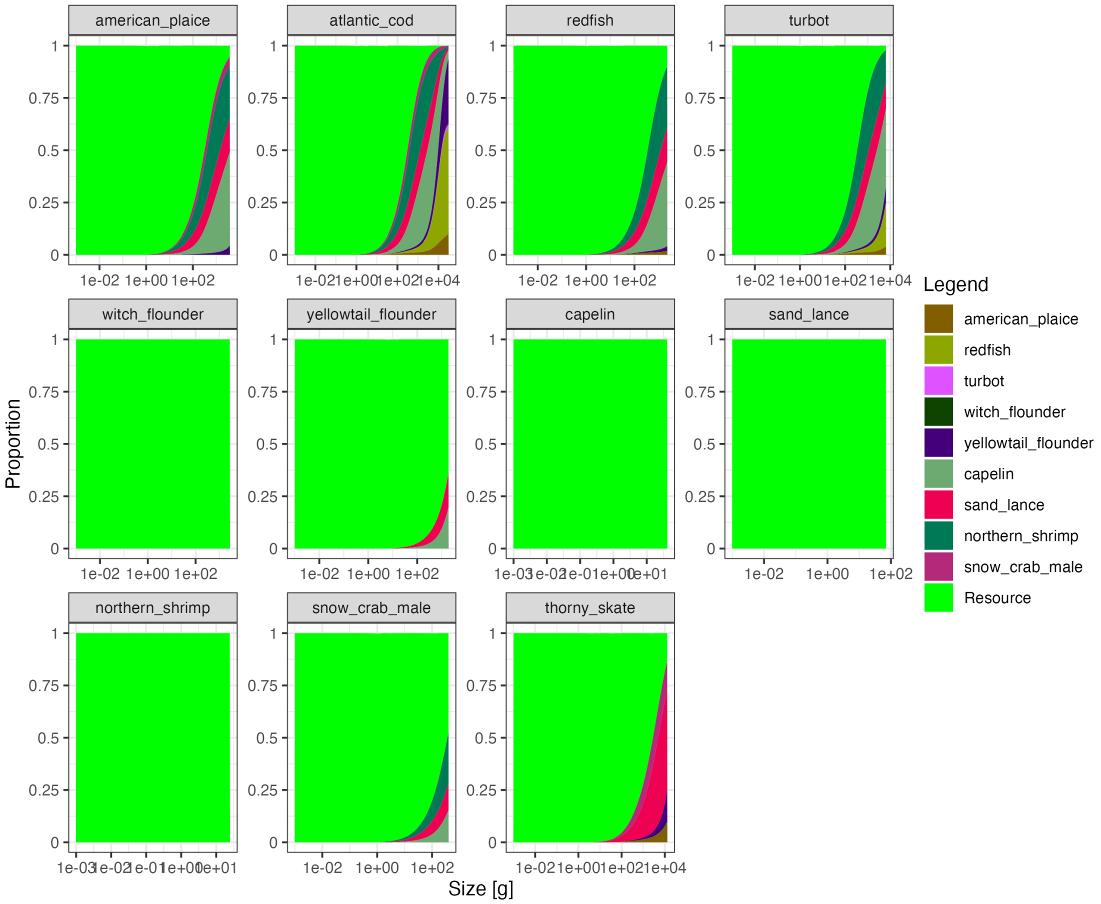


FIGURE C.7: Proportion of species in the diet

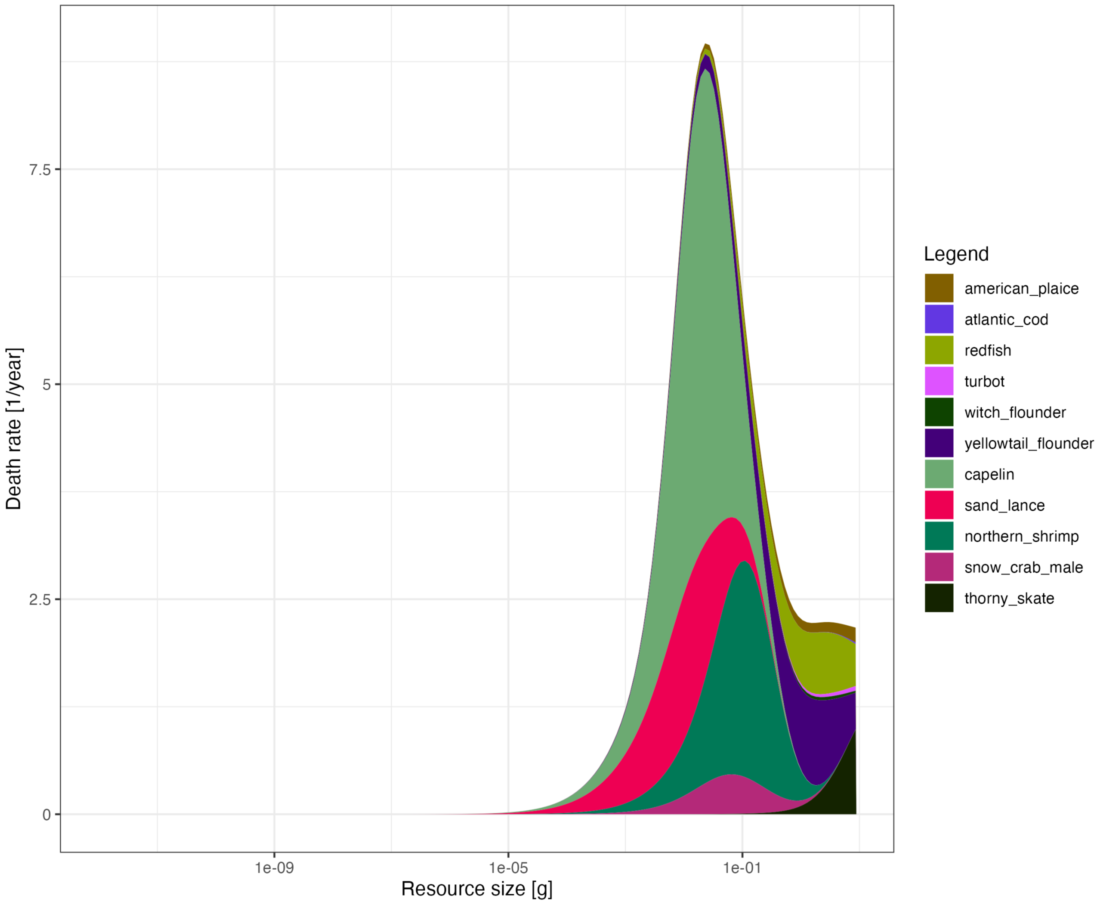
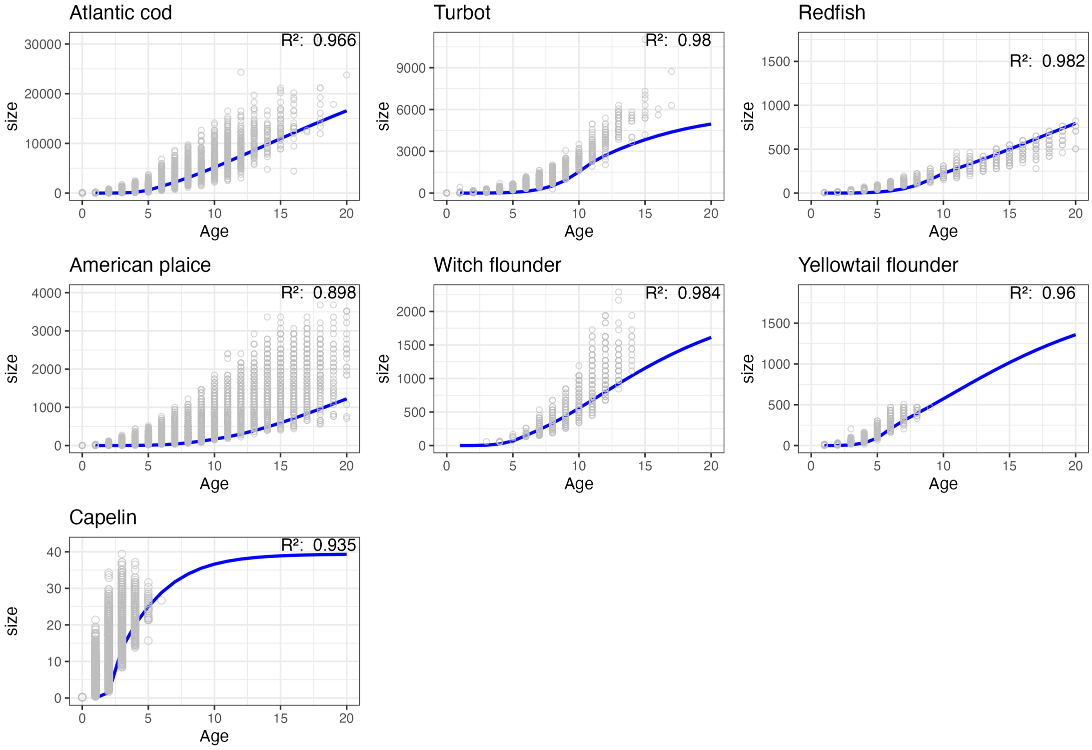


FIGURE C.8: Predation mortality by resource size


Atlantic cod

Turbot

Redfish

American plaice

Witch flounder

Yellowtail flounder

Capelin

FIGURE C.9: Predicted (blue line) and observed (gray circles) individuals size-at-age data for each species. R2 is the proportion of variance for predicted growth that is explained by the observed growth. Note that size-at-age information was not available for snow crab, northern shrimp, sand lance and thorny skate.

Forcing the model with time series of fishing mortality

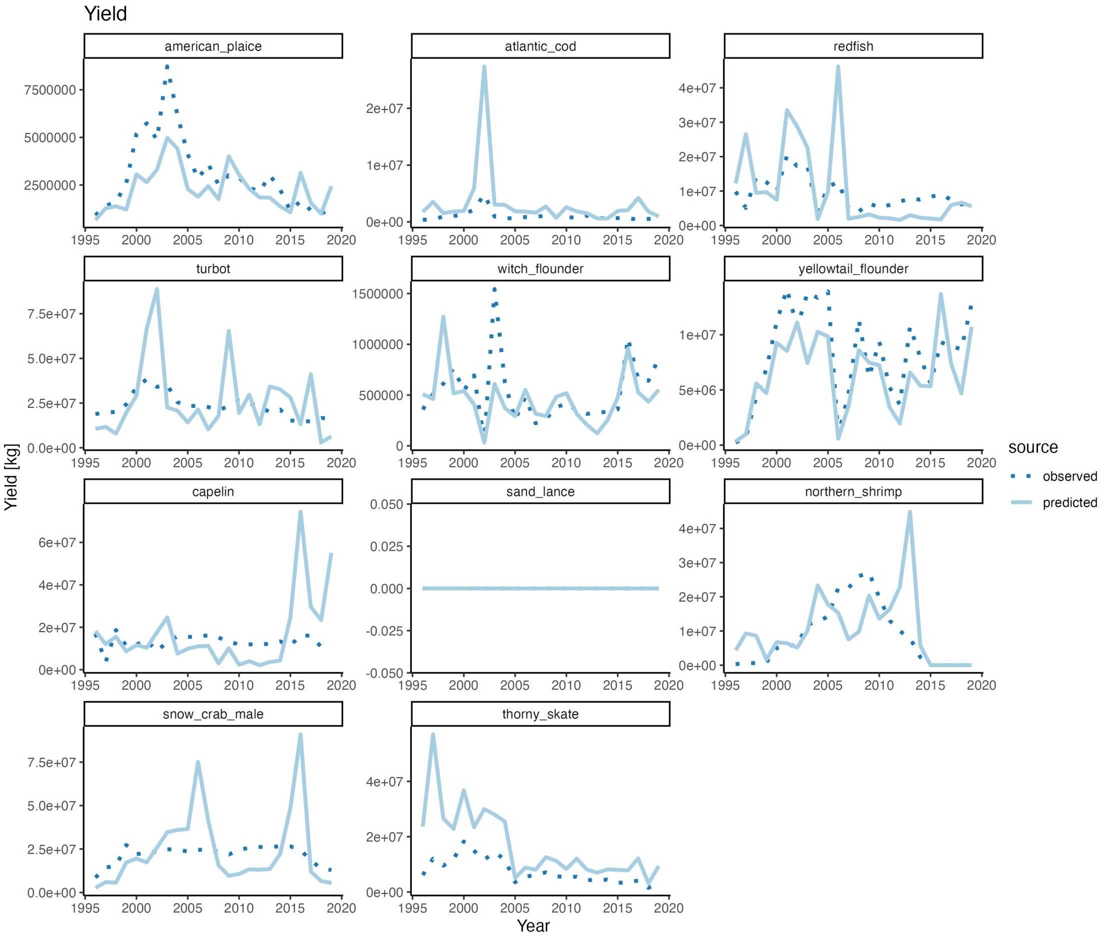


FIGURE C.10: Observed and predicted yield over time

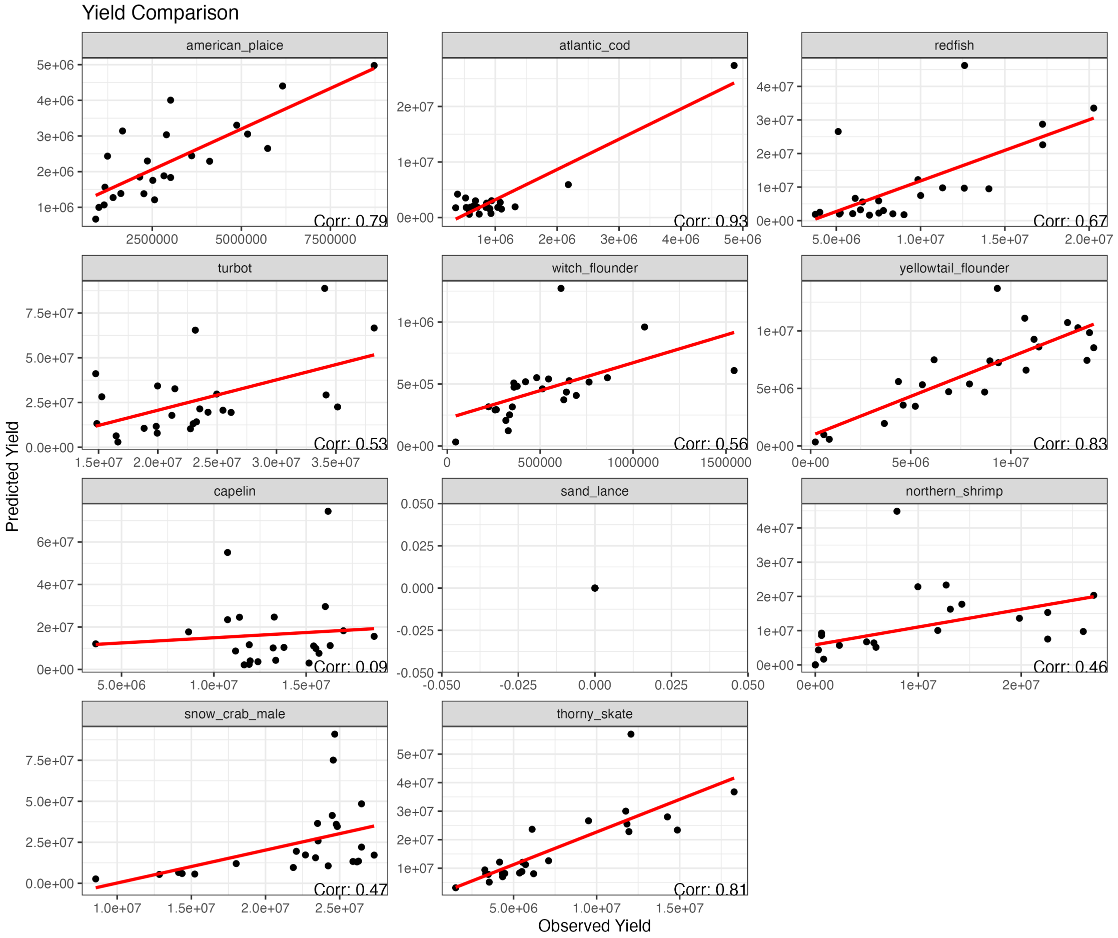


FIGURE C.11: Predicted vs observed yield. Corr represents Pearson correlation values

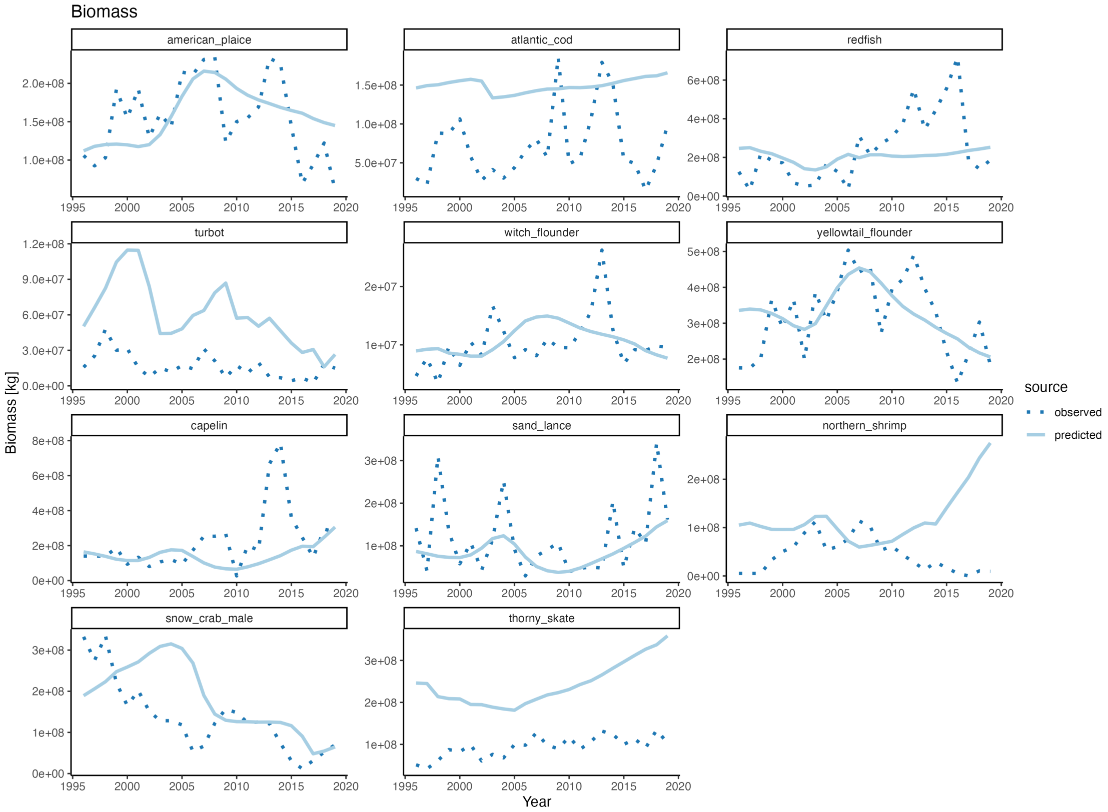


Figure C.12: Observed and predicted biomass over time

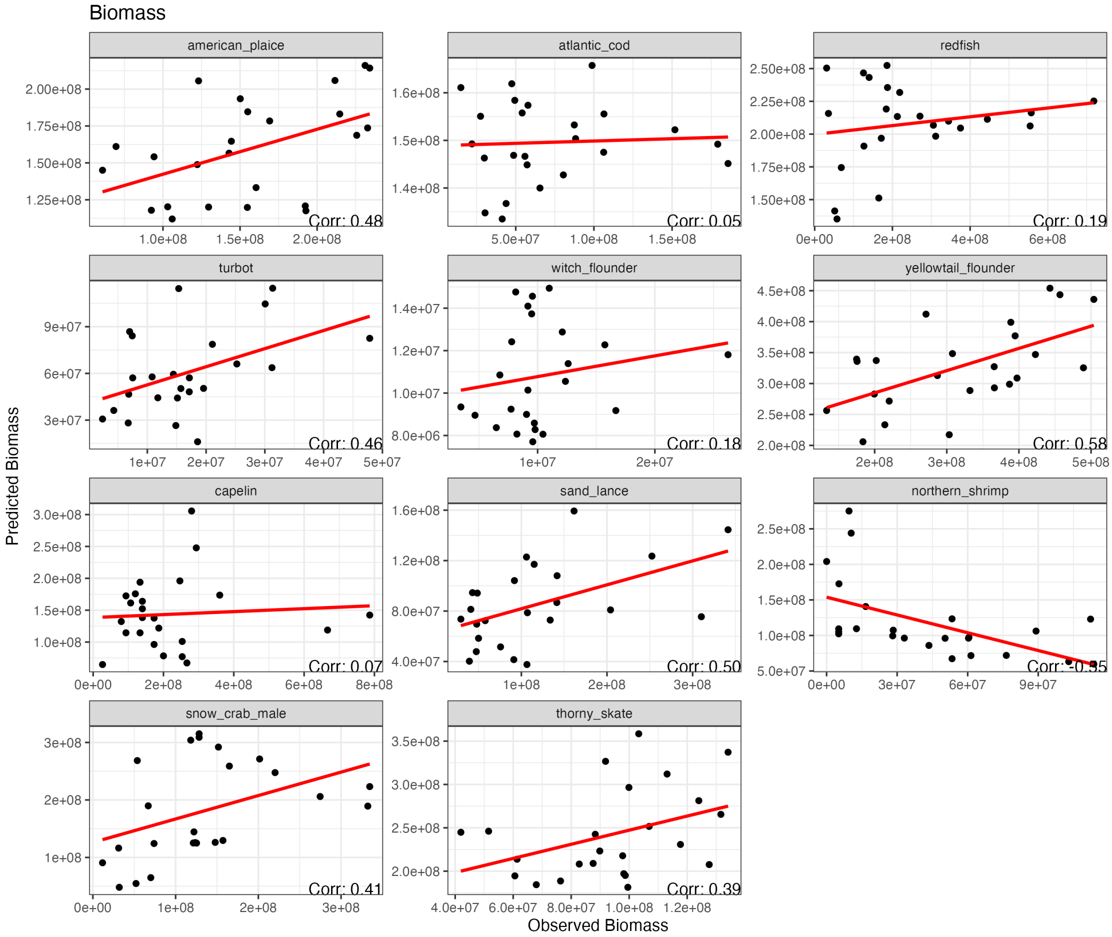


FIGURE C.13: Predicted vs observed biomass. Corr represents Pearson correlation