

**INTEGRATING BIODIVERSITY, CATCH RECONSTRUCTION, AND ECOSYSTEM
MODELING TO INFORM SUSTAINABLE FISHERIES IN SAINT PIERRE AND
MIQUELON (FRANCE): A MULTI-SCALE APPROACH**

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Abstract

Saint Pierre and Miquelon (SPM) is a small French archipelago in the Northwest Atlantic. Its historic dependence on fisheries for local livelihoods gives it heightened socio-ecological vulnerability under changing environmental and anthropogenic pressures. To better understand this vulnerability, this thesis investigates SPM's marine biodiversity, historical fisheries, and ecosystem dynamics through a macroecological and modeling-based approach, linking global biogeographic patterns with local management relevance. Three main objectives guided this work: (1) positioning SPM within global insular gradients of marine biodiversity and testing the application of Island Biogeography Theory (IBT) to marine species; (2) reconstructing SPM's total marine catches from 1950 to 2022 and the evolution of fishing pressures; and (3) evaluating the effects of historical and projected fishing activity on the surrounding ecosystem (NAFO Subdivision 3Ps) using Ecopath with Ecosim (EwE) modeling.

This work established a biodiversity baseline for SPM, and also showed that latitude and continental shelf surface area are significant predictors of marine species richness in 40 archipelagos and islands around the world, consistent with IBT principles. The reconstructed marine catch of SPM revealed that actual removals exceeded official statistics by more than 20%. Over seven decades, catches shifted from high-trophic level predators such as Atlantic cod toward lower-trophic level invertebrates, notably sea cucumber, leading to a 37% decline in the mean trophic level of the catch. These data were integrated into EwE mass-balance models for two time periods (1960–1969 and 2000–2009) and dynamic Ecosim and Ecospace simulations were conducted. Results indicated shifts in fishing mortality and ecosystem structure, with increased effort projected to reduce biomass of invertebrate target species and modestly affect higher-trophic fishes like Atlantic halibut.

By linking biodiversity gradients, reconstructed fisheries data, and ecosystem modeling, this research provides the first comprehensive ecological framework for SPM and the first EwE models for NAFO 3Ps. This demonstrates the value of integrating biogeographic theory and trophic modeling to inform local management and emphasizes the vulnerability of small, data-limited island ecosystems. Ultimately, this work contributes to assessing SPM's long-term capacity to sustain ecological integrity and fishery productivity in a changing climate.

Lay Summary

This thesis explored how the marine environment around the small French archipelago of Saint Pierre and Miquelon (SPM) has changed over time, which marine species occur there, and how fishing has shaped the ecosystem. Using data from islands around the world, the study found that latitude and shelf area are key predictors of marine diversity, and that SPM fits this global pattern. Reconstructing SPM fisheries since 1950 revealed that more fish and invertebrates were caught than officially reported, and that fishing gradually shifted from large fishes like cod to smaller species, notably sea cucumbers. This information was put into models to compare the state of the SPM ecosystem through time, and evaluate that an increase in fishing would reduce the populations of some marine species of economic importance for the archipelago. Together, these findings provide new tools to support sustainable fisheries in SPM.

Preface

This thesis and the research presented within is my original work. It contains five chapters: a general introduction (Chapter 1), three data chapters (Chapters 2, 3 and 4) and a general conclusion (Chapter 5). Each data chapter was prepared as a stand-alone manuscript, which may result in some overlap in content across chapters. Feedback from my committee members, Dr. Daniel Pauly, Dr. Fabrice Teletchea and Dr. Villy Christensen, was incorporated into the final thesis draft. Dr. Daniel Pauly and Dr. Fabrice Teletchea helped with the elaboration of the research proposal, and Dr. Christensen helped with the ecosystem models. Dr. Daniel Pauly provided supervision and analytical support for each chapter.

Marine biodiversity data used in *Chapter 2* for other islands and archipelagos than Saint-Pierre and Miquelon were extracted with the help of Dr. Nicolas Bailly from the SeaLifeBase database. Dr. Gabriel Reygondeau provided feedback on the analysis. This chapter is being prepared for submission for peer-review. Material from *Chapter 2* was presented as:

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Chapter 3 used general catch reconstruction methods developed by Zeller and Pauly (2016) under the *Sea Around Us* initiative, regional methods from Bultel and Zylich (2015) and Divovich *et al.* (2015) as well as methods developed by me for the region and focus of this research, using historical information provided by Gilles Poirier, Marc Derible, Fabrice Teletchea and Joel Vigneau, and archives provided by IFREMER. Dr. Maria ‘Deng’ Palomares reviewed the methods I developed and used. This chapter is being prepared for submission for peer-review. Material from *Chapter 3* was presented as:

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Chapter 4 uses the Ecopath with Ecosim modelling software and methods from Christensen and Walters (2024). Dr. Villy Christensen provided guidance and assistance in calibrating the Ecopath and Ecosim models. Dr. Lyne Morissette provided help in the definition of functional groups and on marine mammals data for the NAFO 3Ps area in the Northwest Atlantic. This chapter is being prepared for submission for peer-review. Material from *Chapter 4* was presented as:

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List of Abbreviations

AIC = Akaike Information Criterion

B = Biomass

CPUE = Catch per Unity of Effort

DFO = Department of Fisheries and Oceans

DTAM = Direction des Territoires, de l'Alimentation et de la Mer (Direction of Territories, Food and the Sea)

EBFM = Ecosystem Based Fishery Management

EE = Ecotrophic Efficiency

EEZ = Exclusive Economic Zone

EwE = Ecopath with Ecosim

FAO = Food and Agriculture Organization

GE = Gross Efficiency

IBT = Island Biogeography Theory

ICCAT = International Convention for the Conservation of Atlantic Tunas

IFREMER = Institut Francais pour l'Exploitation de la Mer (French institute for Ocean Science)

IUCN = International Union for the Conservation of Nature

NAFO = North Atlantic Fisheries Organization

NASCO = North Atlantic Salmon Conservation Organization

MRA = Multiple Regression Analysis

MTC = Mean Temperature of the Catch

MTL = Mean Trophic Level

P/B = Production over Biomass ratio

P = Production

PP = Primary Production

P/Q = Production over Consumption ratio

PSD = Particle Size Distribution

Q = consumption

Q/B = Consumption over Biomass ratio

SPM = Saint Pierre and Miquelon

SS = Sum of Squares

t = tonnes

$t \cdot km^{-2}$ = Tonnes per square kilometer

$t \cdot km^{-2} \cdot year^{-1}$ = Tonnes per square kilometer per year

TAC = Total Allowable Catch

TL = Trophic Level

VBGF = Von Bertalanffy Growth Function

VIF = Variance Inflation Factor

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to my partner, for his love for the sea as bright as mine,
to my best friends, for their precious role in helping me stay afloat,
and to the Ocean, my very first love.*

Chapter 1: Introduction

1.1 Small-scale archipelagos as unique socio-ecological systems

1.1.1 Ecological patterns and human dependence on marine resources

Small island states and territories are unique in the way distinct evolutionary processes have shaped their biodiversity in relation to their isolation to mainland continents and their land surface area – a process described by Island Biogeography Theory (McArthur and Wilson, 1967). Small islands are often described as ‘living laboratories’ because of the way their constrained environments allow intricate ecosystem processes to be studied in detail, while also offering critical insights into climate adaptation as their exposure to sea level rise and storms intensification put them on the frontline of climate change vulnerability (Nurse *et al.*, 2001; Martin, 2018; Pathirana, 2025). A smaller land area constrained by the ocean generally exhibits a higher ecological fragility, and offers accelerated perspective on how both natural and anthropological processes can influence socio-ecological systems and shape their resilience to climate variability, resource depletion, and socio-economic challenges (Nurse *et al.*, 2001; Balzan *et al.*, 2017; Refulio-Coronado *et al.*, 2021). Oceanic and continental islands and archipelagos are known to support higher rates of endemism, shaped by their physical constraints and more-or-less isolated state (McArthur and Wilson, 1967; Whittaker and Fernandez-Palacios, 2007).

While marine biodiversity is not as easily spatially described as various groups of species are not constrained by the same physical boundaries, higher number of species, i.e., species richness, have been found on continental shelves (i.e., in water down to 200 m), with even higher numbers on the shelves around islands (deJuan *et al.*, 2023). Similarly, this ecological sensitivity extends to the surrounding marine environment, where strong human dependence on marine resources makes biodiversity patterns particularly responsive to anthropogenic change (McClanahan *et al.*, 2015; Selig *et al.*, 2019). As a result, island-associated marine systems provide an ideal context for examining how fishing interact with natural processes to influence biodiversity and ecosystem resilience. Small island states and small-scale archipelagos are indeed highly dependent on marine ecosystems for their livelihoods, food security and economic growth (Selig *et al.*, 2019): owing to their close proximity to the sea, fisheries often serve as the primary source

of income and are deeply embedded in local history, shaping cultural identity and community traditions (McGoodwin, 2001).

1.1.2 Socio ecological history and concerns in the Northwest Atlantic

In the Northwest Atlantic, small islands have traditionally provided access to important fishing grounds for Indigenous people, notably for the Mi'kmaq Nation (McMillan and Prosper, 2016). Later, when the first European settlers established colonies on e.g., Anticosti Island and Prince Edward Island, their socio-economic systems were built on access to fish resources. Thus, settlers became reliant on fish stocks health and mainly the abundant resource that Atlantic cod (*Gadus morhua*) represented (Lear, 1998). Cod abundance in the Northwest Atlantic not only provided the material basis for settlement and subsistence on these islands, but also positioned the species as a socio-ecological dominant emblem, embedded in local history and cultural identity (Rose, 2007; Kurlansky, 2011). The cod stock collapse and subsequent moratorium pronounced in 1992 marked a profound turning point in fisheries history, and the entire Northwest Atlantic grieved what was once a 'goldfield' for generations of fishers (Rose, 2007).

The history of cod fisheries in the Northwest Atlantic represents a complex interplay of ecological, technological, and socio-economic dimensions that cannot be reduced to a simple narrative. Over centuries, cod served as both a key species in marine ecosystems (Link *et al.*, 2009) and a cornerstone of coastal economies (Kurlansky, 2011), particularly in Newfoundland and Labrador, and Saint Pierre and Miquelon (Forrest, 2022). Progressive advances in fishing vessel technology, gear efficiency and capacity, combined with shifts in fishing rights, jurisdictional boundaries, and access to fishing grounds, intensified exploitation pressure throughout the 20th century (Hutchings and Myers, 1994; Lear, 1998). This intensification, compounded by a predominantly single-species management that often-overlooked broader ecosystem dynamics, contributed to the severe depletion of the cod stock (Link *et al.*, 2011; Hayden *et al.*, 2015). The collapse not only triggered ecological consequences, including trophic restructuring and altered predator-prey relationships (McCain *et al.*, 2011), but also reshaped local socio-ecological systems, disrupting livelihoods, food security, and cultural heritage (Hamilton and Butler, 2001; Rose, 2007; Kurlansky, 2011). Contemporary management frameworks increasingly aim to move beyond the limitations of single-species approaches by adopting ecosystem-based fisheries

management (EBFM) principles (Pikitch *et al.*, 2004; Link *et al.*, 2011). These approaches seek to account for species interactions, environmental variability, and cumulative human impacts, thereby integrating ecological, social, and economic objectives into a more holistic fisheries governance model (Pikitch *et al.*, 2004).

1.1.3 Ecosystem modelling as a key tool for fisheries management

Because species removal through fisheries have cascading effects on both preys and predators in the ecosystem, and in return ecosystem structure and stability influences species recovery, EBFM is based on the necessity of placing ecosystem health as a top priority for management (Pikitch *et al.*, 2004). EBFM relies heavily on the ability to understand species dynamics and fisheries pressures in the context of communities, and the whole ecosystem. Thus, management should be carried out with the goal of prioritizing long-term benefits and fish stock resilience, without compromising other species or habitats (Hall and Mainprize, 2004). This ecosystem perspective has driven the development of new metrics and indices to measure the performance of various biodiversity properties at the system-level, such as trophic structure and productivity (Hall and Mainprize, 2004; Powers and Monk, 2009). These indicators extend beyond single-species assessments, and can be incorporated in ecosystem models where groups of species are conceptualized as functional ‘boxes’ linked through various production and consumption relationships. Such models are a relevant tool to assess energy flows between different groups in the ecosystem, and evaluate trade-offs in management (Craig and Link, 2023).

Ecopath with Ecosim (EwE) is the most widely used modeling software for freshwater and marine ecosystems, and it can be used to address EBFM concerns (Christensen and Walters, 2004; Heymans *et al.*, 2016). Building on mass balance principles and core ecosystem parameters, it allows both static and dynamic modeling of trophic relationships in a marine ecosystems (Christensen and Walters, 2004). It offers ways to analyze the interplay between fisheries and environmental parameters in modulating ecosystem dynamics, and allows projections of alternative anthropological, economic and ecological scenarios, along with their potential impacts on biomass trends and predator-prey relationships within the system (Susini and Todd, 2021). Such a tool is particularly valuable in regions where historical fisheries have undergone dramatic transformations, as it allows scientists to explore the long-term ecological implications of past

exploitation patterns and management regimes (Pauly and Weingartner, 1998; Craig and Link, 2023). Given its capacity to integrate multiple variables, EwE is especially well suited for examining fisheries in contexts where human well-being is closely tied to marine resources.

1.2 Saint Pierre and Miquelon, a prime study example

The archipelago of Saint Pierre and Miquelon (SPM) is a prime example of how closely intertwined fisheries and local livelihoods are in a small archipelago. As the only insular territory claimed by France in the Northwest Atlantic, in the south of the Canadian province of Newfoundland-and-Labrador (Figure 1), SPM was always at a position of choice for French mainland vessels to exploit the abundance of seafood resources of the productive Grand Banks of Newfoundland and Saint Pierre Bank, until permanent colonies were established and SPM became the grounds of a thriving fishing village relying mainly on cod fisheries, until their collapse at the end of the 20th century (Eynaud, 1986; Winston and Le Floch, 2016).

This collapse of a major source of income and food security was accompanied by extended and polarized negotiations between SPM and Canada for exclusive access to fisheries resources, and later management of fish stocks and total allowable catch (McDorman, 1994; Wilson and Le Floch, 2016). SPM has built its economy mostly on the availability and exploitable potential of seafood, and local culture and identity has been forged by a close relationship with the Atlantic Ocean (Geistdoerfer, 1990; Forest, 2022; Teletchea, 2022). Such a pivotal change in resource accessibility had multi-levels impacts on local livelihoods (Teletchea, 2022), and present days efforts reflect a renewed engagement with marine resources, aiming to rebuild a robust fisheries industry laying on more sustainable foundations (Vigneau *et al.*, 2013; Palomares and Pauly, 2022; Teletchea, 2022).

SPM occupies a distinctive location in the Northwest Atlantic, where sub-Arctic and temperate waters converge, which results in strong seasonal variations in temperature, nutrient availability and water stratification (Bridier *et al.*, 2021; Jutras *et al.*, 2023). This intersection of oceanographic regimes supports a diverse marine community, while also shaping the productivity and seasonality of local fisheries (Colbourne and Murphy, 2008; Jutras *et al.*, 2023). With its highly-stratified water column and heavy reliance on the availability of marine resources, SPM is considerably sensitive to climate change impacts (Bridier *et al.*, 2021). An increase in sea surface

temperatures, which have been observed to be alarmingly high on the Newfoundland shelf (Belkin, 2009), could amplify water stratification, a phenomenon influencing marine species distribution, thereby potentially having strong effects on the entire food web (Bridier *et al.*, 2021). Limited terrestrial resources and economic diversification further heighten exposure, as the local economy and cultural identity remain closely tied to the productivity and accessibility of the surrounding marine ecosystem (Ancellin, 1955; Teletchea, 2022). These interacting ecological and socio-economic factors amplify the archipelago's sensitivity to climate-driven perturbations and underscore the importance of adopting adaptive, ecosystem-based management approaches (Teletchea, 2022; Craig and Link, 2023).

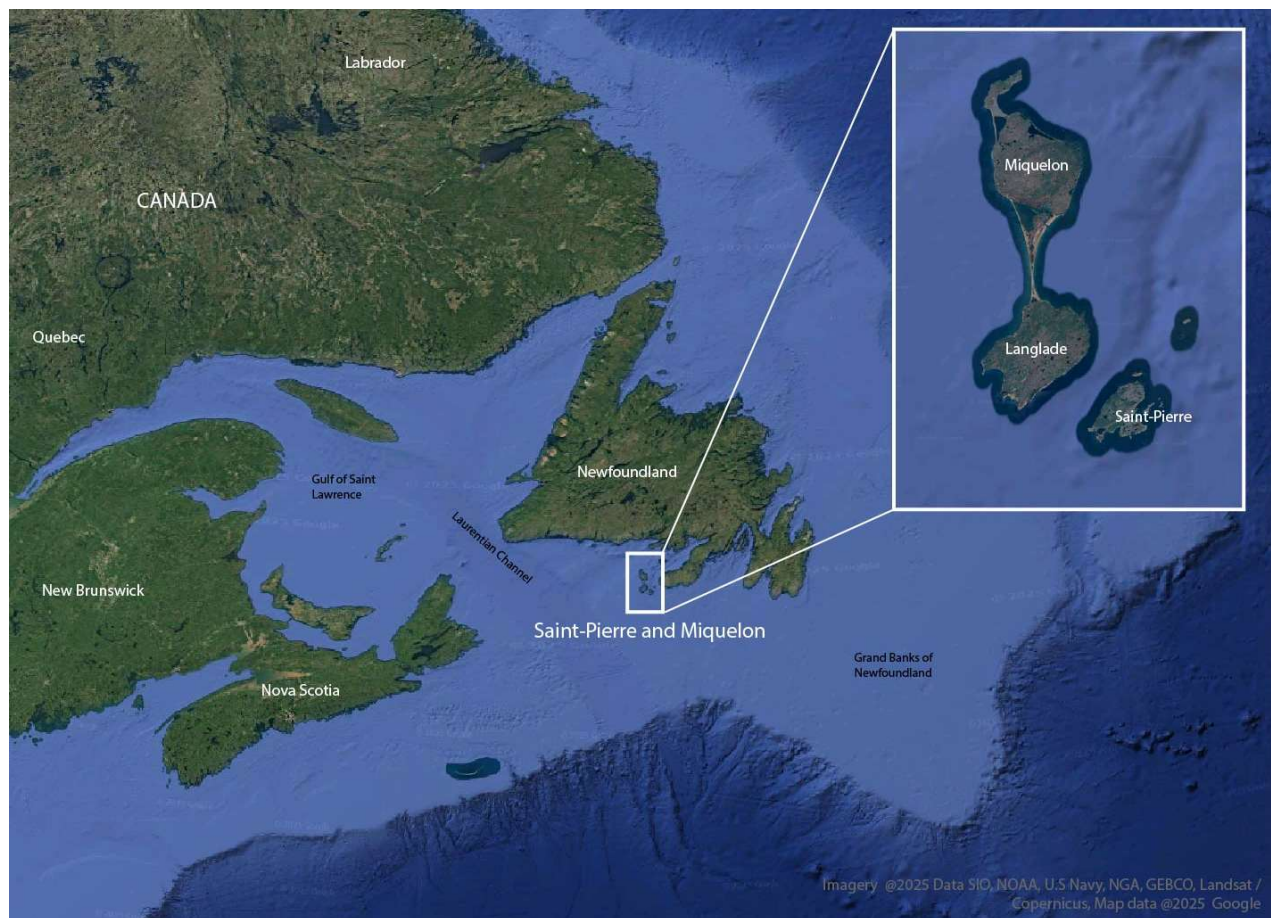


Figure 1.1. Map of Saint Pierre and Miquelon, and its position relative to the province of Newfoundland-and-Labrador, Canada.

1.3 Knowledge gaps and challenges when studying a small archipelago

SPM's unique geo-political position is sufficient in itself to justify the interest of studying with more depth how local fisheries have evolved, and their impacts on the surrounding marine ecosystem. As a small archipelago, SPM shares characteristics common to other data-limited regions, including fragmented or incomplete fisheries statistics, a scarcity of long-term biodiversity surveys, and limited integration between ecological and socio-economic datasets, which can hinder comprehensive ecosystem assessments (Vasconcellos and Cochrane, 2005; Natugonza *et al.*, 2020). Most biodiversity studies in SPM focus on single-species or single-groups assessments (Lormée *et al.*, 2008; Urtizbérrea *et al.*, 2011; Vigneau *et al.*, 2017), and ecosystem links are often sparsely addressed. While a growing number of studies on SPM arise in the hopes of mediating these constraints and moving towards more sustainable management of local resources (Vigneau *et al.*, 2013; Simian *et al.*, 2022; Lepareur *et al.*, 2023), these aforementioned knowledge gaps are yet to be studied comprehensively.

The Northwest Atlantic, as one of the world's most productive and economically important marine regions, has been well-studied through ecosystem modeling in the years succeeding the cod moratorium (Bundy *et al.*, 2000; Morissette *et al.*, 2003; Bundy, 2004; Tam and Bundy, 2019); this, however, is not the case for SPM. Ecosystems model are a tool of choice to bring more clarity on how SPM depends on marine resources, and for evaluating how patterns of local exploitation may influence the trajectory of future ecosystem states (Pauly and Weingartner, 1998; Craig and Link, 2023). Ultimately, complete fisheries records and statistics, extensive biodiversity assessments, and the study of interrelations between fisheries and the ecosystem, are essential to provide advice for marine conservation and the gestion of fisheries in an ecosystem-based management approach (Pikitch *et al.*, 2004; Thurstan *et al.*, 2015; Zeller and Pauly, 2016).

1.4 An integrated approach to understanding and managing the sea around SPM: thesis aims and research objectives

This research situates the archipelago of Saint Pierre and Miquelon within broader ecological and global fisheries contexts and explores the potential impacts of different management scenarios on its marine resources, to inform management efforts. A multi-faceted

approach was chosen to advance ecological and fisheries knowledge of Saint Pierre and Miquelon by combining biodiversity assessment and ecological theory, historical fisheries reconstruction, and ecosystem modelling to evaluate how marine resources shape the archipelago's ecological systems. These research components have been split into three data analysis chapters as follows:

Chapter 2 first addresses the gaps in SPM's presence in marine biodiversity databases, by conducting an extensive literature review to identify the various sources of data on marine species assemblages found in the waters surrounding the archipelago, and input a comprehensive list of (non-fish) marine species from SPM in the SeaLifeBase database (www.sealifebase.org). Building on this list and on the wide availability of fish data from FishBase, and of non-fish data from SeaLifeBase, this chapter tests the application of the Island Biogeography Theory to marine species, and studies the position of SPM relative to other archipelagos around the world in terms of species richness trends. This provides a baseline for marine ecological knowledge in islands and archipelagos, and a framework for understanding SPM's biodiversity patterns in a broader context.

While *Chapter 2* provides a biodiversity context for SPM, *Chapter 3* introduces a comprehensive fisheries background. This is done by reconstructing the total fisheries catches by SPM's boats within and outside of the archipelago's Exclusive Economic Zone (EEZ), from the early 1950s, when official fishing records first became available, to present days. This process falls within the effort of the *Sea Around Us* research initiative (www.seaaroundus.org) to compile reconstructed fishing data for all fishing countries and territories around the world from the year 1950, and to document the impact of fisheries on marine ecosystems worldwide. It includes reported and unreported fishery data disaggregated into multiple sub-categories.

Chapter 4 uses the framework provided by *Chapter 2* and *Chapter 3* to explore ecosystem modeling for the sea around SPM. This third chapter presents the first attempt at modelling the North Atlantic Fisheries Organization (NAFO) management division where SPM and its EEZ are situated, using the Ecopath with Ecosim (EwE) software. The creation of two static ecosystem models for two periods of time, and of a dynamic model for temporal projections, integrates most of the biodiversity and fishery data previously compiled for SPM. These models then allow us to simulate and project in time the ecosystem impacts of different fishery scenarios.

The aforementioned research objectives described for each chapter build on the following hypotheses:

Chapter 1

1. Island Biogeography Theory can be applied to marine ecosystems, and continental shelf surface area used as a proxy for evaluating marine species richness.
2. Island Biogeography Theory can serve as a framework to understand marine biodiversity in SPM, and to position the archipelago on a global marine biodiversity scale.

Chapter 2

3. The reconstructed tonnage caught in the EEZ of SPM will be greater than the reported baseline, when including unreported catches.
4. Fishing pressures in SPM have shifted from higher trophic level species to lower trophic level species through time.
5. The mean temperature of the catch has increased in recent years, matching global trends

Chapter 3

6. Reconstructed catches add greater realism to ecosystem models and allow for modeling and projections of fishing pressures with higher accuracy.
7. The shift to catching lower trophic-level species risks having bottom-up effect on the ecosystem when projected through time.
8. Continuous fishing pressure directed to a limited number of species will lead to measurable shifts in ecosystem structure over time, including declines in target species biomass, and potential cascading effects on non-target species.

Chapter 2: The Biodiversity of Saint Pierre and Miquelon, and application of Island Biogeography Theory to marine species

2.1 Introduction

‘Marine biodiversity’ is a term that encompasses an array of meanings: if biodiversity is defined as ‘all species,’ as is most commonly done, this should include all “the variety of life,” i.e., all genes and ecosystems as well (DeLong, 1996; Swingland, 2001; Cochrane *et al.*, 2016). Biological diversity can also be defined to include several types of diversity measures, namely taxonomic (i.e., the number of species) ecological (i.e., the diversity of ecosystem and environmental processes), genetic (i.e., the variety of genes) and functional (i.e., the number of functional traits) (DeLong, 1996).

Describing marine biodiversity is essential not solely for a better understanding of the components of an ecosystem, but involves acknowledging the intrinsic value of biodiversity. Describing the taxonomy, occurrence and abundance of various species in a marine region can inform environmental management on invasive species, allow the exploring of future distribution scenarios, and enable the study of their repercussions on the ecosystem (Costello *et al.*, 2017). But bringing more attention to marine biodiversity doesn’t just enable the expansion of our knowledge of the ocean: it highlights its intrinsic right to exist and strengthens our ethical responsibilities towards the conservation of marine life (Boero and Bonsdorff, 2007).

2.1.1 Marine biodiversity patterns

Marine biodiversity can be challenging to assess as an additional spatial layer – depth – has to be considered when looking at the number of species in an area (Sala and Knowlton, 2006; de Juan *et al.*, 2023). But it is also difficult to assess in terms of clear geographical borders, as a considerable number of marine mammals and fish are migratory species that do not stay confined to specific areas. This is why marine biodiversity is commonly assessed for marine ecoregions, and in terms of latitude, longitude, and depth (Sala and Knowlton, 2006; Costello *et al.*, 2010; de Juan *et al.*, 2023).

However, when trying to assess marine biodiversity for specific islands and archipelagos, biodiversity levels are known to be higher on shelves, i.e., the inshore areas down to 200 m, which offers guidance on which scale can be used to evaluate island-specific marine species richness, i.e., the total number of marine species (Townsend *et al.*, 2006; de Juan *et al.*, 2023). For benthic invertebrates and sessile organisms, higher diversity is strongly correlated to a high diversity of shelf habitats. This high diversity of habitats provides, in turn, a high food availability for primary consumers, then secondary consumers and thus shapes an ecosystem's trophic interactions (de Juan and Hewitt., 2011; Costello and Chaudhary, 2017).

Marine biodiversity patterns are also strongly influenced by geographical and oceanographic factors (Briggs, 1966; Lalli and Parsons, 1997). Ocean temperature drives patterns of species diversification that are dependent on food availability, predation and competition for the resources. Food availability is driven by primary productivity gradients, which vary according to an array of oceanographic conditions, notably water temperature, salinity, nutrients and oxygen levels, in addition to physical controls such as oceanic currents that distribute nutrients (Lalli and Parsons, 1997; Macpherson, 2003; Costello and Chaudhary, 2017). Marine species are also influenced by depth and latitudinal gradients, which are linked to temperature and productivity gradients. Depths and temperature gradients create biogeographical boundaries, which result in the zonation of marine species ranges, and define depth domains such as the continental shelf (Briggs, 1966; Macpherson, 2003; Briggs and Bowen, 2013). At higher latitudes and colder temperatures, species richness tends to decline, but can nonetheless be influenced by regional oceanic drivers (Peck *et al.*, 2016).

In the Northwest Atlantic Ocean, upwelling zones near Newfoundland and river inputs from the Gulf of Saint-Lawrence support high nutrient inputs to the surface waters, and high primary productivity along coastal regions. Seafloor topography with features like the Grand Banks of Newfoundland provides diverse habitats, supporting species richness and different benthic and pelagic assemblages (Gomes *et al.*, 1995; Townsend *et al.*, 2006).

2.1.2 Geographic and oceanographic contexts of Saint Pierre and Miquelon

The archipelago of Saint Pierre and Miquelon (SPM) is a French overseas territory located 46.8°N and 56.2°W, about 25 km south of the Canadian Island of Newfoundland, in the province

of Newfoundland-and-Labrador. It is the only territory claimed by France that is located in the Northwest Atlantic Ocean and is composed of eight islands: Saint-Pierre, Miquelon-Langlade (two islands connected by a tombolo), Isle-aux-Marins, Ile aux Vainqueurs, Ile aux Pigeons and Grand Colombier. The sovereignty of the eighth island, Ile Verte, is disputed between France and Canada, but accepted as being part of the Saint Pierre and Miquelon archipelago (Symmons, 1980). SPM is the summit of the Miquelon Bank submarine plateau, and is located north of the larger Saint Pierre Bank, which is part of the group of submerged banks making up the Grand Banks of Newfoundland. The Miquelon and Saint Pierre banks depths reach 100 to 200 meters, with an average depth between 50 to 100 meters (Cermakian *et al.*, 1970; Simms, 2007).

SPM is a sub-Arctic Archipelago with a strongly thermally stratified marine ecosystem. (Bridier *et al.*, 2021). The regional oceanographic dynamics on the banks are greatly conditioned by the adjacent density and wind-driven Labrador current, and mainly its inshore branch (Bezaud *et al.*, 2020; Jutras *et al.*, 2023). The Labrador current originates in the Arctic Ocean and brings cold and oxygen-rich water to the southern banks (Jutras *et al.*, 2023). The water temperature on and around the Saint Pierre Bank is characterized by sharp seasonal thermal variations: in summer, surface temperatures warm up to average 15 to 18 °Celsius, and in early fall a massive water temperature drop can be measured to an average of 0-2 °Celsius at 80 meters depth (Anonymous, 1975; Lazure *et al.*, 2018; Bridier *et al.*, 2021). The colder winter waters from the Arctic at 100 meters depth in December-January still persist under a 150 meters thermocline in the summer (Anonymous, 1975). A recent study of temperature oscillations around the archipelago by Lazure *et al.* (2018) highlighted the existence of strong diurnal bottom temperature oscillations in SPM, which can reach up to 11.5 °Celsius at a depth of 70 m. However, the high seasonal stratification of the water column leads to a weak transfer of nutrients and energy between the benthic and pelagic communities (Bridier *et al.*, 2021).

A particularity of the marine habitat around SPM lies in the fact that two specific oceanographic regimes are at play depending on the influence of adjacent currents. The aforementioned Labrador inshore current creates a regime influenced by cold and oxygen-rich Arctic waters on much of Saint Pierre Bank (around 0-2 °Celsius), while the western parts of the Saint Pierre Bank adjacent to the Laurentian channel are influenced by warmer currents (of around 3-6 °Celsius) from the south and the slope of the Bank (Colbourne and Murphy, 2008; Jutras *et al.*,

2023). The convergence of these currents in the area generates an upwelling where nutrient-rich waters rise to the surface, which leads to a high primary production. Such differences in temperature and regimes have an influence on the distribution of fish and invertebrates, both intraspecifically through seasonal distribution and vertical migrations, and interspecifically with spatial differences in species diversity (Anonymous, 1975; Lalli and Parsons, 1997; Colbourne and Murphy, 2008). The vertical stratification of the water column results in pronounced temperature and depth zonation, shaping clear differentiation between benthic and pelagic communities (Briggs, 1966; Macpherson, 2003; Briggs and Bowen, 2013).

2.1.3 Island biogeography of marine organisms

Whereas terrestrial biodiversity of islands and the processes that shaped its diversification have been well studied on numerous oceanic and continental islands, the processes shaping insular marine biodiversity, particularly of mobile and migratory species, still remain understudied. Studying marine biodiversity in archipelagos such as SPM is of particular relevance when trying to understand marine ecosystem interactions, as islands and archipelagos are unique “natural laboratories” (Sinigaglia *et al.*, 2024) and key study areas to explore biogeographical and evolutionary theories (Warren *et al.*, 2015; Hirschfeld *et al.*, 2023). This is illustrated through the high diversity of habitats (and thus, ecological niches) usually provided by islands, the high land-sea connectivity shaping critical predator-prey interactions, and through their isolation from the mainland (Warren *et al.*, 2015; Sandin *et al.*, 2022).

The lack of connectivity to the mainland shaped unique evolutionary processes, notably a higher rate of species diversification and endemism. Many islands demonstrate a high degree of genetic divergence in marine species from the continental mainland as a result of isolation and the evolutionary mechanisms at play (Costello *et al.*, 2017; Sinigaglia *et al.*, 2024).

Island Biogeography Theory (IBT) emerged in 1967 through the work of MacArthur and Wilson (1967) on insular biodiversity and the processes shaping species distribution patterns. The theory states that the number of insular species should follow a lognormal distribution influenced by the surface areas and the degree of isolation of islands. Hence, islands with a larger surface area should provide a higher diversity of habitats suitable for a higher diversity of species. Comparably, islands that are less isolated (i.e., closer to the continental mainland) should have a higher diversity

of species. These conclusions are drawn from the observation of lower rates of extinction when island size increases, and higher rates of immigration where the isolation of an island decreases (MacArthur and Wilson, 1967).

While primarily developed through the study of ants, and for application to terrestrial insular species, Island Biogeography has been applied to marine organisms in recent studies, which yielded negative correlations between marine speciation and immigration rates, as well as other factors relevant only to marine systems, such as eustatic sea level changes (Hachich *et al.*, 2015, Pinheiro *et al.*, 2017). In the marine environment, the coastal areas of islands, like continental shelves, harbor most of the marine diversity. Immigration, speciation and extinction are the evolutionary mechanisms that shape the biodiversity patterns of both terrestrial and marine species.

However, the diversification patterns derived from terrestrial organisms may not apply to marine organisms, which likely to be influenced by different variables, specific to the oceanic environments, such as temperature and oceanic currents (Costello and Chaudhary, 2017; Pinheiro *et al.*, 2017). Inherently, the fact that mobile and migrating marine species are most often exhibiting distributions that are not constrained by physical borders, unlike terrestrial species, plays a substantial role in shaping these differences. Rather, patterns of depth and temperature will create borders for the distribution of marine species, less distinct for highly mobile groups such as marine mammals (Robinson *et al.*, 2011). These variables shaping marine species distribution remain understudied by scientists working on Island Biogeography.

2.1.4 Chapter overview and research objectives

Marine biodiversity in SPM is under strong anthropogenic pressures, to which the exploration of offshore marine mining and gas opportunities on the Saint Pierre Bank are a recent addition. This potential for gas exploitation has been the subject of considerable discussions, and disputes for the access of resources, between Canada and SPM through the years (Day, 1992; Le Floc'h *et al.*, 2016). Such tangible threat requires the planning conservations measures, which themselves require to be based on comprehensive understanding of the local biodiversity.

While marine biodiversity in the broader Northwest Atlantic has been well studied and documented over the years, very few published sources mention the archipelago of SPM specifically as being part of the distribution area of most marine species, resulting in online marine

biodiversity databases being incomplete for SPM. A few biodiversity assessment campaigns have been conducted in SPM mostly geared towards providing an assessment of fish, and benthic and planktonic species (Lazure and Foucher, 2017; BeBest, 2019. Simian *et al.*, 2022). Other groups of species have been studied around the islands in independent studies, such as pinnipeds (Vincent *et al.*, 2022) and seabirds and shorebirds (Abraham and Etcheberry, 2014). However, aside from local naturalists' species lists, no effort was previously undertaken to integrate these various data sources into a comprehensive database, for example SeaLifeBase (www.sealifebase.org), to generate an extensive inventory of marine species present in SPM.

Moreover, there are very few to no studies evaluating the application of the island biogeography theory for marine organisms in relation to water temperature, i.e., influenced by latitude, or attempting to show which dependent variable explains most of the distribution of marine species across islands and archipelagos, as can be straightforwardly achieved through a multiple regression approach. Understanding the variables influencing marine biodiversity is essential to inform management policies, in particular for identifying areas of high conservation interest (Richardson and Whittaker, 2010). Additionally, comparing SPM in terms of marine species richness to other archipelagos around the world gives a useful insight into the relative position of SPM with regard to its marine biodiversity, and the need for increased conservation efforts, e.g., in the form of Marine Protected Areas (MPA). Eventually, SPM could develop policies which could serve as an example of informed management policies, designed to overcome the legacy of overfishing in the Northwest Atlantic.

This chapter thus explores the relative position of SPM on a global insular gradient of marine biodiversity, and the broader application of Island Biogeography Theory to archipelagos. It presents firstly an up-to-date checklist of marine species in the waters around Saint Pierre and Miquelon, including all groups except fish, as a checklist of fishes in SPM has previously been established by Simian *et al.* (2022). This list is, however, subject to being updated with the data collected in potential new assessment field studies in the future. Secondly, a test of Island Biogeography Theory with marine species is performed, using marine species richness in various archipelagos around the world, with SPM as a focus area. This test focuses on identifying which parameters have the most influence insular marine species richness, and on whether SPM stands out as an archipelago of high biodiversity, given its latitudinal position and the size of its shelf, i.e.

the coastal waters down to 200 m depth. This is based on the hypotheses that, following the lognormal species-area relationship (SAR) that is part of Island Biogeography Theory, (1) archipelagos with a large shelf area should have a higher species richness than areas with a smaller shelf, (2) the surface area of the shelf should be the main driver of species richness gradients, over latitude and (3) the species-area exponent of the SAR equation should reflect the strength of the relationship between island size and species richness and be close to its theorized value between 0.3 and 0.5.

While measuring marine biodiversity requires accounting levels of complexity which include not only the number of entities in a marine system, but their abundances and distribution, their genetic divergence and their functional role in the ecosystem, species richness as a single measure of marine biodiversity was considered for the purpose of this chapter. Species richness can be defined in terms of alpha diversity, or the number of species in a particular area with no diversity comparison between area (Whittaker, 1972). This choice was made knowing that it is not enough of a measure of total marine biodiversity, but can be a useful proxy to describe local biodiversity and explore some of the application of biodiversity theories (Sala and Knowlton, 2006).

2.2 Materials and methods

2.2.1 Checklist of the local marine biodiversity

A checklist of marine species occurring in SPM was created and added to SeaLifeBase (www.sealifebase.org), whose lists of marine species occurring in SPM was very incomplete. To provide a checklist as accurate and complete as possible, and given the limited data collections undertaken locally for certain groups, multiple sources and global databases were considered, such as the World Register of Marine Species' (WoRMS, <https://www.marinespecies.org/index.php>), documented distribution maps and datasets (such as the Marine Species Register for the North Western Atlantic Ocean), the Ocean Biodiversity Information System (<https://obis.org/>) and Fisheries and Ocean Canada's (DFO) Maurice Lamontagne Institute databases. Oceanographic and taxonomic campaigns conducted around the archipelago were also considered, such as the phytoplankton and bivalve components of the 2017 Ifremer campaign in SPM and the 2019 BeBest mission on establishing a benthic biodiversity inventory (Lazure and Foucher, 2017; BeBest, 2019).

Additionally, an extensive bibliographic study was undertaken to collect information from various publications pertaining to systematic studies for local fauna and flora (in order to include marine algae in the checklist), to local or exotic species monitoring, and to seafood exploitation or exosystemic studies (Delamare *et al.*, 1888; Rallier du Baty, 1927; Raup *et al.*, 1951; Ancellin, 1955; Lormée *et al.*, 2008, 2012; Zellhuber and Detcheverry, 2009; Abraham and Etcheberry, 2014; Sellier *et al.*, 2014). When SPM-specific studies were not available, species distribution ranges were studied through publications encompassing larger areas, with the rule that said area of study must include the archipelago (Deichmann, 1936; Warburton, 1958; Marti, 1962; South and Hooper, 1980; Weerdt, 1986; Murillo *et al.*, 2016; Savouré-Soubelet *et al.*, 2016; Marine Mammal Observation Network, 2022).

Local knowledge was also sought to confirm the presence of certain species where sources were missing or were incomplete, through personal communications with marine researchers working on various SPM projects including species-specific diet studies, acoustic surveys and ecological monitoring (C. Vincent, CNRS, and F. Urtizbérrea, DTAM, may 2024, personal communication; L. Morrissette, UQAR, October 2024, personal communication). Local naturalist photo observations, such as DORIS and iNaturalist (doris.ffessm.fr, www.inaturalist.org), and databases (naturespm.com) were also reviewed in the context of this study.

2.2.2 Application of the Island Biogeography Theory to marine species

In order to perform a comprehensive comparison of species richness between diverse archipelagos around the world, 40 islands and archipelagos including SPM were selected, varying in their position on latitudinal and longitudinal gradients, and in the total surface area of their continental shelf. These 40 archipelagos were chosen on the basis of having an Economic Exclusive Zone (EEZ) separate from any mainland country's EEZ (e.g., the Yemeni archipelago of Socotra having its own EEZ, separate from the Yemen EEZ), and consequently a continental shelf separate from the mainland shelf. Additionally, the sample group was ensured to cover a wide range of sizes (i.e., shelf surface area, SSA, expressed in km²), including islands as small as Saint Paul and Amsterdam (SSA = 291 km²) and archipelagos as large as Indonesia (SSA = 1,975,420 km²), and a wide range of latitudes, including northernmost archipelago of Svalbard (78°N) and Ecuadorian archipelago of the Galapagos (0°). Shelf surface areas were obtained from

the Sea Around Us website, as earlier calculated with the ESRI software, from the shore to a depth of 200 m, using the United States National Geophysical Data Center's ETOPO GLOBAL 2' elevation data (Zeller and Pauly, 2016).

The basis of the Island Biogeography Theory by MacArthur and Wilson (1967) postulates that biodiversity, expressed through species richness, can be plotted against island surface area in a lognormal relationship based on the species-area equation:

$$S = cA^z \quad (1)$$

where S is the number of species (species richness), c is a constant reflecting the baseline level of species richness for a given habitat, varying with each ecosystem, A is the surface area (here, surface area of an island or archipelago's shelf) and z is the species-area exponent or slope of the area-species curve, quantifying the strength of the relationship between species richness and habitat area (Arrhenius, 1921).

2.2.2.1 Multiple regression analysis for fish species

For the 40 islands and archipelagos considered for this study, a series of regressions and multiple regression analyses (MRA) were run to evaluate the effect of latitude and shelf surface area on fish species richness. MRA was chosen as it allows for the assessment of how several variables influence the variance of the dependent variable, while controlling for confounding effects, and allow to visualize the strength of the relationship between these variables (Zuur *et al.*, 2010). Fish species richness data were extracted from FishBase (www.fishbase.org; Froese and Pauly, 2010) for each of the archipelagos. Data extraction was performed by querying the database by geographic area using the "Country/Island Ecosystem" function and recording the number of "saltwater" fish species reported in that area as the species richness. The dependent variable in this analysis was species richness. The independent variables included latitude and shelf surface area, which were selected based on their theoretical relevance (Macpherson, 2003).

The multiple regression model was specified as follows:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \varepsilon \quad (2)$$

where Y represents the dependent variable, X_1 and X_2 are the predictor variables, β_0 is the intercept, β_1 and β_2 are the regression coefficients and ε represents the error term (Nimon and Oswald, 2013; Groß, 2003).

The two independent variables were plotted in a multiple regression to evaluate their relationship with the dependent variable, the portion of the variation predictable from the independent variables (i.e., the coefficient of determination R^2), and the strength of the species-area relationship (i.e., the slope or species-area exponent z). Additionally, the total number of threatened fish species according to the International Union for the Conservation of Nature's (IUCN) assessments was compared for these islands and archipelagos to evaluate the position of SPM relative to other archipelagos in terms of the number of threatened species on total number of species ratio.

2.2.2.2 Multiple regression analysis for other marine species

MRAs were conducted for 36 of the 40 islands and archipelagos for each of the following marine groups separately: marine mammals, molluscs, crustaceans, and cnidarians, to determine the independent contributions of each independent variable in predicting marine species distribution. Species richness data was collected from SeaLifeBase (www.sealifebase.org). As the online interface allows limited options for taxon-specific filtering, data extraction was manually performed where species counts were sorted by major taxonomic groups from the underlying species occurrence files for each study region. Upon consultation with a SeaLifeBase expert, the four islands and archipelagos for which data on marine species were considered to be incomplete or non-representative of the actual species richness in SeaLifeBase (N. Bailly, biodiversity informatics specialist and Q-Quatics taxonomy coordinator, UBC, personal communication, March 2024) were excluded from the MRAs.

2.2.2.3 Standardized β coefficients

In addition to the unstandardized coefficients given by the MRA output, and for direct comparison of the strength and direction of the relationship between each independent variable and the dependent variable (Nimon and Oswald, 2013), standardized β coefficients were calculated for each variable in each model according to the following equation:

$$\beta_j = B_j \cdot \frac{\sigma_{X_j}}{\sigma_Y} \quad (3)$$

where B is the unstandardized coefficient of the independent variable j , σX_j is the standard deviation of predictor X_j and σY_j is the standard deviation of the dependent variable Y . The standard deviation for all variables was calculated using the formula:

$$\sigma = \sqrt{\frac{\sum (X_i - \bar{X})^2}{N - 1}} \quad (4)$$

where X_j represents individual observations, $\bar{X}$ is the sample mean, and N is the number of observations. This formula accounts for sample variability by using $N-1$ (Bessel's correction) in the denominator (Cook and Upton, 2008).

2.2.2.4 Variable assessment and model significance testing

Prior analysis, all variables (i.e., species richness, latitude and shelf surface area) were assessed for missing data, linearity, normality and multicollinearity to ensure compliance with regression assumptions (Graham, 2003; Zuur et al., 2010). Scatterplots of residuals versus predicted values were examined to confirm linear relationships and the Shapiro-Wilk test was used to evaluate the normality of residuals. Durbin-Watson test was used to evaluate the autocorrelation of residuals. The Variance Inflation Factor (VIF) was calculated with values below 10 indicating acceptable collinearity with the following equation:

$$VIF = \frac{1}{1 - R^2} \quad (5)$$

where R^2 is the coefficient of determination obtained from the regression model, representing the portion of variance that can be predicted from the independent variables (Groß, 2003).

The overall significance of the regression model was evaluated using an F-test, with significance set at $\alpha = 0.05$. Model explanatory power was assessed using R^2 (coefficient of determination) and adjusted R^2 to account for the number of predictors. Individual predictors were evaluated based on their t-statistics and p-values. The analysis was conducted using Microsoft Excel and R, using the *car* (Fox and Weisberg, 2019) and *lmtest* (Zeileis and Hothorn, 2002) packages.

2.3 Results

2.3.1 A description of the marine biodiversity in Saint Pierre and Miquelon

The full list of non-fish marine species found in SPM is available in SeaLifeBase (www.sealifabase.org). The following sections mention all species for groups containing less than 20 species present in SPM, and only some of interest for the groups containing more than 20 species.

Marine mammals

Cetaceans

The SPM archipelago provides feeding grounds that are located on the migration route of several large cetacean species, and presents a quite large variety of both Mysticetes (baleen whales) and Odontocetes (toothed whales) marine mammals, with 15 species identified (Nguyen Hong Duc *et al.*, 2021). While humpback whales (*Megaptera novaeangliae*) are the most abundant cetaceans in the area, other piscivorous (i.e., feeding principally on fish and small invertebrates), species belonging to the Mysticetes subgroup are observed such as minke (North Atlantic sub-species, *Balaenoptera acutorostrata acutorostrata*), right (*Eubalaena glacialis*) and fin whales (North Atlantic sub-species, *Balaenoptera physalus physalus*). Several species of the Odontocetes subgroup are additionally found in the area, sperm (*Physeter macrocephalus*), pygmy sperm (*Kogia breviceps*), and long-finned pilot whales (North Atlantic sub-species, *Globicephala melas melas*), but also harbour porpoise (*Phocoena phocoena*), short-beaked common (*Delphinus delphis*), white beaked (*Lagenorhynchus albirostris*), striped (*Stenella coeruleoalba*) and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) (Zellhuber and Detcherry, 2009; Nguyen Hong Duc *et al.*, 2021; Marine Mammal Observation Network, 2022).

While a few beluga whales (*Delphinapterus leucas*) have been observed in the waters around the islands, these sightings are only of transient individuals as belugas distribution range does not extend to SPM (F. Urtizbéréa, DTAM, January 2025, personal communication). One specimen of Sowerby's beaked whale (*Mesoploddon bidens*) has been found stranded on the island of Langlade in 2024; while the distribution range of this species usually stretches to Labrador, it is very rarely locally observed as it mainly frequents deeper waters outside of the Saint Pierre Bank limits (Mahé *et al.*, 2024).

Two species of planktivorous cetaceans can be found sporadically around the islands: blue whales (*Balaenoptera musculus*) and sei whales (*Balaenoptera borealis*), although the latter species seems to not have been observed or recorded around the islands since 2009 (Zellhuber and Detcheverry, 2009). While most Odontocetes are present more abundantly in summer and autumn, Mysticetes seemed to be mostly recorded in the area in winter (Nguyen Hong Duc *et al.*, 2021).

Only one species of carnivorous cetaceans can be found around SPM: killer whales (*Orcinus orca*) (Marine Mammals Observation Network, 2022). Killer whales hunting around the archipelago have been recently studied to be feeding almost exclusively on seal species, such as grey and harbour seals (L. Morissette, UQAR, October 2024, pers. comm.).

Pinnipeds

Pinnipeds in SPM have a key position in the ecosystem, as their higher trophic level places them among the main predators for many large fish species (Vincent *et al.*, 2022). Among the four seal species frequenting the waters around the archipelago, two are found in higher abundance: grey (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*), as SPM provides breeding grounds for harbour seals and feeding grounds for both species (Vincent *et al.*, 2022; C. Vincent, CNRS, May 2024, pers. comm.). However, in the surrounding area including the Saint Pierre Bank, hooded seals (*Cystophora cristata*) seem to be found in higher abundance, as the bank is part of their route between their breeding grounds and foraging grounds. Harp seals (*Pagophilus groenlandicus*) are also found frequenting the bank sporadically, as neither their breeding or foraging grounds are located in SPM (Hammill and Stenson, 2005). A fifth species, the bearded seal (*Erignatus barbatus*) was observed on a few occasions in the archipelago, while its distribution range does not normally extend to SPM (F. Urtizbérrea, DTAM, January 2025, pers. comm.).

Seabirds

Piscivorous seabirds

The island of Grand Colombier, part of the SPM archipelago, harbours the largest local concentration of seabirds. Several local monitoring and counting expeditions have been conducted on the small island in the past few years. Some piscivorous species have their local population concentrated uniquely on Grand Colombier, such as the Atlantic puffin (*Fratercula arctica*), and

the Leach's storm petrel (*Hydrobates leucorhous*), with around 150,000 pairs present in summer, as the island is their breeding and nesting location (Lormée *et al.*, 2008, 2012; Letournel *et al.*, 2018). In total, 36 species of piscivorous seabirds are found in SPM, among which are razorbills (*Alca torda*), the only extant members of the genus *Alca*, black-legged kittiwakes (*Rissa tridactyla*), staying almost all year long in the archipelago, black guillemots (*Cepphus grylle*), breeding on the archipelago every year, northern fulmars (*Fulmarus glacialis*), circumpolar species pushed (mainly by rising pollution discards from trawlers in the Arctic) to expand its breeding and nesting areas to SPM, and Northern gannets (*Morus bassanus*), locally nicknamed 'marga' (used in SPM to refer to someone voracious) for the large quantities of fish it feeds on (Abraham and Etcheberry, 2014). Piscivorous seabirds in SPM feed primarily on small fishes, such as capelin (*Mallotus villosus*) and sand lance (*Ammodytes* sp.) (Letournel *et al.*, 2018).

Planktivorous seabirds

Planktivorous seabirds are represented by a single species in SPM, the dovekie (*Alle alle*). Dovekies are a Holarctic species, whose breeding and feeding grounds are located in the Arctic. In SPM, they can be observed every year around mid-October and in winter (Abraham and Etcheberry, 2014). The winter presence of the species in SPM is influenced by the current systems and temperature patterns themselves influencing plankton density, as dovekies tend to select zooplankton species that have high calorific values (Brown, 1988; Jakubas *et al.*, 2007).

Benthivorous seabirds

Benthivorous seabirds feed mainly on small organisms on the sea floor and are represented by 14 species in and around SPM, among which are the common eider (*Somateria mollissima*), horned grebe, feeding in the shallow water along the coast, red-necked grebe (*Podiceps grisegena*) found in both the calmer waters along the coast and the natural lagoon of the Grand Barachois in Miquelon, and the red-throated loon (*Gavia stellata*), where SPM is at the northern range of their winters distribution (Abraham and Etcheberry, 2014; Tam and Bundy, 2019). Most of the benthivorous species are Holarctic species expanding their winter-feeding areas to the southern waters of Newfoundland, and are found in smaller groups than the piscivorous seabird species in the archipelago (Abraham and Etcheberry, 2014).

Shorebirds

Shorebird species are often forgotten from marine biodiversity studies, as they are not traditionally considered ‘marine’ birds. They are, however, of importance in the marine ecosystem as shorebirds use marine habitats and forage for small invertebrates including bivalves and small shrimps (Warnock *et al.*, 2001). For the purpose of this study, only the species of shorebirds frequenting marine habitats were considered and added to SeaLifeBase. The 36 species listed in SPM include mostly species of sandpipers, phalaropes and plovers, such as the buff-breasted sandpiper (*Tryngites subruficollis*), the sanderling (*Calidris alba*), the semipalmated plover (*Charadrius semipalmatus*) and the ruddy turnstone (*Arenaria interpres*) (Abraham and Etcheberry, 2014).

Fishes

The fish species occurring in the SPM archipelago have been described by Simian *et al.* (2022). Among the 111 species of demersal and pelagic marine fishes listed in SPM, notable species include Atlantic cod (*Gadus morhua*), of strong economic importance as the main species historically targeted by local fisheries, capelin (*Mallotus villosus*), species of high cultural significance on the archipelago, Atlantic halibut (*Hippoglossus hippoglossus*), Atlantic salmon (*Salmo salar*), mainly targeted by local recreational fisheries, and porbeagle shark (*Squalus acanthias*), an abundant benthopelagic species in the Northwest Atlantic commonly targeted by local fisheries (Paturel, 1976; Eynaud, 1986; Rago *et al.*, 1998; Simian *et al.*, 2022).

Marine invertebrates

The SeaLifeBase database has been supplemented with 597 invertebrate species in 102 orders and 13 phyla: Annelida (10 orders, 23 families), Arthropoda (13 orders, 54 families), Brachiopoda (2 orders, 2 families), Bryozoa (2 orders, 9 families), Chaetognatha (1 order, 1 family), Cnidaria (13 orders, 45 families), Echinodermata (16 orders, 22 families), Mollusca (36 orders, 113 families), Nematoda (2 orders, 2 families), Nemertea (1 order, 1 family), Porifera (4 orders, 4 families), Priapulida (1 order, 4 families) and Xenacoelomorpha (1 order, 1 family). The results presented below only include the groups that matter to local fisheries, and the entire list can be found on SeaLifeBase.

Crustaceans

The crustacean group in SPM consists of 96 species, and includes crabs (e.g. *Pagurus acadianus*), shrimps (e.g., *Lebbeus polaris*), prawns (e.g., *Pandalus montagui*), lobsters (*Homarus americanus* being the only species in the Northwest Atlantic), krill (e.g., *Meganyctiphanes norvegica*), barnacles (e.g., *Balanus crenatus*), amphipods (e.g., *Stegocephalus inflatus*), isopods (e.g., *Calathura brachiata*), copepods (e.g., *Paraheterorhabdus robustus*) and other small crustaceans. Illustrating this invertebrate group are species commonly targeted for local consumption and export by SPM commercial and small-scale fisheries, such as snow crabs (*Chionoecetes opilio*), Arctic lyre crab (*Hyas coarctatus*) and northern prawn (*Pandalus borealis*) (Marti, 1962; Murillo *et al.*, 2016; BeBest, 2019; DFO, 2022). The presence of the exotic and invasive green crab (*Carcinus maenas*), locally monitored for its potential impact on the local crustaceans, can also be noted (Sellier *et al.*, 2014).

Echinoderms

Echinoderms are a phylum of benthic invertebrates which fall into five classes, including starfish, sea urchins, sea cucumbers, sand dollars, and occupy various ecological niches on the sea bed (Amemiya *et al.*, 2005). Echinoderms are represented by 39 listed species in SPM, including the orange-footed sea cucumber (*Cucumaria frondosa*), commercially exploited since the early 2000s in the archipelago (Palomares and Pauly, 2022), but reported much earlier from St Pierre Bank, e.g., by Marti (1962).

Molluscs

Molluscs are made up of several subgroups including bivalves, cephalopods and gastropods, the most diverse subgroups within the phylum. They are known to be occupying a broad ecological spectrum in terms of habitats, motilities and feeding behaviors (Vinther, 2015). A total of 319 species has been listed under the Mollusca phylum for SPM, including the locally exploited waved whelk (*Buccinum undatum*), soft-shell clam (*Mya arenaria*), Atlantic deep-sea scallop (*Placopecten magellanicus*), Iceland scallop (*Chlamys islandica*) and blue mussel (*Mytilus edulis*) (Marti, 1962; Van Guelpen *et al.*, 2005).

2.3.2 Testing the application of island biogeography theory

To examine the relationship between species richness and both latitude and shelf surface area, MRAs were conducted for each of the five marine groups considered: fishes, marine mammals, molluscs, crustaceans, and cnidarians. These analyses informed on SPM's position along richness gradients, and on the extent to which the independent variables predict species richness.

2.3.2.1 Relation between species richness and the two independent variables

The MRAs show that both latitude and the shelf surface area are significantly related to species richness for three of the five groups: fish, molluscs, and cnidarians. The variance in species richness of the two remaining groups (i.e., marine mammals and crustaceans) is only explained by surface area.

For fish species, the overall model was significant, $F(2,37) = 34.33$, $p\text{-value} < 0.05$, explaining 65% of the variance in species richness ($R^2 = 0.65$, Adjusted $R^2 = 0.63$). Latitude is a significant negative predictor, indicating that lower latitude values are associated with an increase in species richness, while surface area is a significant positive predictor, with greater surface area associated with an increase in species richness (Table 2.1).

Table 2.1. Regression coefficients and significance for predictors of fish species richness in 40 islands and archipelagos. Summary of regression coefficients (B), standard errors (SE), standardized coefficients (β -value), t-statistics and p-value for the multiple regression model predicting species richness.

Predictor	<i>B</i>	SE	β -value	t-stat	p-value
Intercept	2.09	0.19	<i>N/A</i>	10.88	$4.35e^{-13}$
Latitude	-0.02	0.003	-0.72	-7.24	$1.36e^{-09}$
Surface area	0.27	0.05	0.55	5.46	$3.38e^{-06}$

The standardized β coefficients indicate that both predictors were significant. The higher β value of 0.72 for latitude suggests it has a stronger influence on fish species richness than surface area. An increase in latitude is associated with a greater decrease in species richness than an increase in shelf surface area (Figure 2.1). The observed values plotted against predicted values by

the regression model showed a strong linear relationship. This indicates that the multiple regression model provided a good fit to the data (Figure 2.2).

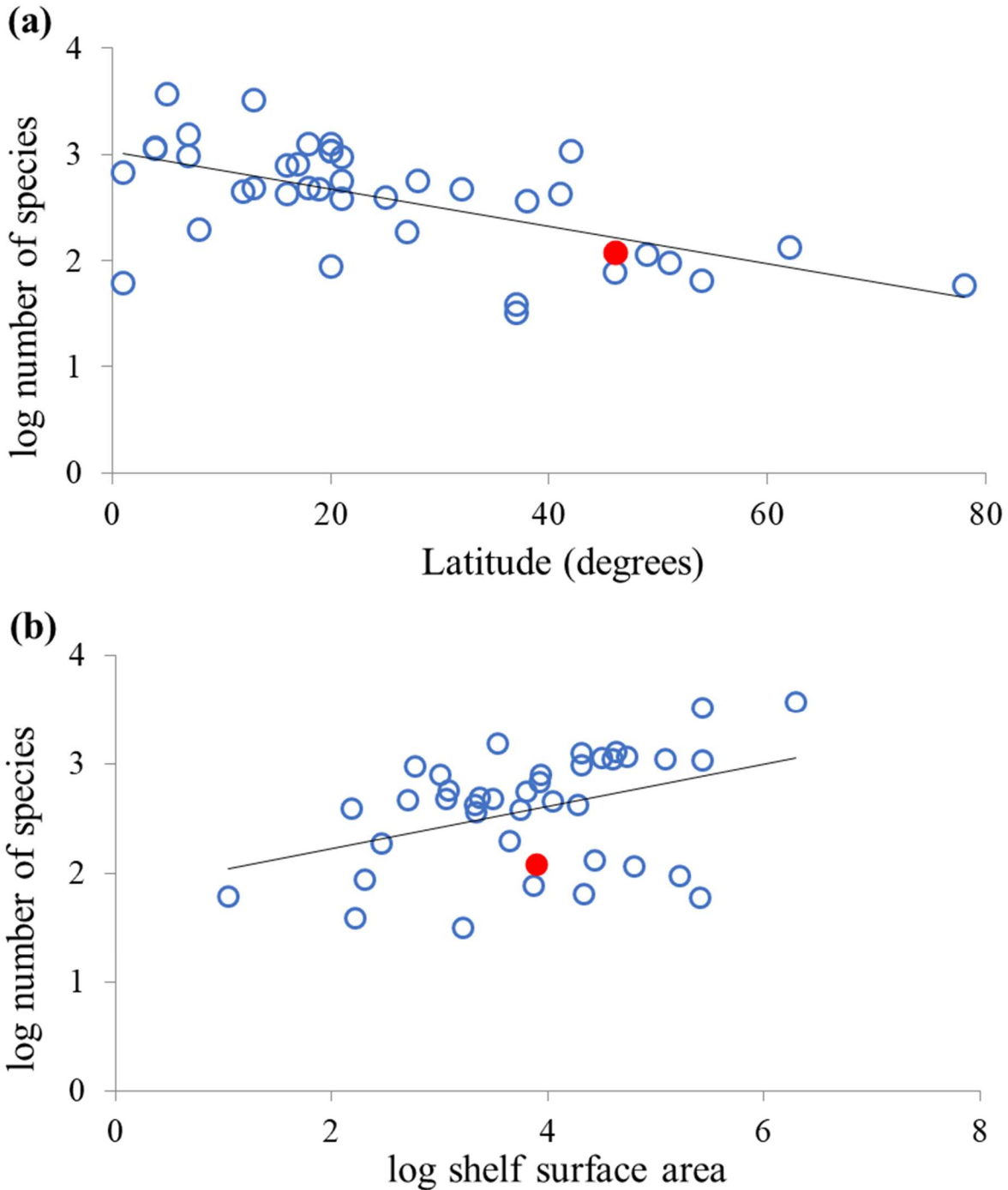


Figure 2.1. Multiple linear regression analysis of fish species richness with latitude (a) and shelf surface area (b) in 40 islands and archipelagos. SPM is represented by a red data point.

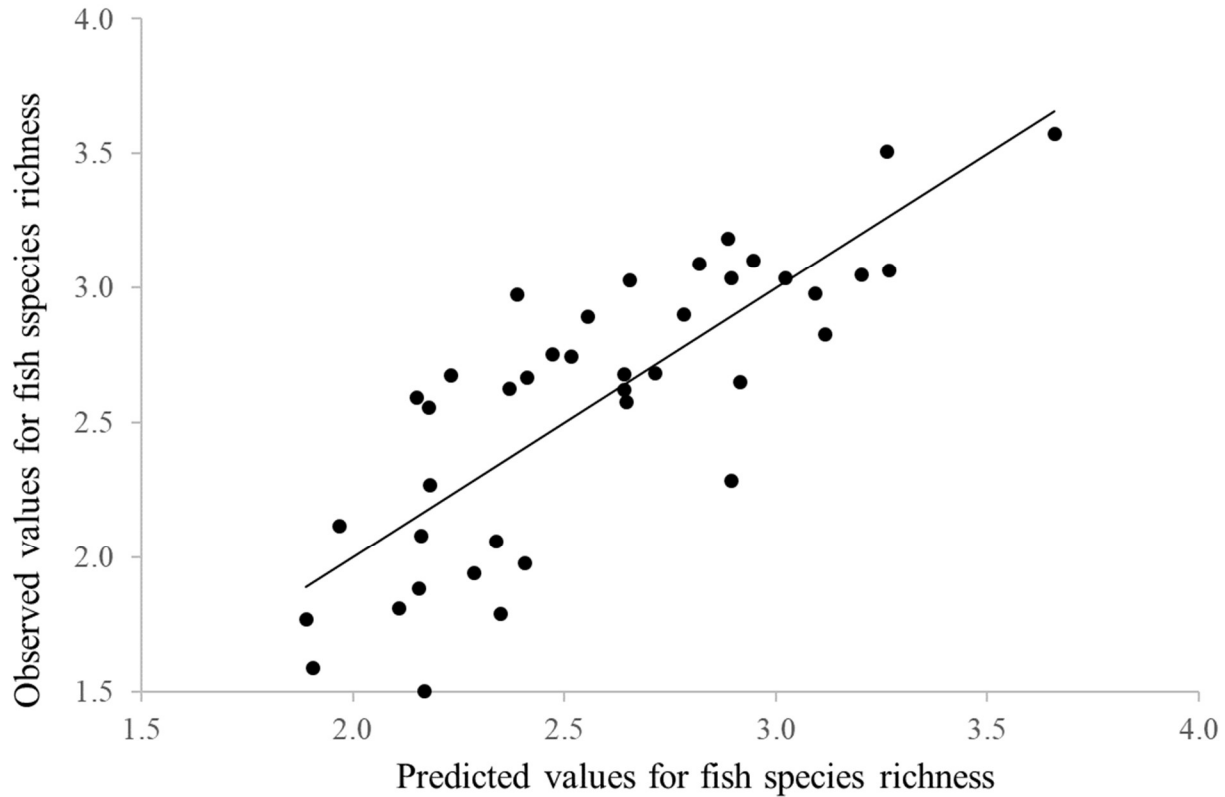


Figure 2.2. Observed versus predicted values for fish species richness from the multiple linear regressions model. Data points close to the x:y line indicate higher accuracy in the predictions.

For marine mammal species, latitude was not a significant predictor ($p = 0.11$) in explaining the variance in species richness, while surface area was a significant positive predictor ($p = 0.01$), indicating that surface area values are associated with an increase in species richness (Table 2.2, Figure 2.3). The overall model with $F(2,33) = 4.31$ explains 21% of the variance in species richness ($R^2 = 0.21$, Adjusted $R^2 = 0.16$) (Table 2.2).

Table 2.2. Regression coefficients and significance for predictors of marine mammal species richness in 36 islands and archipelagos. Summary of regression coefficients (B), standard errors (SE), standardized coefficients (β -value), t-statistics and p -value for the multiple regression model predicting species richness.

Predictor	B	SE	β -value	t-stat	p-value
Intercept	0.98	0.14	N/A	7.21	$2.85e^{-08}$
Latitude	-0.003	0.002	-0.10	-1.62	0.11
Surface area	0.08	0.03	0.18	2.62	0.01

For molluscs, the overall model was significant, $F(2,33) = 9.53$, $p\text{-value} < 0.05$ (Table 3), explaining 37% of the variance in species richness ($R^2 = 0.37$, Adjusted $R^2 = 0.33$). Both predictors are significant: latitude is a negative predictor, indicating that lower latitudes are associated with an increase in species richness, while surface area is a positive predictor, suggesting that greater surface area is associated with an increase in species richness (Table 2.3).

The standardized β coefficients show values for shelf surface area, suggesting that an increase in surface area has a stronger influence on mollusc species richness than an increase in latitude (Figure 2.3, 2.4).

Table 2.3. Regression coefficients and significance for predictors of molluscs species richness in 36 islands and archipelagos. Summary of regression coefficients (B), standard errors (SE), standardized coefficients (β -value), t-statistics and p -value for the multiple regression model predicting species richness.

Predictor	B	SE	β -value	t-stat	p-value
Intercept	1.60	0.30	N/A	5.38	$6.01e^{-06}$
Latitude	-0.01	0.004	-0.38	-2.78	0.009
Surface area	0.26	0.07	0.54	3.67	$8.40e^{-04}$

For crustacean species, latitude was not a significant predictor ($p = 0.11$) in explaining the variance in species richness, while surface area was a significant positive predictor suggesting that an increase in surface area is associated with a greater increase in species richness ($p < 0.0001$) (Figure 2.4). The overall model with $F(2,33) = 14.66$ explains 47% of the variance in species richness ($R^2 = 0.47$, Adjusted $R^2 = 0.44$) (Table 2.4).

Table 2.4. Regression coefficients and significance for predictors of crustacean species richness in 36 islands and archipelagos. Summary of regression coefficients (B), standard errors (SE), standardized coefficients (β -value), t-statistics and p -value for the multiple regression model predicting species richness.

Predictor	B	SE	β -value	t-stat	p-value
Intercept	1.04	0.25	N/A	4.15	$2.21e^{-04}$
Latitude	-0.005	0.003	-0.18	-1.64	0.11
Surface area	0.32	0.06	0.66	5.32	$7.20e^{-06}$

For cnidarians species, the overall model was significant, $F(2,33) = 17.06$, $p\text{-value} < 0.05$ (Table 2.5), explaining 51% of the variance in species richness ($R^2 = 0.51$, Adjusted $R^2 = 0.49$). Both latitude and surface area are significant predictors in explaining the variance in cnidarian

species richness. While an increase in latitude results in a decrease in cnidarian species richness, an increase in surface area indicates an increase in species richness. The standardized β coefficients are similar, but suggest surface area has a slightly stronger influence on species richness (Figure 2.3, 2.4).

Table 2.5. Regression coefficients and significance for predictors of cnidarian species richness in 36 islands and archipelagos. Summary of regression coefficients (B), standard errors (SE), standardized coefficients (β -value), t-statistics and p -value for the multiple regression model predicting species richness.

Predictor	B	SE	β-value	t-stat	p-value
Intercept	1.44	0.26	<i>N/A</i>	5.60	3.17e ⁻⁰⁶
Latitude	-0.02	0.003	-0.52	-4.57	6.43e ⁻⁰⁵
Surface area	0.26	0.06	0.53	4.15	2.20e ⁻⁰⁴

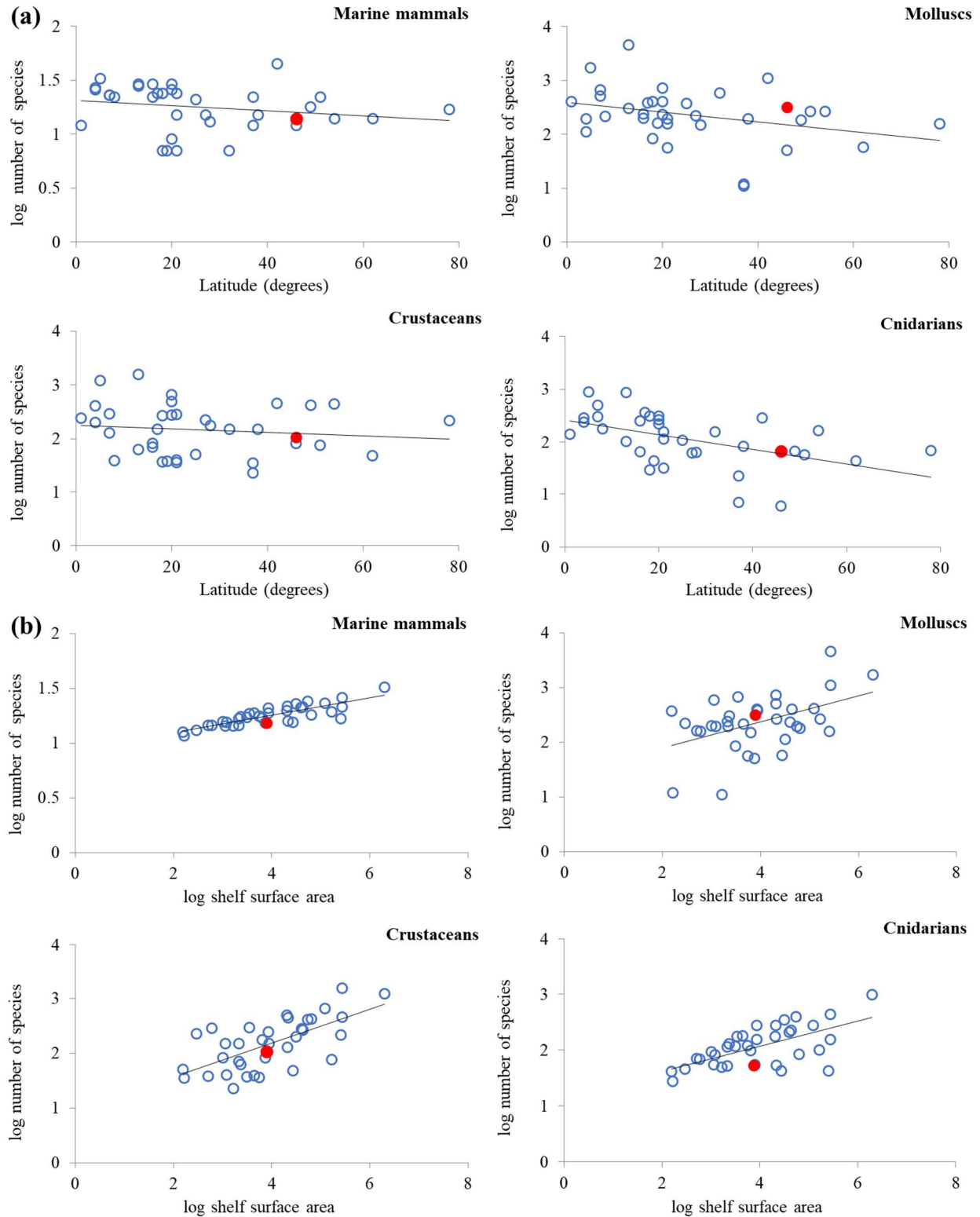


Figure 2.3. Multiple linear regression analysis of species richness with latitude (a) and shelf surface area (b) for four groups of marine species in 36 islands and archipelagos. SPM is represented by a red data point.

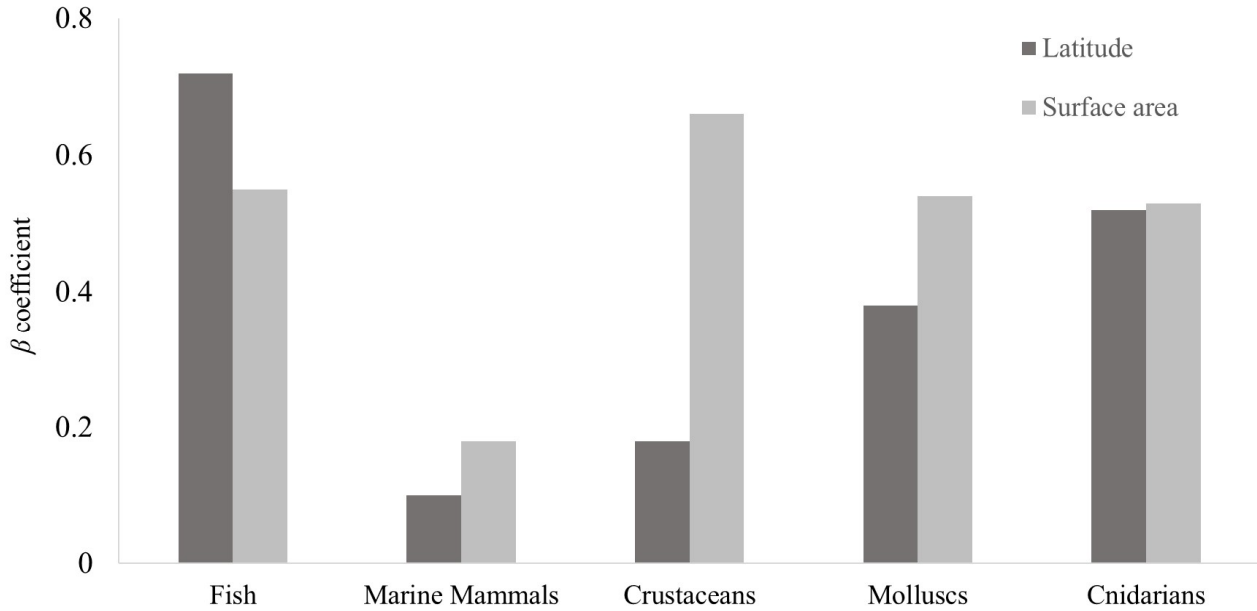


Figure 2.4. Absolute standardized β coefficient values for each of the five groups considered. The MRA for fish species richness was done for 40 islands and archipelagos, while the MRAs for other groups were done for 36 islands and archipelagos.

Additionally, when looking at the species-area exponent Z defined as the slope of the species-surface area relationship plotted on a log scale, or the B coefficient for the surface area predictor, its value varies between 0.08 (marine mammals) and 0.32 (crustaceans) with an average value of 0.25.

2.3.2.2 The position of SPM on species distribution gradients

When comparing the position of SPM along a latitudinal and surface area gradient of species distribution, the archipelago does not stand out as an area with particularly high marine biodiversity compared to islands of similar sizes or in similar latitudes (northern or southern). Rather, it is positioned where it would be expected to be given its latitude and the size of its shelf. This is true for marine mammals, crustaceans and cnidarians (Figure 2). For fish species (Figure 1), SPM even shows a below-average species richness, while it is slightly above-average for molluscs.

However, SPM stands out when comparing the ratio of threatened fish species to the total number of fish species. The archipelago is slightly above average both in terms of the total number of threatened fish species in comparison to other archipelagos of similar latitude and in comparison to other archipelagos of similar shelf surface area. Additionally, SPM has the highest ratio of threatened fish species of all 40 islands and archipelagos of this study, with 23 species with a threatened IUCN status out of 121 total fish species (19%).

2.4 Discussion

Understanding species diversity and the factors shaping species distribution is essential for effective conservation management. This is especially relevant in the context of smaller islands or archipelagos of which the marine biodiversity is understudied, while they are situated in regions of high ecological significance. Saint Pierre and Miquelon (SPM) is a prime example. This chapter aimed to assess the marine biodiversity (i.e., expressed in terms of species richness) in SPM by compiling an updated checklist of marine species present in the waters around the archipelago, and to investigate the environmental factors influencing marine species trends in islands and archipelagos. This study positioned Saint Pierre and Miquelon (SPM) within a global framework of relative species diversity by drawing comparisons with 40 globally distributed islands and archipelagos. The key findings reveal that SPM is home to 14 phyla and 727 assessed marine species. Among the main groups assessed, we counted 14 species of marine mammals distributed among 5 families and 103 species of seabirds and shorebirds distributed among 14 families. Marine invertebrates are represented by 13 phyla, 30 classes, 102 orders, 278 families and 522 species. The results of the multiple regression analyses indicate that both latitude and shelf surface area are significant predictors of species richness in SPM, situated on the average trendline when compared to other archipelagos of same size and latitude.

2.4.1 Biodiversity patterns in SPM

Marine species richness in SPM has only recently started to be assessed in terms of published species checklists on global and peer reviewed marine databases. While sporadic work had been done to enter a few marine species occurring in SPM in the SeaLifeBase and FishBase databases, following assessment campaigns around the archipelago (Lazure and Foucher, 2017;

BeBest, 2019; Simian *et al.*, 2022), Simian *et al.* (2022) were the first to publish a comprehensive checklist of diadromous and marine fishes occurring in SPM. Following this project to supplement FishBase, the present work was the first attempt at providing a comprehensive checklist of non-fish marine species around SPM, published on the global database SeaLifeBase (www.sealifebase.org). This work allowed to add to the checklist of fish a checklist of more than 700 marine species, including seabirds, marine mammals and marine invertebrates.

When comparing the fish species assessed for SPM to biodiversity patterns in adjacent areas of the Northwest Atlantic, several species can be observed on Saint Pierre Bank but not in the Gulf of Saint Lawrence, such as Bigelow's ray (*Rajella bigelowi*) (Simian *et al.*, 2022). Dissimilarities can be comparably observed for non-fish marine species. Marine mammals such as the blue whale (*Balaenoptera musculus*) and beluga whale (*Delphinapterus leucas*) are only rarely observed around SPM while being much more abundant in the Gulf of Saint Lawrence. Killer whales (*Orcinus orca*), on the other hand, are abundant on the Saint Pierre Bank while rare in the Gulf (Marine Mammals Observation Network, 2022). Another notable pattern lies in the distribution of the giant sea scallop (*Placopecten magellanicus*), which ranges from Newfoundland to Maine; scallop beds are especially abundant on Saint Pierre Bank, while only occasional on the adjacent Grand Banks (Packer *et al.*, 1999). Similarly, the orange-footed sea cucumber (*Cucumaria frondosa*), known for its uneven distribution patterns with regions of high abundance (DFO, 2019), is present in high concentration around the SPM archipelago.

An explanation for such patterns in invertebrate diversity can be found in the bathymetry and oceanographic regimes at play around SPM. While both regions are influenced by the cold and oxygen-rich Labrador current, Saint Pierre Bank is exposed to a warmer and nutrient-rich influx from the Laurentian Channel influenced by strong upwelling (Hachey, 1961; Colbourne and Murphy, 2008). Warmer temperatures and a high nutrient input on the bank favor the establishment of a high diversity of species (Macpherson, 2002). Such factors can contribute to explaining why some species are recorded in particularly high abundance on Saint Pierre Bank (i.e., *Cucumaria frondosa*, *Placopecten magellanicus*, Ophiuroidea) (Coughlan *et al.*, 2020; Boët *et al.*, 2025).

2.4.1.1 The position of SPM on a global island scale

On a global scale, SPM was compared to the 40 islands and archipelagos considered for this study on a latitudinal and area size gradient for the five species groups assessed. When compared to archipelagos of similar size range like Crozet Islands and Kerguelen, both situated at the same range of latitudes (i.e., 46-49° North or South), SPM presents a similar average number of fish and marine mammal species. These numbers slightly vary for crustaceans, molluscs and cnidarians, with SPM being slightly richer in molluscs species. Similar alpha diversity values (i.e., total number of species) can be attributed to similar thermal conditions (Macpherson, 2002; Chaudhary *et al.*, 2021). The SPM and Crozet archipelagos, and the island of Kerguelen, are situated respectively in the Northwest Atlantic Ocean and in the Southern Ocean. Both regions experience inter-annual variabilities in sea surface temperatures and are influenced by cold nutrient-rich currents (i.e., the Labrador current in the Saint Pierre Banks area, and the Antarctic Circumpolar current in the Southern Ocean) (Hukuda *et al.*, 1989; Sloyan, 2005). These cold, well-oxygenated environments are ideal to support niche specialization for cold-adapted fauna, and long-lived, slow-growing species (Peck, 2016). Both regions present shallow submarine plateau habitats adjacent to deep ocean basins, and experience strong mixing and topography-influenced upwelling (Hukuda *et al.*, 1989; Sloyan, 2005; Li *et al.*, 2015; Guillaumot *et al.*, 2018). These conditions promote nutrient-rich surface waters and high primary productivity, which enhances benthopelagic coupling essential for nutrient transfers in the food web (Raffaelli *et al.*, 2003; Griffiths *et al.*, 2017). Similarities in oceanographic conditions can explain resemblances in species richness, and a general poleward decrease in species diversity (Chaudhary *et al.*, 2016).

An additional interesting observation arising from the aforementioned species richness comparisons is the high ratio of threatened fish species found around SPM, according to the IUCN Red List of Threatened Species assessments. SPM has the highest ratio of threatened fish species for the total number of fish species out of the 40 islands and archipelagos of this study. Such a high ratio may stem from a history of heavy exploitation of the Saint Pierre and Grand Banks ecosystem: groundfish fisheries, particularly for cod, were intensely developed throughout the 20th century in the region and led to severe stock declines (Lear, 1998; Schijns *et al.* 2021). This legacy of overfishing, combined with the slow recovery of certain species (Lilly *et al.*, 2008; Swain and Benoit, 2015), has likely contributed to the elevated conservation concerns in the area. These

concerns may nowadays be heightened by climate-driven changes in the ocean conditions, and by habitat degradation (Ruiz-Diaz *et al.*, 2024).

2.4.1.2 Ecological significance and conservation implications

The taxonomic checklist assembled for this study is expected to assist in further taxonomic assessments in the waters surrounding SPM. While previously exclusively focused on studying species of commercial interest to local fisheries, there has been a growing shift toward biodiversity assessments driven by conservation priorities. Recent work by Boët *et al.* (2025), for instance, confirmed the occurrence of several epibenthic invertebrates around the archipelago using video monitoring and quadrat sampling techniques. The present checklist contributes to this evolving framework by enhancing taxonomic knowledge of the region, with the aim of developing updated and comprehensive species databases that can support informed management decisions. These data are essential not only for conservation planning, but also for subsequent assessments of ecosystem functioning and dynamics. Such assessments are critical for achieving sustainable fisheries management and for understanding the cascading ecological effects of harvesting fish and invertebrates on predator-prey interactions within the broader ecosystem.

Marine species each play a distinct role in maintaining ecosystem processes such as nutrient cycling and food web dynamics; cataloguing marine biodiversity at the taxonomic level allows for insights into the specific contributions of individual species or functional groups. This creates a more comprehensive framework for assessing the diversity of ecosystem services and their ecological, social, and economic value (Palumbi *et al.*, 2009; Barbier, 2017). Some of these values are species-specific and abundance-dependent, with the example of marine species used as food resources, while some services rely on the inter-relations at play within the community (Duarte, 2000; Tilman *et al.*, 2014). A detailed taxonomic understanding of the SPM ecosystem enhances comprehension of the links between ecological roles and social and economic values. For instance, identifying species of commercial, cultural, or ecological importance enables better estimation of the benefits derived from local fisheries, ecotourism potential, and ecosystem resilience. It also supports more accurate assessments of how human activities, such as harvesting or habitat modification, may affect species assemblages and long-term ecosystem dynamics.

Without proper taxonomic assessments, these links remain overlooked and the value of the ecosystem underestimated (Palumbi *et al.*, 2009; Barbier, 2017).

Furthermore, the high ratio of threatened fish species around SPM provides valuable insight into the direction that conservation and management efforts should take in the region. As an archipelago with a long-standing dependence on fisheries, prioritizing the conservation of fish species could serve as a catalyst for encouraging the local fishing sector to adopt more sustainable practices. By aligning conservation goals with fishery interests, there is potential to foster improved stock monitoring and management. In turn, this could support the rebuilding of the fishery industry in SPM on more stable, resilient, and scientifically informed foundations, ensuring both ecological sustainability and long-term economic viability (Link *et al.*, 2011)

2.4.2 Alignment with the island biogeography theory

2.4.2.1 Key drivers of marine species trends

MacArthur and Wilson's (1967) Island Biogeography Theory introduced ecological rules driving the distribution of insular species richness along physical gradients, rooted in the key evolutionary patterns of immigration and extinction in islands and archipelagos. The theory conceptualizes species richness as a dynamic equilibrium, in which richness remains relatively stable as rates of immigration and speciation balance the rates of extinction. The theory is based on two main variables for these rates: island area and isolation from the mainland. As larger islands typically support more species due to higher habitat diversity and larger population sizes, extinction risk is reduced; this area effect links island size with higher species richness. Similarly, the area effect links island isolation from the mainland with lower rates of immigration: remote islands tend to have lower species richness (MacArthur and Wilson, 1967). While this theory is well documented for terrestrial species, gaps exist in its application to marine species, especially in how the species-area relationship applies to migrating versus sessile marine organisms. By having a global marine focus that spans diverse taxonomic groups and continuous gradients, this study sought to bridge some of these gaps, to reflect the complexity and scale of marine biodiversity patterns.

The present study identified both latitude and area (here defined as shelf surface area) as significant drivers of marine species richness. The identification of surface area as a significant

driver aligns with the core principles of IBT (MacArthur and Wilson, 1967). In this context, the shelves surrounding islands and archipelagos function as marine analogues to terrestrial islands. By comparing 40 islands and archipelagos globally distributed along both latitudinal and size gradients, the MRAs results captured spatial patterns consistent with equilibrium theory (Simberloff, 1974): islands and archipelagos with larger continental shelf surface areas demonstrate higher species richness, i.e., support more marine species. In a marine context, where the ecosystem is characterized by fluid boundaries and higher connectivity (Cowen *et al.*, 2007), environmental gradients and habitat size both drive species richness. However, results show that predictor importance varies across different groups, indicating different responses based on marine taxa's different ecological niches, mobility, and life histories.

Additionally, island area and latitude were tested as predictors because these variables capture the primary habitat-area and climatic gradients hypothesized by classical island biogeography theory (MacArthur and Wilson, 1967). It was chosen not to include a simple geographic isolation metric (e.g. nearest-land distance) because, for marine benthic and reef-associated taxa, isolation is governed primarily by species-specific larval dispersal and oceanographic connectivity (e.g., currents) rather than Euclidean distance alone. Consequently, two islands at equal Euclidean distance from a source can have very different effective connectivity if currents favor or oppose transport between them (Kinlan and Gaines, 2003; Cowen *et al.*, 2006). Reliable, globally comparable oceanographic connectivity data were not available for the full set of islands included in this study.

2.4.2.2 Latitude as a proxy for biogeographic constraints

Latitude has been demonstrated to drive most of the regional richness in marine assemblages around the world in a general unimodal gradient peaking on both sides of the equator (Ekman, 1967; Hillebrand, 2004b; Tittensor *et al.*, 2010). Marine species richness declines at higher latitudes in a steeper gradient than freshwater species, which has been found to be influenced by fundamental differences in dispersal capacity and habitat connectivity. Marine species demonstrating planktonic larval stages have broad dispersal capabilities and can colonize habitats effectively; moreover, habitat continuity is greater in the marine realm without sharp physical constraints and facilitates species sorting along depth and temperature gradients,

contributing to pronounced latitudinal patterns (Hillebrand, 2004a; Costello and Chaudhary, 2017; Miller, 2021).

Latitude acts as a stand-in for temperature, productivity, and seasonality, all three of these environmental variables acting as biogeographic constraints influencing marine biodiversity (Bohdalková *et al.*, 2021). Lower latitudes closer to the equator experience higher sea surface temperatures, which increase the metabolic rates of fish and invertebrates (Pauly, 2021) and thus, various ecological processes, including species interactions and food web dynamics (Brown *et al.*, 2004; Bruno *et al.*, 2015). Similarly, primary productivity expressed through chlorophyll *a* concentration tends to be higher at lower latitudes in regions with patterns of equatorial upwelling (Fiedler *et al.*, 1991). Phytoplankton richness presents hotspots located around the equator (Righetti *et al.*, 2019). Diversity gradients also seem to be stronger for higher trophic level species (Hillebrand, 2004a). Tropical and subtropical upwelling zones with primary productivity support more prey biomass, in turn sustaining more predators. Likewise, tropical regions like coral reefs, mangroves and seagrass beds provide complex habitats supporting diverse prey communities, allowing niche partitioning among predators and therefore increasing species coexistence and richness at higher trophic levels. However, while equatorial waters can exhibit high productivity in upwelling zones, many tropical ocean regions are nutrient-limited and less productive (Howarth, 1988). Primary productivity is more strongly controlled by nutrient supply than latitude alone (Fiedler *et al.*, 1991), which emphasizes that species richness in islands and archipelagos is shaped not solely by latitude, but by a broader set of ecological and environmental factors.

Our results suggest that latitude is a significant negative predictor of species richness in fishes, molluscs, and cnidarians. However, this pattern does not hold for crustaceans and marine mammals, which show no significant correlation between species richness and latitude. In the case of marine mammals, this feature can be explained by their high mobility and broad ecological niches. Most marine mammals are capable of extensive migrations, often spanning multiple latitudinal zones, and are more strongly influenced by prey availability, oceanographic features, and migratory corridors than by climatic or latitudinal gradients (Pompa *et al.*, 2011; Kiszka *et al.*, 2015). Although latitude can act as a proxy for primary productivity, which does influence prey abundance, marine mammals are not restricted to narrow thermal or ecological zones. Their capacity to exploit a range of habitats, from polar to tropical waters, and their reliance on dynamic

ecological factors such as upwelling zones and seasonal prey aggregations, make latitude a poor standalone predictor of their species richness (Kaschner *et al.*, 2011; Pompa *et al.*, 2011).

Crustacean species richness not being strongly influenced by latitude is consistent with the weaker latitudinal diversity gradient (LDG) that has been observed globally (Rivadeneira and Poore, 2020). This could be explained by the high diversity of ecological niches they occupy, evolutionary history, regional environmental factors, or the sampling biases that will be further explored in the following sections. Previous studies on crustacean distribution patterns have found that different crustacean groups tend to show different LDG strength: amphipods may show peak species richness at mid-latitudes rather than at the equator, indicating a more complex distribution pattern (Arfianti and Costello, 2020; Rivadeneira and Poore, 2020). The trends observed in both crustaceans and marine mammal groups support the idea that species traits can override spatial biogeographic predictors.

Additionally, fish are the only group in the study for which latitude has a stronger effect than surface area in predicting the variance in insular species richness. This suggests that fish species richness is highly sensitive to latitudinal gradients, likely due to thermal sensitivity and life history factors, which is consistent with the latitudinal diversity gradient (LDG) global patterns (Hillebrand, 2004b). Indeed, changes in ocean temperature have been found to have a considerable effect on distribution patterns, with ocean warming causing range shifts in fish populations (Cheung *et al.*, 2009; Tittensor *et al.*, 2010; Dahms and Killen, 2023). High thermal sensitivity acts as the main driver of latitudinal gradients in fish diversity. On an evolutionary time scale, higher tropical temperatures influence higher rates of mutations, leading to higher rates of speciation in fish species (Costello and Chaudhary, 2017; Lin *et al.*, 2021).

2.4.2.3 Species area relationships and shelf area effect

Demonstrating latitude as a proxy for marine species richness distribution is not new; however, it is interesting to identify which other factors are at play, and the relative importance of latitude compared to surface area in explaining the variance in species richness. Shelf surface area had a consistent positive effect on species richness, and was found to be a more significant predictor of species richness for all groups in this study, except for fish, where latitude was a stronger predictor.

In Island Biogeography Theory the positive relationship between island area and species richness is commonly attributed to lower extinction rates and greater niche diversity on larger islands (MacArthur and Wilson, 1967). Here, ‘Area’ in the marine context represents more than physical size: it reflects productivity, bathymetric complexity, and habitat diversity. The role of island shelf surface area in explaining the variance in marine species richness can likely be inferred from habitat and resource diversity, and the reliance of marine organisms on niche availability. Indeed, a larger continental shelf area is typically associated with greater habitat diversity, as it is more likely to exhibit increased environmental heterogeneity. This heterogeneity supports a broader range of ecological niches, either by expanding the range of existing niches or through new niches becoming available (Hutchinson, 1957; St. Pierre and Kovalenko, 2014). A higher niche availability and complexity promote the coexistence of a wider range of species, and the occurrence of more habitat specialists, which present features uniquely adapted for highest performance in certain types of habitats (Devictor *et al.*, 2010; Romoth *et al.*, 2023). This niche diversity, combined with the relatively high connectivity on continental shelves, further enables species with complex life histories to exploit various habitats throughout their life cycles (Dethier *et al.*, 2003). For instance, shelves presenting a high habitat diversity and complexity have been linked with higher benthic species richness, highly dependent on the heterogeneity of substrate types on the sea floor (Taniguchi and Tokeshi, 2004; de Juan *et al.*, 2023; Romoth *et al.*, 2023).

Moreover, primary productivity is generally higher on shelves, as nutrient availability is increased by coastal upwelling, river runoff, and resuspension of nutrients from sediments due to shallower depths (Mann, 2000). Primary productivity has a positive effect on zooplankton biomass (Hernández-León *et al.*, 2020). Food availability through zooplankton contributes to shaping consumer population size: larger and more stable populations are in turn linked with reduced extinction risks (Legendre *et al.*, 2008; Ball *et al.*, 2024). Reduced extinction risk on larger, more productive shelves could contribute to explaining the role of shelf area in predicting marine species diversity, according to IBT core principles.

2.4.2.4 Species-area exponent

In accordance to IBT, the species-area exponent z expresses the strength of the relationship between the species richness and the surface area of the island (i.e., in this case, of the shelf surface

area) (MacArthur and Wilson, 1967). It is typically comprised between 0.3 and 0.5 for oceanic islands, and a higher value identifies a stronger species-area relationship. The value of z being closer to 0.5 expresses a steeper increase in species richness with area, while a smaller value of z expresses a more gradual increase in species richness as area expands, which is usually typical of mainland habitats (MacArthur and Wilson, 1967; McGuinness, 1984). The average value of z for all groups considered in this study was 0.25, implying a weaker species-area relationship and a more gradual increase, and more homogeneous species distribution. This can potentially be explained by the higher rate of dispersal in marine habitats, a result of the lack of strong physical barriers in oceanic systems and high connectivity of marine habitats (White *et al.*, 2019). The third dimension of species distribution, depth, prevails in influencing the distribution of some marine species like highly migratory marine mammals, for which z had the lowest value of 0.08 (Piacenza *et al.*, 2015). The group with the highest z values was the crustaceans, generally characterized by a lower dispersal rate, especially in juveniles and species without a larval stage (Daly *et al.*, 2021; Iwasa-Arai, 2024). Low z values suggest that other oceanographic factors play a crucial role in shaping marine species distribution patterns.

2.4.3 Challenges and limitations of the study

2.4.3.1 Challenges and limitations in applying Island Biogeography Theory to marine species

Limitations exist in the reliance on IBT to predict trends in species richness in oceanic and continental islands. The theory assumes that islands reach an equilibrium between extinction and immigration rates, on which most of the theory lays (MacArthur and Wilson, 1967): this doesn't take into consideration ecosystems that might be subject to continual disturbances and might not achieve any equilibrium. By assuming equilibrium theory is true for all islands, the theory may fail to account for the role of disturbances in shaping species richness and community composition. In such cases, species richness may fluctuate unpredictably, and the assumption of a steady-state equilibrium becomes unrealistic, limiting the theory's predictive accuracy in the context of these islands (Villa *et al.*, 1992).

Moreover, choosing to conduct a study with several marine groups of interest at once is a challenge in itself, in terms of taxonomic breadth and ecological heterogeneity (Kolasa and Pickett, 1991). If this study is broadly informative on the possibility to apply IBT to marine species, and the relevance of studying marine biodiversity within the scope of this theory, it may lack ecological specificity. Indeed, the marine groups chosen for this study each encompass a wide spectrum of ecological strategies, ranging from highly mobile pelagic species to benthic taxa with restricted dispersal. For example, ‘fishes’ include everything from reef-associated species with restricted dispersal to highly migratory pelagic fish (Shackell and Frank, 2003), while ‘Molluscs’ range from sessile bivalves to widely-ranging squids (Wanninger and Wollesen, 2018). For species with restricted ranges and strong habitat dependence, area may be a powerful determinant of occurrence, whereas for wide-ranging or highly dispersive taxa, island size may be far less relevant (Pineiro-Corbeira *et al.*, 2025). However, two subsequent arguments may temper the actual effect of the point previously discussed. Diversity in ecological strategies exists within sub-groups or species, a prime example being jellyfish (Phylum: Cnidaria) of which the life cycle includes both a sessile stage (i.e., the polyp phase) and a mobile stage (i.e., the medusa phase) (Licandro *et al.*, 2015). Secondly, most marine species (excluding marine mammals) possess a mobile larvae stage which determines most of the species’ dispersion within its marine habitat, with a stronger effect than dispersal at the adult stage (Gaines and Lafferty, 1995).

Nonetheless, using a careful approach is warranted, and by aggregating such diverse organisms, the analysis may obscure finer-scale patterns, as the colonization and extinction dynamics underpinning IBT (MacArthur and Wilson, 1967) are unlikely to operate uniformly across such disparate life histories. This taxonomic breadth therefore represents both a strength and a weakness of the study. On one hand, it allows for a broad exploration of the applicability of IBT across multiple marine phyla. On the other, it limits the interpretability of the results at finer ecological scales. Further explorations of the application of IBT to marine species with taxa split into more ecologically homogeneous groups would still be relevant to consider, and would potentially align more closely with theoretical assumptions of IBT.

2.4.3.2 Limitations of multiple regression analyses and marine species databases

Multiple regressions were used by Hamilton *et al.* (1967) and Watson (1964) to corroborate MacArthur and Wilson's (1967) species-area relationship, and evaluate the extent to which different degrees of island area would influence species richness. Further studies looking at global comparisons between islands' species diversity used MRAs as a method of choice to assess drivers' weight and the degree of variance (Lomolino, 1984; Gentile and Argano, 2005; Kalmar and Curie, 2006). Nonetheless, this method presents several limitations. One lies in the high correlation that can be exhibited by ecological predictors tested in an MRA. While not reducing the predictive power of the model *per se*, this high correlation can result in an inflation of the variance of coefficients estimates, consequently making it challenging to discern predictor's individual effect on the response variable, potentially resulting in misleading conclusions (Graham, 2003). This highlights the need to test predictors for multicollinearity prior to MRAs with tools like the Variance Inflation Factor (VIF). Additionally, ecological systems are inherently complex, and multiple regression models often explain only a small fraction of the variance in response variables. This limitation suggests that important predictors may be missing or that the relationships are non-linear or involve interactions not captured by the model.

Moreover, while databases such as SeaLifeBase (www.sealifebase.org) provide valuable repositories of marine biodiversity data, their use in ecological studies presents several limitations. A primary constraint lies in the uneven taxonomic coverage and geographic sampling effort across regions. Specifically, the availability of reliable species occurrence data is contingent upon the existence of comprehensive taxonomic assessments, which are not uniformly conducted for all islands or marine taxa. For instance, the Socotra Archipelago illustrates this limitation well: although it has been extensively surveyed for fish species by staff of the Frankfurt-based Senckenberg Museum (Zajonz *et al.*, 2000) and is thus well represented in FishBase, it had to be excluded from the broader multiple regression analyses in this study due to incomplete data for other taxonomic groups in SeaLifeBase, i.e., unrealistically low species counts for certain groups. This example highlights a broader issue of sampling bias: regions with higher ecological, economic, or political interest often receive more attention and investment in biodiversity assessments, while other areas remain underrepresented. Consequently, species richness estimates and ecological inferences drawn from these datasets may disproportionately reflect patterns in

well-studied areas, potentially skewing conclusions about broader biogeographic trends. Another related example of sampling coverage issue occurs in the tropics, where limited survey efforts have led to underrepresentation of species diversity. This under-sampling effect has been widely noted in tropical regions, with the need for more comprehensive studies with greater spatial coverage (Stroud and Thompson, 2019; Cardoso *et al.*, 2024). Interestingly, this bias is somewhat counterbalanced in databases like FishBase and SeaLifeBase, which have integrated a higher number of studies covering tropical latitudes (Froese and Pauly, 2010). It could also be argued that another issue is the potential effect of the non-inclusion of very small taxa, notably small molluscs, in SeaLifeBase. However, the bias towards large species this represents is likely to be the same, or broadly similar, among different archipelagos, and is thus not likely to generate counter-factual trends.

Nonetheless, databases such as FishBase and SeaLifeBase remain crucial resources for marine biodiversity research. They provide standardized, accessible, and regularly updated data that enable large-scale comparative analyses and ecological modeling. Their continued development and expansion, particularly through initiatives that support taxonomic surveys in underrepresented regions, are crucial to improving the reliability and inclusiveness of global ecological studies.

2.5 Conclusion

The study conducted in the present chapter underscores the multifaceted drivers of marine biodiversity patterns in insular environments, revealing how both area size and latitude influence species richness in the waters surrounding Saint Pierre and Miquelon, as well as in oceanic and continental islands and archipelagos around the world. The significant negative relationship between latitude and species richness in fishes, molluscs and cnidarians affirms the role of large-scale environmental gradients – particularly temperature – in shaping biodiversity. Yet, the absence of this trend in crustaceans and marine mammals highlights the taxon-specific nature of these patterns, cautioning against universal assumptions about latitudinal diversity gradients across marine taxa.

Together, the effects of latitude (i.e., a proxy of temperature) and area size (i.e., a proxy of habitat diversity) reinforce a marine extension of Island Biogeography Theory, suggesting that

area-dependent extinction risk and dispersal-limited colonization processes also structure species richness in the marine realm. These findings support the broader utility of island biogeographic principles in understanding and predicting biodiversity beyond terrestrial systems. Though, ecological limitations might come into play and require more homogeneous taxa split to account for ecological heterogeneity, and finer scale patterns. Parsing out such differences through more ecologically resolved analyses would help disentangle the mechanisms behind the observed richness–area relationship, and clarify the extent to which island biogeography processes, versus marine-specific factors, govern biodiversity patterns in the ocean.

Importantly, this contributes to the foundational taxonomic knowledge necessary for evaluating the ecological, social, and economic value of ecosystem services in the historically overexploited, but ecologically rich region SPM is located in. The marine ecosystem of Saint Pierre and Miquelon is shaped by complex oceanographic conditions and ongoing pressures from both climate change and fishing activity. Establishing a robust, region-specific biodiversity baseline is critical for identifying species that play key ecological and for ensuring these contributions are factored into sustainable resource management.

Aligning conservation priorities with fisheries management goals holds particular promise in this context. A taxonomically informed approach can enhance ecosystem modelling assessments and guide adaptive strategies, ensuring decisions are grounded in the full complexity of local biodiversity. As species distributions continue to shift in response to warming waters and other anthropogenic pressures, a nuanced understanding of marine biodiversity across space, taxa, and time will be essential for safeguarding both ecosystem function and the human communities that depend on it.

Chapter 3: Reconstructing what Saint Pierre and Miquelon has caught from 1950 to 2022

3.1 Introduction

The catch reconstruction approach originates from the need to assess discrepancies between the amount of seafood caught officially reported to fisheries management agencies and what is actually caught in practice, acknowledging that such gaps often arise from limitations in government reporting systems and the exclusion of certain fishing sectors. (Zeller and Pauly, 2016). Globally, it was estimated that catches are underestimated by over 50% in official reports and databases (Pauly and Zeller, 2016). It has been shown through various studies that worldwide aquatic resources are largely subject to overfishing leading to the depletion of exploitable stocks, amongst other alarming impacts on resource abundance and diversity (Pauly, 1987; Pitcher, 2001; Coll *et al.*, 2008; Dulvy *et al.*, 2021). However, the true extent of overfishing is challenging to evaluate, as governmental catch records used in most scientific work to assess fish stocks or ecosystem health are missing essential components that are unaccounted for in the process of reporting the catch (Zeller, 2007; Pauly and Zeller, 2016). The need to account for more representativity and accuracy in fisheries data aligns with the global need to conceptualize fisheries within their ecosystem, e.g. in the practice of Ecosystem Based Management (Pikitch *et al.*, 2004). Providing a better reconstruction of the seafood amounts removed from the ocean by each fishing country allows for an improved understanding of the impact of removals both within each species populations and marine ecosystems (Pikitch *et al.*, 2004; Zeller and Pauly, 2016). Reconstructions can inform more sustainable management policies considering the ecological footprint of fishing on different trophic levels within the ecosystem (Pikitch *et al.*, 2004; Harvey *et al.*, 2020).

3.1.1 Catch reconstructions by the *Sea Around Us*

The *Sea Around Us* project aims at reconstructing marine catches in a country's Exclusive Economic Zone (EEZ) claimed or defined according to the United Nation Convention on the Law of the Sea (UNCLOS), for each year where local or foreign fisheries were active in the EEZ,

starting from 1950 onwards (Zeller and Pauly, 2016). The starting point of 1950 connects with the year the Fisheries and Agriculture Organization (FAO) produced its first annual '*Yearbook on Fisheries Statistics*', covering global fishery data reported by its member countries and the colonies several still had (Pauly, 2008). Each year, member countries supply reports of their fishery catches to the FAO, which produces a yearly report of landed nominal catch (weight in tonnes) disaggregated in three categories: fishing country, FAO fishing area and species or group name. Catch reconstructions focus on the amounts that are not included in these official reports, but also on a more detailed disaggregation, including fishing sectors and gear.

The methods for reconstructing marine catch data are based on demystifying the widespread notion of “no data” in fishery science. It involves using a variety of national and international sources to fill in gaps in official governmental reports, providing a conservative estimation of a country’s total catch in the form of catch time series (Zeller, 2007). Catch reconstruction aims at providing this estimate for each of four defined fishing sectors: industrial, artisanal, subsistence and recreational (Zeller and Pauly, 2016). Industrial refers to large-scale commercial fisheries generally operating offshore or internationally and using moving gears (e.g., trawlers or seiners), while artisanal refers to small-scale commercial fisheries operating in inshore waters, generally involving smaller vessels and fixed fishing gear. The subsistence sector refers to the small-scale catch that is usually caught for personal consumption, and the recreational sector applies to catches made for recreative purposes (Zeller and Pauly, 2016). The small-scale fisheries sectors are the most commonly underreported sectors, but catches of certain taxa and by certain gears, illegal and unregulated fisheries, and amounts that are discarded at sea (whether species caught as bycatch or individuals not meeting the regulated sizes or quotas) are most likely to be underreported or unreported as well (Pauly and Zeller, 2016). Discarded catch is not landed by fishing vessels and therefore unaccounted for in official FAO reports, and represent globally around 10 to 20% of total annual catch (Zeller *et al.*, 2018). Reconstructing these amounts is done using a conservative approach, to avoid the potential issue of overestimation but still comprehensively accounting for unreported fisheries components (Zeller *et al.*, 2018).

The global trend to account mainly for the commercial landings in FAO and NAFO reports at the detriment of small-scale landings and industrial scale discards left unreported reflects a bias towards industrial fishing, which aligns not only with the priorities of larger economic

stakeholders, but also those of tax and subsidy structures (Jacquet *et al.*, 2010; Arthur *et al.*, 2019). Additionally, giving a more precise spatial resolution to the reported catch, here within the limits of a country's EEZ, allows more fitted policy applications of fishery management (Zeller *et al.*, 2016). The process of catch reconstruction focuses on the EEZ as a delimiting area, but accounts for all the amounts that were caught by a country inside and outside of its EEZ (Zeller, 2007).

3.1.2 The Exclusive Economic Zone of Saint Pierre and Miquelon

The Saint Pierre and Miquelon (SPM)'s Exclusive Economic Zone (EEZ) falls within the FAO Area 21 (Atlantic, Northwest) and the North Atlantic Fisheries Organization (NAFO) management subdivisions 3Ps and 4Vs, which implies that SPM must submit catch records to both organizations (Palomares and Pauly, 2022). The EEZ is an enclave completely surrounded by the Eastern Canadian EEZ and is one of the few EEZs in the world in this peculiar situation (Figure 1). This implies that all fishing outside of this home EEZ that is not in the High Seas is subjected to Canadian fisheries management policies (Day, 1992). The EEZ as it is delimited today was established in 1992, as the result of an arbitration by the International Tribunal of New York to solve the maritime boundary and exclusive fishing rights dispute between France and Canada, which was caused mainly by the distribution of cod stocks on the Saint Pierre Bank (Marston, 1993; Teletchea, 2022). The EEZ encompasses an area of 12,400 km², consisting of a territorial sea of 24 nautical miles south and west and 12 nautical miles east of the archipelago, and a 200 nautical miles long and 10 nautical miles wide corridor stretching from the south of the islands past the limit of the Saint Pierre Bank (Wilson and Le Floc'h, 2016). It is contrastingly smaller than the previously claimed area of almost 50,000 km², following the 1972 agreement on fishing relations between France and Canada (Marston, 1993; Forest, 2022). This agreement contributed to establish a framework for France-Canada seasonal consultations on fishing rights and quotas, and delimited territorial waters for both parties largely on the principle of equidistance (Marston, 1993; Teletchea, 2022).

In 1977 and with the intention to reduce fishing activity on both Grand Banks and Saint Pierre Bank by foreign vessels, Canada extended its EEZ to 200 nautical miles, prompting SPM to do the same (Fleury, 2004; Forest, 2022). The dispute emerged as the two EEZ overlapped and almost the entirety of the Saint Pierre Bank – most of which is the NAFO subdivision 3Ps – was

covered by the zone claimed by SPM (Marston, 1993). The status of “independent state” was a tumultuous subject in the dispute: Canada argued that SPM didn’t possess the authority to be granted more than a territorial sea of 12 nautical miles, while France based its claim of a 200 nautical miles exclusive fishing zone on this status (Day, 1992). Ultimately, these disagreements led to the intervention of an arbitral tribunal in the matter of defining each party’s EEZ (Marston, 1993). The area designated as the ‘Exclusive Economic Zone’ of SPM between 1972 and 1992 therefore underwent a major shift in 1992, the same year the infamous Atlantic cod (*Gadus morhua*) moratorium was implemented in the Northwest Atlantic (Lear, 1998).

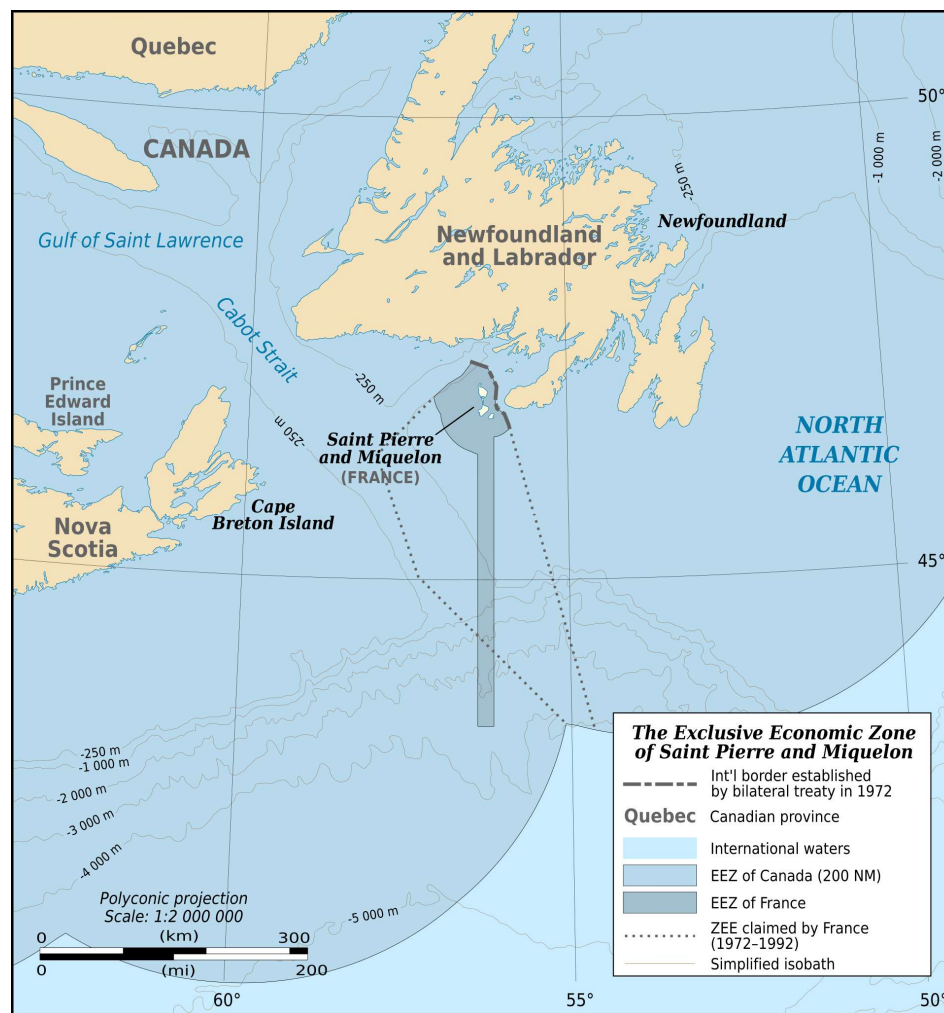


Figure 3.1. The EEZ of Saint Pierre and Miquelon (France) before and after the 1992 arbitration (Gaba, 2021; Government of Canada, 2021). The dashed line represents the EEZ from 1972 to 1992.

3.1.3 The cod fishery in Saint Pierre and Miquelon, a *raison d'être*

As an archipelago whose economy relied almost exclusively on Atlantic cod, 1992 marked a turning point for SPM's fishing rights and access to aquatic resources (Forest, 2022). Small insular economies deeply tied to fishing for livelihoods (through employment) and other industries (such as processing and transport) are highly vulnerable to shifts in the fishing sector, such as fluctuations in fish stocks and the global market. While small-scale fisheries are a source of income, they are also deeply embedded in local culture and play a crucial role at ensuring food security and sustainability. Industrial-scale fisheries, on the other hand, provide locally numerous sources of employment and income, mainly through export revenues in the global seafood market (Cermakian et al., 1970; Hussain, 2008; Guillotreau *et al.*, 2012). The moratorium on cod fishing in 1992 highlighted this vulnerability and left many local fishers facing strong economic challenges (Schijns *et al.*, 2021). To fully grasp this impact, exploring the historical context of fisheries on the islands is needed. The first French fishery practices in SPM trace back to the 16th century when the islands were used as temporary settlements by French fishers during seasonal fishing trips along the coast of Newfoundland. In the 17th century, French fishers established permanent settlements on the archipelago (Livingston and Losier, 2021). As cod proved to be a then-abundant and reliable resource, it drove thousands of people in the 18th century to leave mainland France to settle in SPM and set the foundations of a thriving new fishery exploitation (Sauvage *et al.*, 2023).

Atlantic cod was for centuries not only the main species targeted by local small-scale, then industrial-scale fisheries, but also an enduring symbol for the maritime culture of the islands: cod fisheries provided livelihoods for over 600 fishers in the beginning of the 1900s, and were a family endeavour where other members contributed to processing duties such as drying and salting the fish (Rallier du Baty, 1927; Geistdoerfer, 1990). In addition to mostly catching cod, small-scale fishing also targeted other species such as capelin (*Mallotus villosus*), herring (*Clupea harengus*) or northern shortfin squid (*Illex illecebrosus*) (Ancellin, 1955). It was practiced almost every day from May to October, using artisanal wooden boats called *doris*, capable of holding two men and the number of lines or other fishing gear needed for one day of fishing (Ancellin, 1955; Geistdoerfer, 1990). During this *golden age* of the cod fishery, some *doris* were hauled on larger schooners permitting access to cod fishing locations farther offshore, on the Grand Banks of

Newfoundland (Sauvage et al., 2023; M. Derible, local historian, October 2024, personal communication).

However, while cod still had a central place in local practices, the 1950s marked the beginning of the small-scale fisheries decline, following the rapid decline in cod biomass in the Northern Atlantic, the opening of the Société de Pêche et de Congélation (SPEC, *Fishing and Freezing Company*) in 1951, Saint Pierre's first fish processing plant, and the introduction of industrial trawlers in 1952 (Geistdoerfer, 1990; Teletchea, 2022). Succeeding the start then halt of operations of the SPEC in the 1970s, Interpêche was created as a new fish plant, and new trawlers were added to the local fleet. As these larger industrial trawlers became responsible for most of the catch, small-scale fishers saw their profession become a less stable source of income, and the number of *doris* steadily declined between 1950 and 1992, when the last *doris* stopped operating for small-scale fisheries (Eynaud, 1986; Geistdoerfer, 1990; F. Teletchea, University of Lorraine, October 2024, personal communication). Following the cod moratorium, Interpêche's profit rapidly declined as catches declined, until bankruptcy forced it to close, taking away even more local jobs in the fishing industry (Teletchea, 2022). Ultimately, if the small-scale sector underwent what can rightfully be called a collapse, both sectors declined considerably following rapid biomass changes in the Northwest Atlantic. The sharp decline of the cod fisheries led to the slow emergence in the 2000s of invertebrate species as new fisheries (such as sea cucumber (*Cucumaria frondosa*), lobster (*Homarus americanus*), crab (*Chionoecetes opilio*), and squid), demonstrating a clear example of the fishing down the marine food web concept, where fisheries focus shifts to lower trophic level species, when higher trophic level species become less or unavailable (Pauly et al., 1998). Nowadays, all fish and seafood processing on an industrial scale has been relocated: local trawlers, trap setters and longliners export their catch to other countries such as Canada, the United States and Europe for processing and consumption. The local market is very small, with only two local structures processing artisanal catch and selling it locally (deBeauregard, 2013; Wilson and Le Floc'h, 2017; Teletchea, 2022).

The evolution of catches by SPM can be observed in the FAO database of reported landings, but information about which sector the catch is pertaining to is missing. As SPM reports catches to two management entities (FAO and NAFO) that use different species names in their databases, discrepancies between actual catch and reported catch can be seen: for SPM, this shows

through some species missing from the NAFO database where they are reported in the FAO database, and some landing amounts being higher in the FAO database. Furthermore, no information is available in either FAO or NAFO on the volume of fish caught as bait by SPM *doris*, or the amount discarded at sea by SPM trawlers, quantities that are most likely omitted in ‘total’ landings. Such information can only be obtained by conducting a complete reconstruction of the archipelago’s fisheries along the years.

3.1.4 A new reconstruction of Saint Pierre and Miquelon’s catches

A first reconstruction was conducted for SPM by Bultel and Zylich (2015) in the context of the *Sea Around Us* project. This was followed by an update by Page *et al.* (2020), using the same methods as developed by Bultel and Zylich (2015) and an updated approach to reconstructing recreational American lobster (*Homarus americanus*) and Atlantic salmon (*Salmo salar*) catches. Upon careful study of the first reconstruction, several parts of the methods to reconstruct unreported catch were estimated to be either (1) not elaborated with enough links to available scientific literature, (2) not sufficiently considering the extent of SPM’s fleet and fishing grounds, (3) not representative of the historical evolution of industrial and artisanal fishing at the local scale, or (4) not accounting for similar fishing practices in the Northwest Atlantic when no SPM-specific literature was available. In addition to these observations, several large errors were committed: some FAO or NAFO reported amounts were not correctly transcribed in the reconstruction database, leading to inaccurate catch time series, and some species included in the reconstruction were in reality not occurring in the Atlantic Northwest. To account for the aforementioned deficiencies and ensure SPM’s catch would be reconstructed comprehensively and as accurately as possible, a new reconstruction was undertaken, starting anew from 1950.

Reconstructing the catch in SPM is crucial for two main reasons. Firstly, it allows for a better understanding of how catches have evolved at a local level, and how this evolution has shown through the different fishing sectors. Uncovering gaps between reported data and reality can give a clearer picture of historical fishing dynamics in SPM. Understanding sector-specific trends shines a light on how fishing practices and the local economy are evolving. Secondly, reconstructing the past and present catch and obtaining comprehensive time series enables us to understand more precisely the impact fisheries and species removal can have on the marine

ecosystem (Zeller and Pauly, 2016). When this reconstructed fisheries data is used in ecosystem modeling, it adds an additional layer of precision to the dynamics affecting the ecosystem. Ultimately, reconstructing local catches is crucial for designing sustainable and comprehensive fishery management strategies around the archipelago, which will have an impact at both the species and ecosystem levels (Pitcher, 2001).

Thus, this chapter presents the attempt at the full reconstruction of Saint Pierre and Miquelon's total catch from 1950 to 2022 in and around their home EEZ, disaggregated by year, species, fishing sector, and fishing gear. Reconstructed data will secondly allow the calculation of two catch indices for SPM: the mean trophic level of the catch (MTL) and mean temperature of the catch (MTC). This attempt rests on the following hypotheses: (1) accounting for unreported data will produce catch assessments with a higher tonnage than the baseline catches reported by NAFO and FAO, and (2) fishing pressures in SPM have shifted from higher trophic level species to lower trophic level species through time.

3.2 Methods

3.2.1 Reported 'baseline' catch

SPM reports marine catches per species to four official reporting bodies, the Food and Agriculture Organization of the United Nations (FAO), the International Commission for the Conservation of Atlantic Tunas (ICCAT), the North Atlantic Salmon Conservation Organization (NASCO) and the Northwest Atlantic Fisheries Organization (NAFO), which succeeded to the International Commission of Northwest Atlantic Fisheries (ICNAF) in 1979 as the Convention for the management of all exploitable marine resources in the area (Maguire, 2001). NAFO divides the Northwest Atlantic Convention Area – which includes the 200 nautical miles EEZ of the adjacent coastal state – into subareas, divisions, and sub-divisions (Koen-Alonso *et al.*, 2019). NAFO reported catches by SPM offer a more detailed baseline for a reconstruction, as they are spatialized by NAFO sub-divisions (Figure 3.3). Since the FAO data covers the years 1950 to 2022 and the NAFO data started in 1960, the FAO dataset was used as the reported baseline for the 1950-1959 period and the NAFO dataset was used for the 1960-2022 period. From 1950 to 1959, since no spatialization was available for the catch, it was spatialized using the closest available ratio between NAFO divisions and sub-divisions averaged over five years (1960-1964) for each

species. Species caught exclusively in specific NAFO areas from 1960 onward were allocated only to those areas. NAFO zones where the five-year ratio was less than 1% were excluded from the spatialization, as were zones with catches occurring for fewer than two years between 1960 and 1964. Only the zones where catches were recorded starting in 1960, according to NAFO reports, were included in the spatialization, assuming fishing did not begin in the other zones in the 1950s.

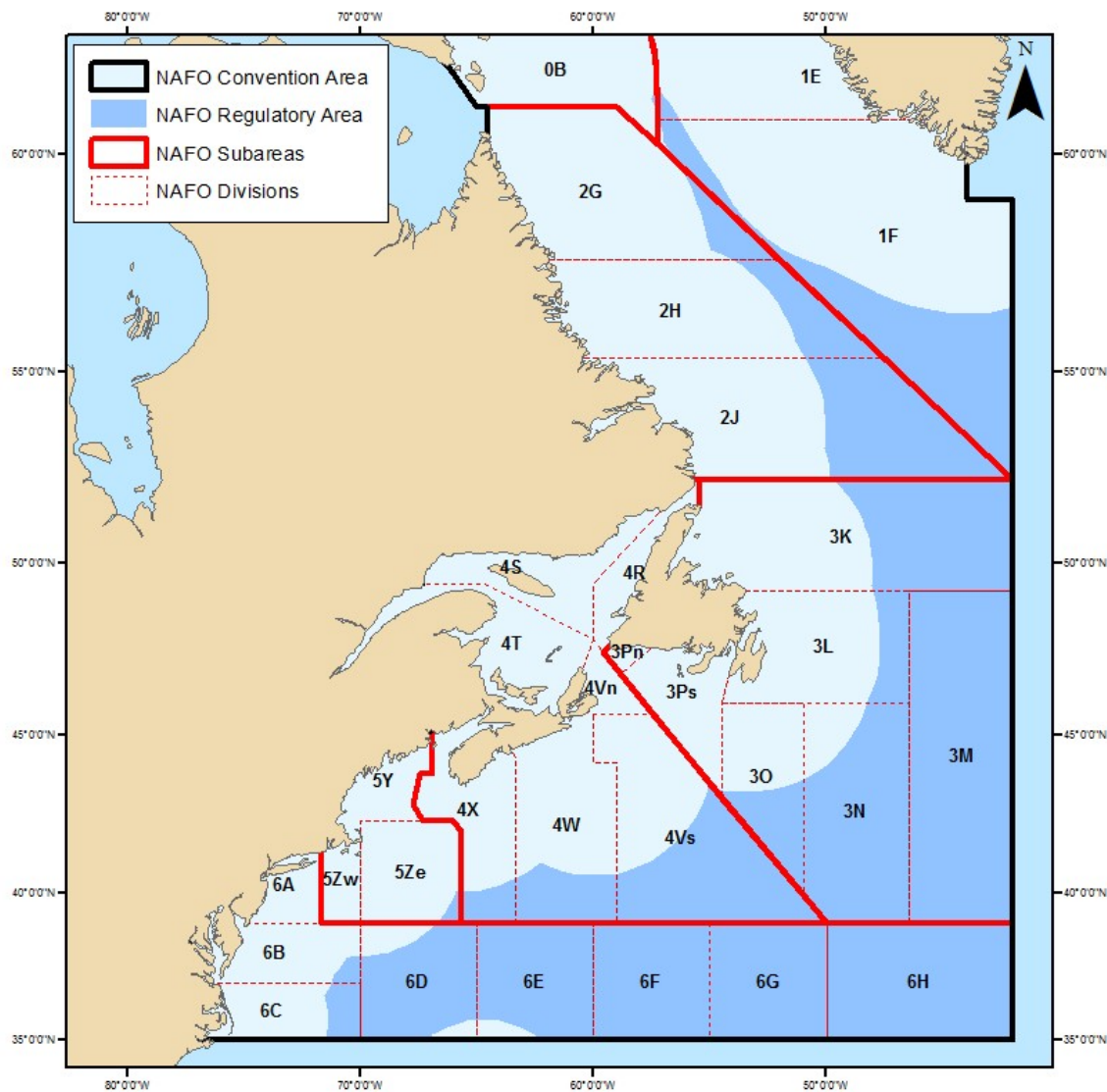


Figure 3.2. Map of the North Atlantic Fisheries Organization (NAFO) convention area (6,551,289 km²), including the NAFO divisions and sub-divisions (©Northwest Atlantic Fisheries Organization).

Some methods were taken over from the first reconstruction conducted by Bultel and Zylich (2015). These include the choice of using the spatialized NAFO dataset as the reported

baseline from 1960 onwards despite the FAO dataset being higher for some years by a 2% average, as well as using the FAO dataset to supplement the years where the catch was reported in FAO but unreported in NAFO, or different by more than 500 tonnes between the two datasets. For the five most recent years, the FAO dataset was as well used when catches were higher than in the NAFO dataset, as recent years can contain discrepancies between databases that haven't been revised yet (Table 3.1). These catches were allocated between NAFO sub-divisions using the same ratio as the NAFO dataset for the same years. Several species were never reported in the NAFO dataset but reported to FAO, such as sea cucumber. The FAO dataset was likewise used as the reported baseline source for the concerned species.

Table 3.1. NAFO taxa for which the catch was replaced by FAO amounts for the most recent five years reconstructed, when FAO catches were higher. Not included are the species only present in FAO databases.

NAFO taxa name	2017	2018	2019	2020	2021	2022
American plaice	-	-	-	X	-	-
American lobster	X	-	X	X	X	-
American sea scallop	X	-	X	X	X	X
Atlantic mackerel	-	-	-	X	-	X
Atlantic redfishes	-	-	X	-	-	-
Lumpfish	-	-	-	-	-	X
Northern shortfin squid	X	-	-	X	-	-
Queen crab	X	-	X	X	X	X
Waved whelk	-	-	X	X	-	-
Witch flounder	-	-	X	-	-	-
White hake	-	-	-	-	-	X

The NASCO dataset was used as a baseline for reported Atlantic salmon (*Salmo salar*) catches as the reported amounts were higher than the NAFO dataset amounts. For all species, several datasets were made available upon request by the national Ministry of Maritime Affairs covering the years 1980 to 2006 and 2010 to 2020 for both industrial and artisanal catches. For the years where catches were higher in the national datasets, these were used as a supplementary baseline source.

Another case where the same methods as Bultel and Zylich (2015) were used concerns catches in the EEZ of SPM by French mainland vessels, also reported through FAO and NAFO. FAO was used as the baseline dataset for 1950-1959 and NAFO spatialized data was used as the baseline dataset for 1960-2022. For 1950 to 1959, the methods consisting of keeping the NAFO's sub-divisions spatial allocation ratio calculated from the years 1960-1964 to spatialize the FAO data were used. The same methods were applied to the few years where NAFO data was not available.

3.2.1.1 Sector allocation

The first trawlers were introduced in 1952 in SPM, marking the beginning of the industrial fishing sector (Eynaud, 1986). Prior to 1952, the artisanal fishing sector was the dominant sector in SPM. Artisanal fisheries gradually decreased from 1952 to 1992, year when the last *doris*, which were used for artisanal fishing, stopped operating, with the exception of a few exploited species that have always been caught using artisanal fishing gear (G. Poirier, local fisher, October 2024, personal communications). All artisanal fishing took place inside the home EEZ, within the few nautical miles radius known as the Inshore Fishing Area (IFA) defined as “the area that extends from shore to either 50 km offshore or to the 200 m depth contour, whichever comes first” (Chuenpagdee *et al.*, 2006).

With this knowledge, all catch in 1950 and 1951 was allocated to the artisanal sector. Catch reports per sector made available by the SPM's department of Maritime Affairs for the 1980-2006 and 2010-2020 periods allowed the calculation of sector ratios for all species, and the identification of species caught solely by industrial or artisanal vessels. For the species caught by both sectors, like cod, sector ratios were available for the years 1960 and 1970 from Eynaud (1986). These ratios were used in complement to the 1980 ratio as anchor points to interpolate the proportions of artisanal/industrial landings between 1952-1960, 1960-1970, and 1970-1980. All catches of species previously caught by both sectors were allocated to the industrial sector from 1993 onwards, following the collapse of the artisanal fishery. The 2020 artisanal/industrial ratio was applied to 2021 and 2022. Landings from French mainland vessels were all allocated to the industrial sector.

Some species reported only as industrially fished to the Maritime Affairs of SPM were allocated to the industrial sector exclusively, like haddock (*Melanogrammus aeglefinus*) or pollock (*Pollachius virens*), while other species reported only as artisanally fished or caught using artisanal gear like traps or other hand tools, like American lobster, waved whelk (*Buccinum undatum*), Shortfin squid (*Illex illecebrosus*) or Atlantic salmon (Forest, 2022), where allocated to the artisanal sector exclusively.

3.2.1.2 Spatial allocation

SPM's vessels used to fish in sixteen NAFO divisions and sub-divisions: 2J, 3KLMNO, 3Pn, 3Ps, 4RST, 4Vn, 4Vs, 4WX and 5Ze (Figure 3.3). The EEZ of SPM overlaps with two of these divisions: 3Ps and 4Vs. The previous reconstruction allocated the catch between the SPM EEZ and the rest of the NAFO 3Ps and 4Vs zones according to the assumption that since SPM's EEZ represents respectively 10.2% and 0.8% of 3Ps and 4Vs, the catches should be allocated using these same percentages "in absence of a better alternative" (Bultel and Zylich, 2015). This assumption does not consider the evolution of the Canada-France maritime boundaries and the French-claimed fishing area of approximately 50,000 km² between 1972 and 1992, the year when the current official maritime boundaries were established (Keske *et al.*, 2016; Forest, 2022). From 1972 and 1992, catches reported as caught "inside the home EEZ" in the literature were geographically considering this larger area and not the current boundaries of the EEZ.

The spatial allocation of the catches in the NAFO 3Ps sub-division between the SPM and Eastern Canada's EEZs was done according to the ratios calculated by Eynaud (1986) in his analysis of the decline of artisanal fisheries in SPM. Cod was said to be caught 90% in the home EEZ, and 10% in the rest of 3Ps from 1978 to 1984 included. In 1985, the ratio was 59% of cod caught in the home EEZ and 41% in the rest of 3Ps, and in 1986 it changed to 75% in the home EEZ and 25% in the rest of 3Ps. These ratios make more sense in the context of the formerly claimed fishing zone area which represented 46% of the 3Ps area. As cod was the main targeted species by local fisheries, these ratios were assumed to be the same for all other fish species caught in 3Ps in the absence of a more precise alternative. Since this period aligned with the formerly claimed 50,000 km² EEZ, the catch was allocated to a zone called "Triangle" for the purpose of spatial allocation within the database of *Sea Around Us* (www.searoundus.org). The 1978 ratio

was kept and applied to the catch from 1950 to 1977, and the 1986 ratio was kept and applied to the catch from 1987 to 1992 when the new fishing boundaries were delimited, assuming this new surface area of the EEZ would influence the spatial allocation of catches.

Since no other spatial ratios were available in the literature or upon discussions with local fishers for the years onwards, ratios were calculated using the Global Fishing Watch (2024) reports on SPM's trawlers' fishing effort from 2014 to 2022. The number of fishing events was available in both the SPM EEZ and the Eastern Canada EEZ for each year. Since not all but only the most active vessels were reported, the three vessels with the most fishing events (*Cap Marie*, *Cap Jean* and *Beothuk*) were used as a reference to calculate a ratio to allocate the 3Ps catch between both EEZs. As 1992 marked both the collapse of artisanal fisheries and the delimitation of new maritime boundaries, the 2014 ratio was applied to the 1993-2014 period, assuming it is reflective of the official and smaller home EEZ.

Some catches were spatially allocated using other information considering fishing agreements and the location of some fishing areas. Thus, several species are said to be “local species” as they are solely managed locally in the SPM EEZ, including waved whelk, sea cucumber, snow crab, American lobster and Atlantic deep-sea scallop (*Placopecten magellanicus*). The fisheries for these species are regulated under a national decree, and there is no co-gestion agreement with Canada for their exploitation (deBeauregard, 2013). Another species, lumpfish (*Cyclopterus lumpus*), was listed as being locally managed in the 2004 annual IEDOM report for the archipelago (IEDOM, 2004). All catch of the aforementioned species reported in NAFO 3Ps was allocated to the home EEZ. The allocation of *Placopecten magellanicus* catches to the home EEZ was further confirmed by the assessment of the 3Ps stock showing the species abundance being concentrated within the home EEZ (Foucher, 2018).

All catch occurring in the 4Vs subdivision was allocated between the SPM and Canadian EEZ using the same methods as the allocation done for the subdivision 3Ps, given that both the formerly claimed EEZ and the present regulated EEZ overlap with 4Vs, and from information on effort derived from fishing effort maps from 1986 to 1991 (Bez and Moguedet, 1992).

Given that mainland French vessels used to fish off the Northern Coast of Newfoundland and in the Gulf of Saint Lawrence, and given the 1972 fishing agreement between Canada and

France where France renounced its fishing right in the Northwest Atlantic (Forest, 2022), French metropolitan vessels' catches in the 3Ps and 4Vs zones were all allocated to SPM's EEZ.

Catches from SPM's vessels occurring in all the other NAFO divisions and sub-divisions not overlapping with the home EEZ were all allocated to the Eastern Canada EEZ, with the exception of the 3N and 3M divisions. Upon consideration of the NAFO 3N portion the Canadian EEZ covers, and the relative distance SPM industrial trawlers usually cover (Bez and Moguedet, 1992), catch in the 3N division was allocated between the Eastern Canada EEZ and the High Seas using the respective percentages of overlap (16.7% and 83.3%). Other divisions overlap with both the Eastern Canada EEZ and High Seas, such as divisions 3O and 3L, where all catch was allocated to the Canadian EEZ upon consideration of the limits of the Newfoundland Grand Banks, where most exploitable fish stocks are concentrated (Nogueira *et al.*, 2015). All catch in division 3M was allocated to High Seas as this division does not overlap with the Eastern Canada EEZ.

3.2.2 Unreported industrial catch

Discards of marine fishes and other organisms occur either when some individuals or species are caught while they were not targeted by a fishery (i.e., *by-catch*), or as a result of regulations. Some individuals can be discarded as they do not meet the quota or size restrictions for a specific fishery, or do not satisfy size or quality standards for the fishery (Zeller *et al.*, 2018). Bottom-trawling is the fishing practice leading to the most important amounts of annual discards worldwide (Roda *et al.*, 2019). SPM's 1987 decree on marine resource management and conservation states that all catch not meeting the minimal sizes stated through this decree has to be discarded at sea (deBeauregard, 2013). As discarded catch is usually unreported, very little to no information was available on SPM's discards. Older sources state that enormous quantities of fish were discarded during commercial fishing trips around Newfoundland (Rallier du Baty, 1927; DeLoture, 1994). Since no better option was available and upon comparison of similarities between both countries' fisheries, the methods used to calculate discards in the 3Ps area by Divovich *et al.* (2015) in the Eastern Canada catch reconstruction were used, assuming the discard rate would be the same for SPM's trawlers as NAFO fishing areas are common, and as both countries' fisheries were impacted similarly by the cod collapse in 1992. Discards were calculated

for both the groundfish and northern shrimp (*Pandalus borealis*) fisheries, using the Newfoundland fleet as a reference.

Shrimp trawl related discards were calculated for the years where the northern shrimp fishery was active in SPM, from 2000 to 2013, using a discard ratio and species disaggregation from Kulka (1995, 1999). The NAFO 3L division, one of the two divisions where SPM trawlers catch shrimps, was included in the discard assessments conducted for Newfoundland from 1980 to 1995. The middle of the 1990s marked a strong decrease in shrimp trawl-related discards, linked to the introduction of new gear attachments for trawlers and minimum mesh sizes regulations (Kulka, 1995; Larsen *et al.*, 2018). The rate of 2.5% discards calculated in 1994 was used for 2000 to 2013 (Kulka, 1995). Discards were split using the ratios calculated by Divovich *et al.* (2015) for each NAFO subdivision, between four species: cod, American plaice (*Hippoglossoides platessoides*), brill (*Scophthalmus rhombus*) and redfish (*Sebastes* spp.). Species disaggregation takes into account the decline in cod biomass following the cod moratorium in 1992.

Groundfish-directed fisheries discards were calculated using two sources, the first being Kulka (1986) which provides information on the discarding estimates for the Newfoundland offshore fleet in 1980-1985, with reference to trends in the past five years. The second source used was Jean (1963), which provides insight into discards at sea by northern New Brunswick draggers. In order to calculate discard rates through the years, some components of the fishery were taken into consideration and assumed to be true for SPM's fleet too, such as the introduction of large mesh nets and reduction of sizes retained for landing in 1956, leading to discards being seven times higher in 1956 than 1961 (Jean, 1963). The discard rate was interpolated from 1956 to 1961 to reflect this transition. Discards for the Newfoundland offshore fleet increased from 7.7% at the beginning of the 1980s to 11.0% in 1985 and reflected the effort increase in the cod fishery (Kulka, 1986). This was assumed to be true for SPM as well, giving that reported catches from local trawlers increased substantially from 1980 to 1987, demonstrating an increased effort preliminary to the cod collapse. The 7.7% discard rate was used for 1961-1985. From 1985 to the cod moratorium in 1992, the discard rate of 11.0% was deemed constant, and assumed to return to 7.7% in the years following the moratorium, illustrating a decreased fishing effort translating into a decreased discard rate (Divovich *et al.*, 2015). Using the methods developed by Divovich *et al.* (2015) in the Eastern Canada reconstruction, with emphasis on the discard rates and species

disaggregation estimations from Kulka (1986) and Jean (1963), and an additional comparison with recent studies on discards in the NAFO 4VW divisions (Gavaris *et al.*, 2010), discards were calculated for the groundfish directed fisheries by trawlers in SPM from 1952 (year when the first trawler was introduced) to 2022, in each of the NAFO division and subdivision. Discards calculated in the 3Ps subdivision were allocated between the SPM and the Canadian EEZs using the aforementioned spatial allocation ratios calculated.

Some information on discards for specific fisheries was available through local and Canadian sources. Sea cucumber bycatch ratio was estimated through a DFO survey on the Saint Pierre Bank in 2016 to be 72% of sea cucumber landed for 28% of bycatch discarded. The main species making up respectively 13% and 4% of the total bycatch were identified as sea urchin (*Strongylocentrotus droebrachiensis*) and sand dollar (*Echinarachnius parma*). The other species making up the remaining percentages of bycatch were toad crab (*Hyas* sp., 3%), Iceland scallop (*Chlamys islandica*, 2%), Atlantic deep-sea scallop (*Placopecten magellanicus*, 2%) and polar six-rayed star (*Leptasterias polaris*, 1%). These percentages were applied to disaggregate the calculated discards by species. The last 3% were attributed to “other marine invertebrates” (Pantin, 2018).

3.2.3 Unreported small-scale catch

3.2.3.1 Subsistence catch

The inhabitants of Saint Pierre and Miquelon have relied on fish for their subsistence for centuries, particularly capelin (*Mallotus villosus*), one of the most abundant marine resources around the archipelago (Dumont and Provost, 2008; G. Poirier, local fisher, October 2024, personal communication). As for other coastal communities on the Northern Coast of the Saint Lawrence Gulf and in Newfoundland, capelin was usually either consumed fresh or dried and had multiple uses, not only as bait, but also as a source of fertilizer for the land and as food for dogs. The local saying “Du pain, du beurre, du capelan” (lit. “Bread, butter, capelin”) used when referring to an afternoon snack reflects the omnipresence of capelin as an important resource on the island (Ancellin, 1955; Dumont and Provost, 2008; G. Poirier, local fisher, October 2024, personal communication). There is however no trustworthy source on the amounts caught each year for subsistence. According to Ancellin (1955), families would keep “small quantities for

personal consumption.” Upon discussion with local fishers, families were said to keep around ten bags of twelve capelins per year for personal use. Since capelin was a resource known to be “easy to catch” with small nets off the coast of the islands (J. Vigneau, IFREMER, and G. Poirier, local fisher, October 2024, personal communications), it was assumed that this was true for all families. This assumption allowed the calculation of a yearly tonnage of capelin landed for subsistence, using population data and the average individual weight of *Mallotus villosus*.

Discussions with local fishers allowed to identify that other species were kept for subsistence during the years when artisanal fisheries were prominent. According to G. Poirier (local fisher, October 2024, personal communication), every fisher was bringing home an average of 30 kg of fish each week, kept for personal use out of the total caught artisanally. This amount was said to be mostly cod, and “a little bit of all species caught.” For the duration of the fishing season, from May to October (Ancellin, 1955), a yearly amount of fish landed for subsistence was calculated using this new information and the number of fishers available through Eynaud (1986). The number of fishers was interpolated for the years onwards. The larger portion of this subsistence amount was allocated to cod (80%), and the remaining 20% equally split between all other species caught in the artisanal fisheries each year. The distribution of the latter percentage was adjusted for years where some species were caught in amounts below 10 tonnes, to reflect an accurate prevalence of each species in the subsistence catch. Species having a calculated subsistence tonnage below 1 tonne for some years were ignored in the species allocation for subsistence landings.

Subsistence catch was calculated for the years 1950 to 1992, which corresponds to the cease of artisanal fisheries using *doris*, following the cod collapse in the Northwest Atlantic. Recent reports on seafood consumption in SPM suggest that the consumed species are mostly cod, salmon, scallops and crustaceans, which were said to be mostly originating from industrial, artisanal and recreational catches. Crustaceans were said to be solely originating from artisanal fisheries. Additionally, a considerable part of the cod, salmon and scallops consumed was said to be imported. However, a small portion of local people (a third of the 97% consuming seafood in a 286 people sample) was said to be practicing auto-provisioning (Dewals *et al.*, 2019). As this single data point was not sufficient to calculate a subsistence rate, it was conservatively assumed to be around half a tonne per year and per species consumed and potentially caught as subsistence

(namely: cod, salmon and scallops) after 1992 onwards. For salmon, it was assumed to be around 0.05 tonnes per year to match the previous years trends.

3.2.3.2 Recreational catch

There are two species known to be targeted in recreational fisheries in SPM: Atlantic salmon and American lobster (Guellec, 1987; Goraguer, 2010). A campaign in 1975 with the aim to assess the salmon resources and potential for a fishery stated that “no attempt at salmon fishing had been undertaken in Saint-Pierre and Miquelon” since the beginning of the 20th century (Paturel, 1976). The legislation under which salmon fishing is regulated in SPM was implemented in 1987, with permits allocated to professional and recreational fishers (Goraguer, 2010). The year 1987 was therefore assumed to mark the start of the recreational salmon fishery. The number of recreational salmon fishing licenses and the total landings for this fishery are reported to NASCO and were available from 1990 to 2010 (Goraguer, 2010), 2011 to 2020 (NASCO, 2021) and in 2021-2022 (NASCO, 2023). Since no data was available for 1987 to 1989, it was assumed that the number of recreational licenses and the total landings were equal to those in 1990.

Very little data was available for the lobster recreational fisheries. The first legislation to regulate this fishery appeared in 1987, through a decree establishing new regulatory measures for the fisheries resources in SPM (Guellec, 1987). However, this decree did not establish a number of permits. The recreational lobster fishery allows the catch of four lobster per fishing trip, but is said to be poorly controlled, which leads to overuse of this quota with some fishers having more than forty lobster traps in use at once (d’Aboville, 2007). As no data were available on the number of fishing licenses or the total catches, the same methods in Page *et al.* (2020) were used. It was conservatively assumed that the proportion of lobster fishers increased from 0 to 5% of the total population between 1986 and 1992, and made up 5% of the total population from 1992 onwards. The number of lobster fishers was calculated using this ratio and population data from 1987 to 2022. The total population was interpolated between the years where no data were available. The commercial catch of lobster is estimated to be lower than the recreational catch, as there is not enough local demand for lobster on the market since recreational fishers are able to catch them with little to no quota regulation (d’Aboville, 2007). The average rate of lobster landed per recreational fisher was assumed to be 50 kg per year (F. Teletchea, University of Lorraine, October

2024, personal observations), and this amount was multiplied by the estimated number of lobster fisher to obtain an average rate of 15 tonnes per year (Page *et al.*, 2020).

3.2.3.3 Bait

The use of bait for the artisanal cod fishery was first described at the beginning of the 20th century by Rallier du Baty (1927), with the use of several species for consequent quantities of bait, including capelin, scallops (*Chlamys islandica* and *Placopecten magellanicus*), waved whelk, herring (*Clupea harengus*), mackerel (*Scomber scombrus*), northern shortfin squid, propeller clam (*Cyrtodaria siliqua*) and softshell clam (*Mya arenaria*). Starting in 1889, fishers were then forced by law (i.e., the Newfoundland Bait Act) to fish for their own bait on the Saint-Pierre Bank rather than buying it from Newfoundland's fishers (Dashwood, 1899). The two species used in most quantities to bait the lines were waved whelk and shortfin squid: both species were said to be easy to catch at the same fishing location where cod was caught. Whelk was said to be the most abundant and used bait, additionally used to supplement insufficient quantities of squid when needed (Rallier du Baty, 1927). Ancellin (1955), however, described a change in the species selected for bait in the 1950s, stating that the most used species were capelin, followed by squid and clams. Recent sources confirmed that for the artisanal cod fishery from 1950 to 1992, capelin was used in most quantities from June to mid-August, while squid was used from mid-August to the end of the fishing season, and whelk and softshell clam in spring (April and May) before capelin arrived on the Saint Pierre Bank (Ancellin, 1955; J. Vigneau, IFREMER, and G. Poirier, local fisher, October 2024, personal communications). One capelin or one to three bivalves was needed to bait one hook, while one shortfin squid could be used to bait six hooks (Rallier du Baty, 1927; Ancellin, 1955). To be conservative, it was assumed that an average of two bivalves was needed per hook, and since two species were used at the same period, that it represented one individual of each species.

Bait amounts were calculated using the aforementioned species-specific information, in addition to information about artisanal boats and hooks, the number of artisanal boats for each year available through Eynaud (1986), and the average weight of each species. Artisanal boats carried between 2,000 to 2,200 hooks, and the most used hooks were called “*mitraille*” (‘sub-machine gun’), made up of a total of ten hooks (Rallier du Baty, 1927; Desjardins and Huet, 2003; G.

Poirier, local fisher, October 2024, personal communication). Since “only some hooks were baited,” it was assumed a third of the hooks used bait, making up an average of 700 hooks baited per trip (G. Poirier, local fisher, October 2024, personal communication). In one fishing season lasting from May to October, fishers spent around 120 days at sea (Eynaud, 1986). Assuming this represents twenty days of fishing per month, bivalves caught for bait in spring were considered to only be used when the fishing season started in May. For 700 hooks baited per boat during twenty days, the average amount of molluscs used was 2,100 kg per boat. This amount was equally distributed between the two species used, waved whelk and softshell clam. As the use of capelin overlaps with the use of squid in August, this month was split in half and each species assumed to account for fifteen days of fishing. The average amount of capelin caught for bait was calculated for fifty days of fishing, and is equivalent to 1,820 kg per boat per year. The average amount of squid caught for bait was calculated for fifty days of fishing and equals 892 kg per boat per year. These amounts multiplied by the total amount of doris allowed to obtain total bait amounts for all years from 1950 to 1992.

The final equation to calculate bait for these four target species was as follows:

$$700 \cdot D \left((d_i \cdot w_i \cdot n_i) + (d_j \cdot w_j \cdot n_j) + (d_k \cdot w_k \cdot n_k) + (d_l \cdot w_l \cdot n_l) \right) \quad (6)$$

where D is the number of doris operating for the designated year, w is the average weight of one individual from species i, j, k or l , d is the number of fishing days where species i, j, k or l was caught and n is the average number of individuals from species i, j, k or l needed as bait per hook.

Additional information stated that fishers kept around 100 kg of capelin per boat a year for bait. Since this stated amount is well below the calculated amount, and since Ancellin (1955) states that capelin was sometimes caught in higher quantities and frozen to make up for the times when live bait was available in lesser quantities, 100 kg per boat was added to the total amount of capelin caught for bait. This should not represent an overestimation, as the number of hooks baited was a conservative assumption.

As species used for bait were not landed but used directly for the artisanal fishery, they were considered to be unreported. Despite the important decline in artisanal fisheries, some species like snow crab and American lobster are still caught using artisanal fishing gear which most certainly requires the use of bait. There is however no recent information source on which species

are used to bait lines, pots or traps, in which quantities, nor if those species are caught by SPM's fishers or imported from elsewhere in Canada (which is suspected to be the case).

3.2.3.4 Artisanal discards

Very little information was available on artisanal discards, as little to no observer studies coverage was available for artisanal gear such as pots, traps, and handlines. With the available data, it was possible to calculate artisanal discards for only four taxa targeted in the artisanal fisheries. Capelin discards were calculated on the basis that the average male-to-female ratio is 2:1 and that females were usually discarded as they were smaller and not sought for consumption (Rallier du Baty, 1927). Artisanal landings were assumed to represent two-thirds of the catch, and the remaining third was categorized as discards. Lumpfish discards were calculated knowing that males and juveniles were usually discarded at sea, as mature females are the ones sought for their roe (Briand, 1995; Kennedy *et al.*, 2019). With very little information on sex ratios other than females usually being more abundant than males, lumpfish discards were calculated on the basis of an estimated male-to-female ratio of 1:2 (Kennedy *et al.*, 2019).

Snow crab and American lobster discards were additionally calculated, but not included in the final reconstruction file computed in the Sea Around Us database as survival rates are usually very high for crustaceans (Roussel, 2019). Lobster discards calculation was made possible using Roussel's (2019) estimate that an average of 45% of lobsters are discarded alive in the Saint Pierre and Miquelon lobster fishery, most being egg-bearing females and the rest individuals smaller than the 87 millimeters size limit.

3.2.4 Gear disaggregation

Gear information was available for several fisheries in SPM, allowing a more precise gear disaggregation. Within the industrial sector, trawlers started operating in 1952 and represent the entirety of the industrial fleet, with the exception of some targeted fisheries (Bertrand, 1988). Bottom-trawl was the gear attributed to all groundfish industrial catch from 1952 to 2022. A study on the biology of sea cucumbers in Saint Pierre and Miquelon in 2020 informed on the use of dredge as a fishing gear to catch holothurians, which was also used to give insights on dredge related discards and sea cucumber fishing locations (Vigneau *et al.*, 2019). Molluscs fished

industrially (i.e., Iceland scallop and giant sea scallop) were caught using scallop dredges (Foucher, 2018; DFO, 2018a). Recent reports list long-liners as the preferred gear to catch Atlantic halibut (Vigneau *et al.*, 2013); while it was not possible to obtain a precise date for the introduction of longliners as recurrent fishing vessels, Eynaud (1986) mentions the “failed introduction” of longliners in 1981. It was therefore assumed longliners started targeting Atlantic halibut in 1992 onwards.

In the small-scale fisheries, lumpfish were caught using 90-meter-long gillnets installed at sea floor level (Briand, 1995). Crustaceans (snow crab and American lobster) were caught using crab traps and lobster pots and traps (Laurans, 2010). Shortfin squid was caught artisanally using weighed-down jigger lines, a type of vertical line composed of several hooks (Ancellin, 1955; FAO, 2024). Molluscs fished artisanally (i.e., whelk, mussel) were caught by hand (Ancellin, 1955; Rallier du Baty, 1927). As the artisanal fisheries were said to be “almost exclusively line fishing,” the gear for all other species was assumed to be 60% small-scale handlines, 20% small-scale longlines, and 20% small-scale gillnets (Ancellin, 1955). This assumption is conservative and considers the small-scale nets being used occasionally in the artisanal fishing sector (Ancellin, 1955; M. Derible, local historian, and G. Poirier, local fisher, October 2024, personal communication).

Capelin fished for subsistence was assumed to be mainly caught using small-scale nets (80%) as reported by local fishers (G. Poirier, local fisher, October 2024, personal communication) while the rest (20%) was assumed to be the amount caught using small-scale handlines and kept for fishers’s own consumption. Salmon fished in the artisanal and subsistence sectors was caught using gillnets (Paturel, 1976; Forest, 2022). With no precise information for this sector, “recreational fishing gear” was the gear allocated to all recreational catch.

3.2.5 Catch data reliability score

To quantify the uncertainty of the reconstructed data, data reliability scores were attributed to the input data for each sector by periods of five years. These scores developed by Zeller and Pauly (2016) are derived from criteria developed by the Intergovernmental Panel on Climate Change (IPCC) and quantify the reliability of the five years time-series on a scale from 1 to 4, i.e., (1) ‘very low’, (2) ‘low’, (3) ‘high’ and (4) ‘very high’. These scores were first attributed to each

reporting status of the catch (i.e., ‘reported’ or ‘unreported’) in each sector, then averaged for the sector by raising each score to the catch. This attribution relies on a qualitative evaluation and is then computed as an overall score for each time period in the *Sea Around Us* databases.

3.2.6 Taxon specific notes

Some species' scientific names entered in the *Sea Around Us* database as used in previous reconstructions are alternative combinations that have been superseded and are no longer accepted in the taxonomy of these species. This is the case for one species caught by the SPM fleet, Yellowtail flounder, listed as *Limanda ferrugina* but accepted as *Myxopsetta ferrugina* (Froese and Pauly, 2024). The group Anarhichadidae previously listed in the reconstruction for reported “wolffish” catch was replaced by *Anarhichas lupus*, the only species of this group caught around the archipelago. All species taxonomy was verified using the World Register of Marine Species (WORMS, www.marinespecies.org), and the corrected and accepted names were used in the present reconstruction.

3.2.7 Additional analyses with the reconstructed catch

3.2.7.1 Mean trophic level of the catch

With the reconstructed data, an additional analysis of the mean trophic level of the catch was performed, for the species making up the catch within the SPM EEZ, and for the species making up all catch (inside and outside the SPM EEZ). The trophic level of each species was weighted by the amount of that species caught by SPM’s fleets (i.e., all sectors included), and averaged for each year to obtain a trend from 1950 to 2022.

3.2.7.2 Mean temperature of the catch

The final analysis completed with the reconstructed catch implied the calculation of the mean temperature of the catch from SPM fleets within their EEZ. The preferred mean temperature of each fish and invertebrate species was extracted from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org), and weighted by the amount of each species caught by SPM

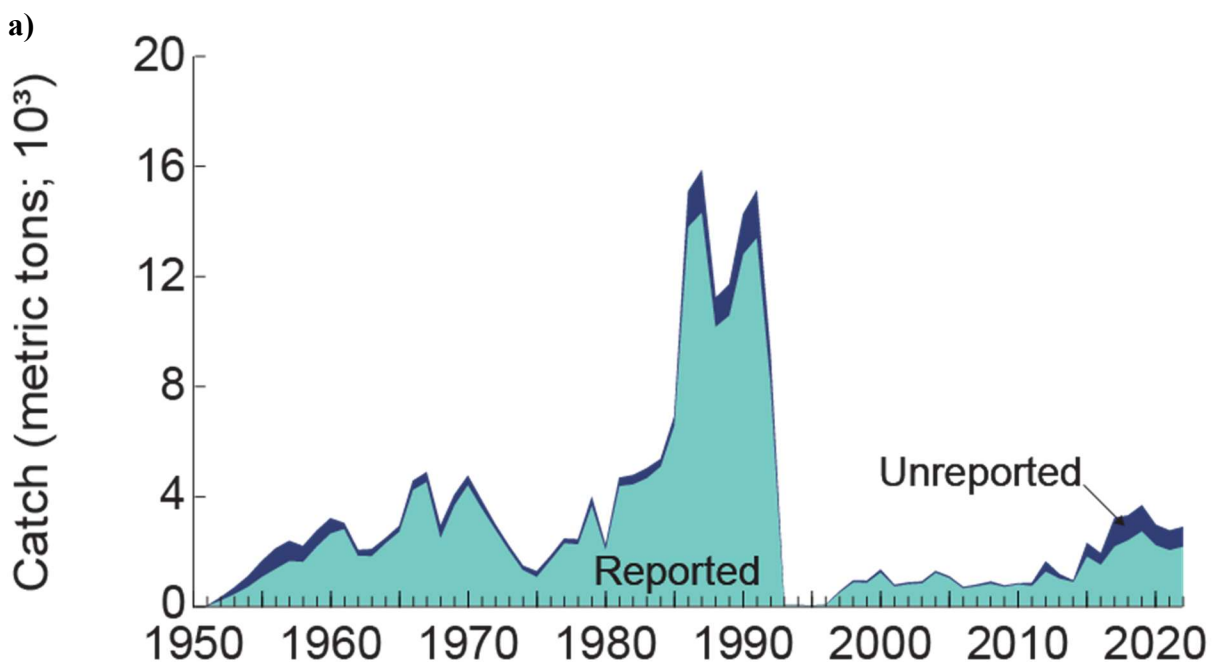
(i.e., all sectors included), then averaged for each year to obtain a trend from 1950 to 2022. A segmented regression through R was performed to better visualize the trend patterns.

3.3 Results

For all sectors, all species, from 1950 to 2022, reported versus total reconstructed amounts caught by the SPM fleet increased from 544,856 tonnes to 629,225 tonnes, with almost 100,000 tonnes of unreported catch. The highest amounts of unreported catch pertain to the industrial sector (52.5%), followed by the artisanal sector (36.5%), subsistence catch (10%) and recreational sector (1%). The main sources of unreported catch are species discarded at sea, mainly in the industrial sector, and species caught as bait, mainly in the artisanal sector.

3.3.1 Industrial catch

Industrial catch makes up 85% of the total catch from SPM trawlers from 1950 to 2022 (Figure 3.3, 3.7). Out of this proportion, an average of 43% of the total catch was caught within the perimeter of the SPM EEZ from 1950 to 2022, while an average of 53% is caught within the Eastern Canada EEZ. The remaining average of 4% is caught in the High Seas.



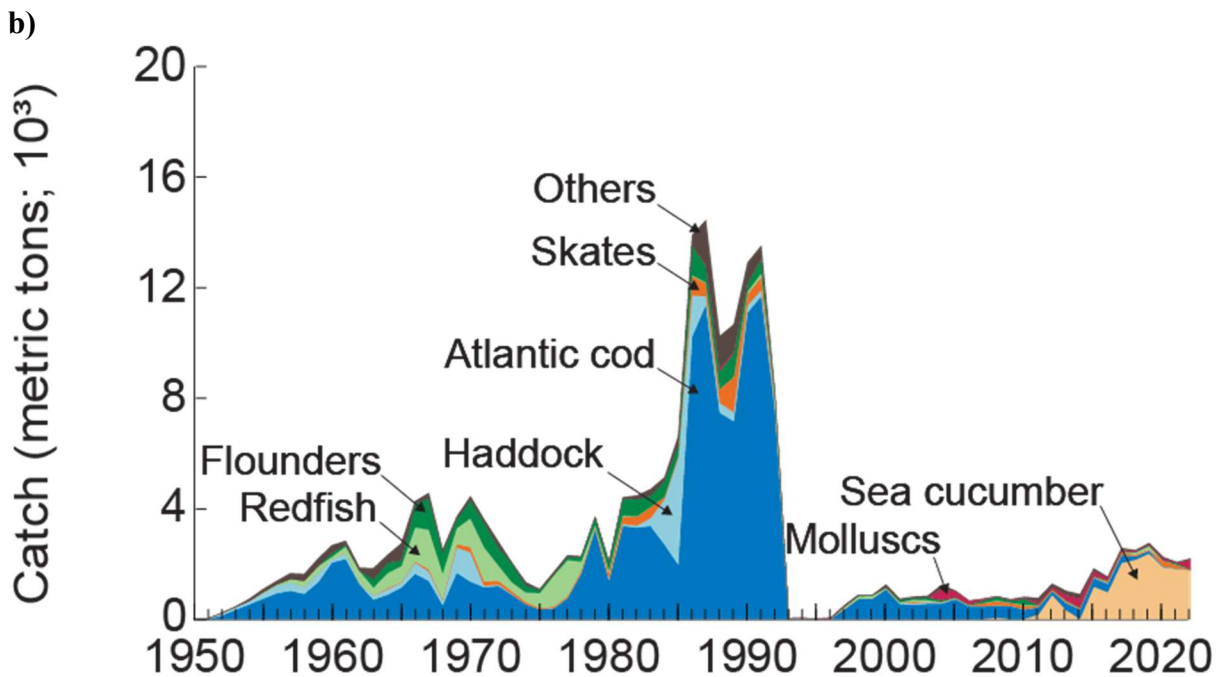


Figure 3.3. Reconstructed industrial catch of the SPM fleet within the SPM EEZ from 1950 to 2022 a) by reporting status and b) by taxa. ‘Others’ include 20 additional taxa.

3.3.1.1 Landings

Within the SPM EEZ, Industrial landings were an average of 1,100 tonnes in the 1950s, before increasing to an average of 3,000 tonnes per year in the 1960s and early 1970s. Industrial landings started declining in 1972, before peaking again in 1977, and increasing substantially in the 1980s to reach an average of 8,500 tonnes per year from 1980 to 1992. Two major peaks can be noted in 1987 and 1991, of 14,300 and 13,400 tonnes respectively. Post-1992 and the Northwest Atlantic cod collapse, industrial landings remained very low between 1993 and 1996, around 30 tonnes per year, before increasing again in 1997 and staying somewhat constant at around 900 tonnes per year throughout the 2000s to mid-2010s. Industrial landings in the EEZ experienced another increase starting in 2015.

The main taxa targeted by the commercial fleet within the home EEZ are Gadidae (67%), Sebastidae (8%), Pleuronectidae (8%) with mainly catches of American plaice and yellowtail flounder, echinoderms (7%), and Rajidae (4%). The remaining 6% is distributed between 15 other

taxa. Some species caught industrially (i.e., using industrial gear such as trawls and dredges) are only caught within the SPM EEZ, including sea cucumber. SPM industrial fisheries used to target mainly Atlantic cod (65%), redfish (8%) and haddock (8%) between 1952 to 1992. Post-1992, the target shifted to mainly sea cucumber (44%), cod (32%) and Atlantic deep-sea scallop (7%).

Outside of the SPM EEZ and within the Eastern Canadian EEZ, four major peaks in catches can be noted: in 1961 (8,400 tonnes), 1986 (9,200 tonnes), 1990 (10,000 tonnes) and 1991 (10,000 tonnes). After the 1992 collapse, industrial catches in the Eastern Canadian EEZ experienced another peak from 1997 to 1999, before fluctuating towards a decrease from 2000 to 2022. While cod stays the main species commercially caught, the composition of the catch varies between different NAFO divisions and sub-divisions. The 3Ps sub-division (excluding the SPM EEZ) sees catches of mainly cod (70%) and haddock (8%), while the 2J3KLMNO divisions (Grand Banks) see catches of mainly haddock (37%), cod (20%) and American plaice (15%). The 4RSTVns divisions catches are predominantly cod (78%) and redfish (16%), while the in the 4WX5Ze divisions (Scotian Shelf) they are mainly haddock (52%), cod (40%) and pollock (3%). Atlantic cod is mainly caught in the 3Ps subdivision (44%), and in the 4R (19%) and 4Vn divisions (18%) (Figure 3.4).

In the High Seas, fluctuations in yearly catch are more significant. Three major peaks of catch can be observed in 1965 (2,000 tonnes), 2007 (1,400 tonnes) and 2010 (1,100 tonnes). The main species caught by SPM trawlers in the High Seas are yellowtail flounder (24%), American plaice (17%), polar shrimp (16%) and Atlantic cod (15%) (Figure 3.4).

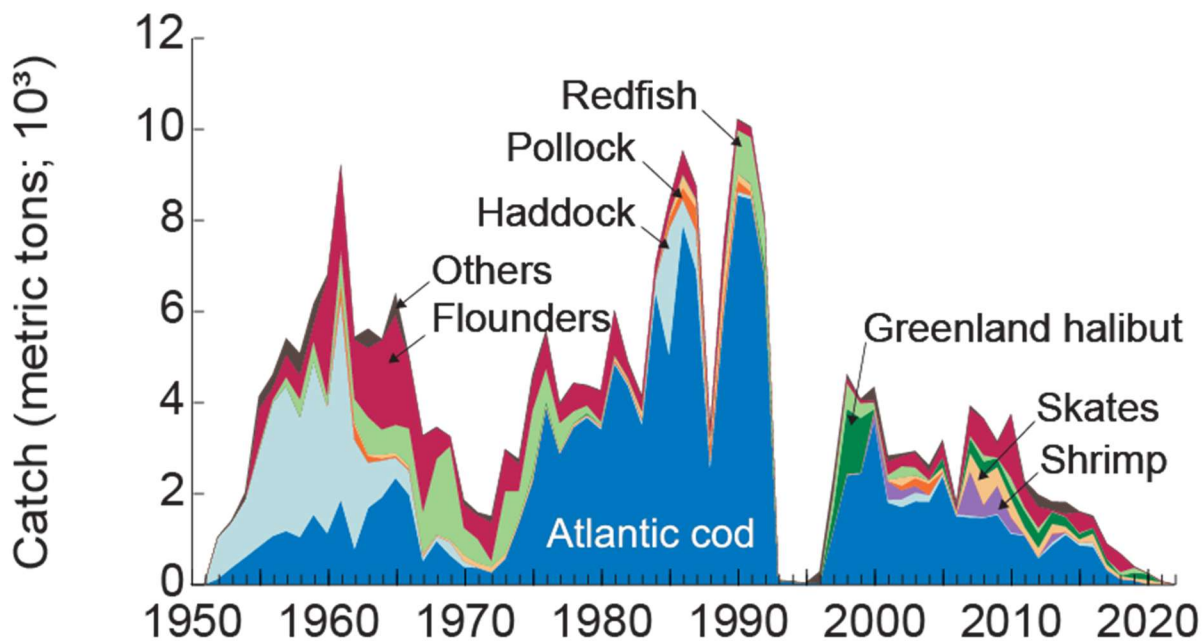


Figure 3.4. Reconstructed industrial landings of the SPM fleet outside of the SPM EEZ from 1950 to 2022 by taxa. ‘Others’ include 20 additional taxa.

3.3.1.2 Discards

Discards make up 100% of the unreported industrial catch and 15% of the total industrial catch. Within the SPM EEZ, discards were estimated to be an average of 500 tonnes per year in the 1950s, declining to an average of 250 tonnes per year throughout the 1960s, 1970s, and early 1980s, and peaking at an average of 1300 tonnes per year in the late 1980s to early 1990s. Discards followed the trend of landings with a sharp decline following the 1992 cod collapse, staying under 3 tonnes per year from 1993 to 1996. Discards increased again to a stable average of 60 tonnes per year throughout the mid-1990s to 2010, when they peaked again at around 500 tonnes per year in the 2010s and early 2020s. Three notable peaks can be observed, in 1987, 1991, and 2018, of respectively 1,540, 1,780 and 830 tonnes discarded at sea (Figure 3.5).

The taxa composition of these discards has some similarities with the landings’ taxa composition, with cod being the main species discarded (18%). While 96% of cod is landed, 4% is discarded. This proportion discarded is estimated to be of mainly small individuals which do not meet the catch size limit. Other taxa majorly discarded include Pleuronectidae (14%) with mainly

American plaice (13%), Rajidae (13%), echinoderms (13%) with mainly green sea urchins (9%) and Sebastidae (12%). The remaining 30% are distributed between 32 other taxa.

Outside of the SPM EEZ and within the Eastern Canada EEZ, discards peaked three times in 1956, 1986 and 1990, with respectively 2,240, 1,000 and 1,100 tonnes discarded. Discards were highest in the 1950s, with an average of 1,400 tonnes discarded. In the High Seas, discards peaked in 1957 with 200 tonnes discarded, and were highest in the 1950s with an average of 115 tonnes discarded per year (Figure 3.5). Outside of the home EEZ, the taxa making up most of the discards are Gadidae (21%), Sebastidae (19%), Pleuronectidae (18%), Rajidae (16%), and Merlucciidae (13%).

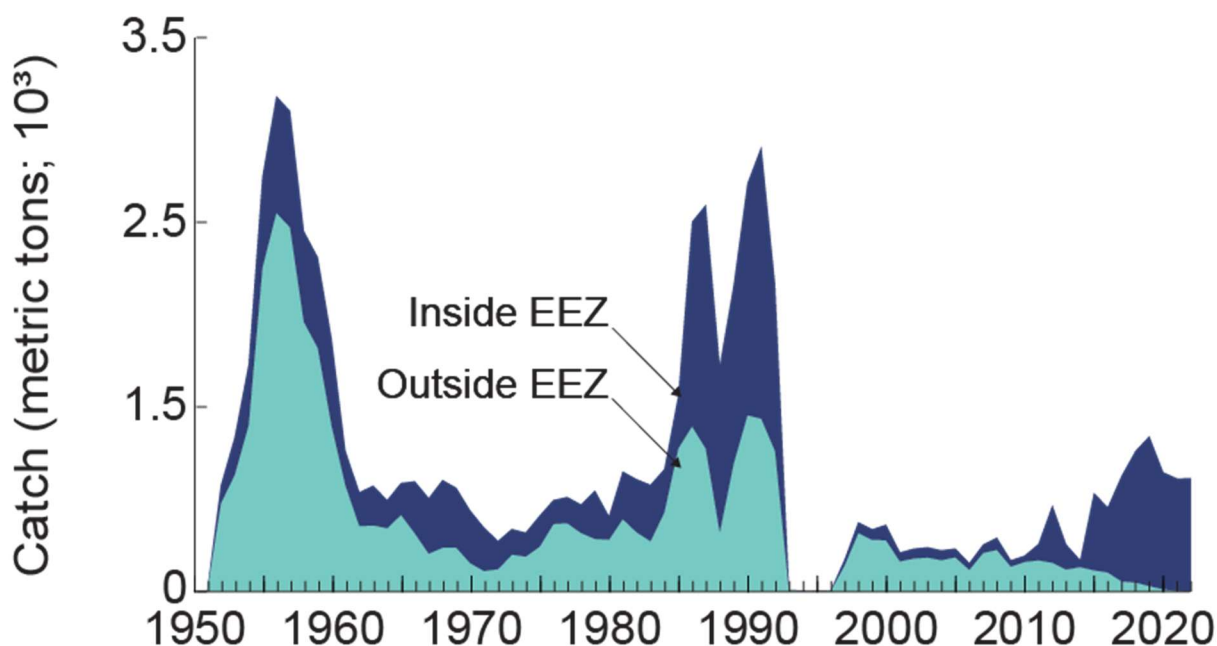


Figure 3.5. Reconstructed industrial discards of the SPM fleet inside and outside the SPM EEZ, from 1950 to 2022.

3.3.2 Artisanal catch

Artisanal catch shows a steady decline from 1950 to 1992. While artisanal landings made up 100% of the total landings in 1950 before industrial fishing gear was introduced, they declined to 29% in 1960, 20% in 1970, 7% in 1980 and 3% in 1990. The strongest decline of 71% was

observed between 1950 and 1960 (Figure 3.6). Artisanal catch makes up 14% of the total catch from SPM trawlers from 1950 to 2022 (Figure 3.7). All artisanal catch was fished within the SPM EEZ.

3.3.2.1 Landings

Artisanal landings amounted to around 3,300 tonnes a year at the beginning of the 1950s, peaking to 4,900 tonnes in 1954, before rapidly declining to around 1,500 tonnes a year in the 1960s and as low as 630 tonnes in 1972. They increased again in the late 1970s to peak at 2,700 tonnes in 1979, before declining again until reaching a low 166 tonnes in 1994. Following the collapse of artisanal fisheries, a rebuilding phase can be observed in the late 1990s when artisanal catch increased to around 1,000 tonnes per year again, followed by periods of highs and lows through the 2000s and 2020s. The lowest artisanal landings occurred in 2017, amounting to 70 tonnes landed.

Artisanal landings from 1950 to 1992 are dominated by two species: Atlantic cod (61%) and northern shortfin squid (13%). Other species commonly caught artisanally include capelin, waved whelk and softshell clam. From 1993 to 2022, artisanal landings are dominated by snow crab (50.0%) and lumpfish (31.4%), representative of a major taxonomic shift in artisanal catch composition following both the cod and artisanal fleet collapses in 1992. Other species fished artisanally include American lobster and waved whelk.

A total of 24 taxa are represented in the artisanal fishery. For the full 1950-2022 time series, the most targeted family is Gadidae (53%), followed by Ommastrephidae (11%), Osmeridae (8%), Oregoniidae (7%), Cyclopteridae (6%) and Buccinidae (5%). Fishes made up 72% of the landings, while molluscs made up 21% and crustaceans 7% of the landings.

3.3.2.2 Discards

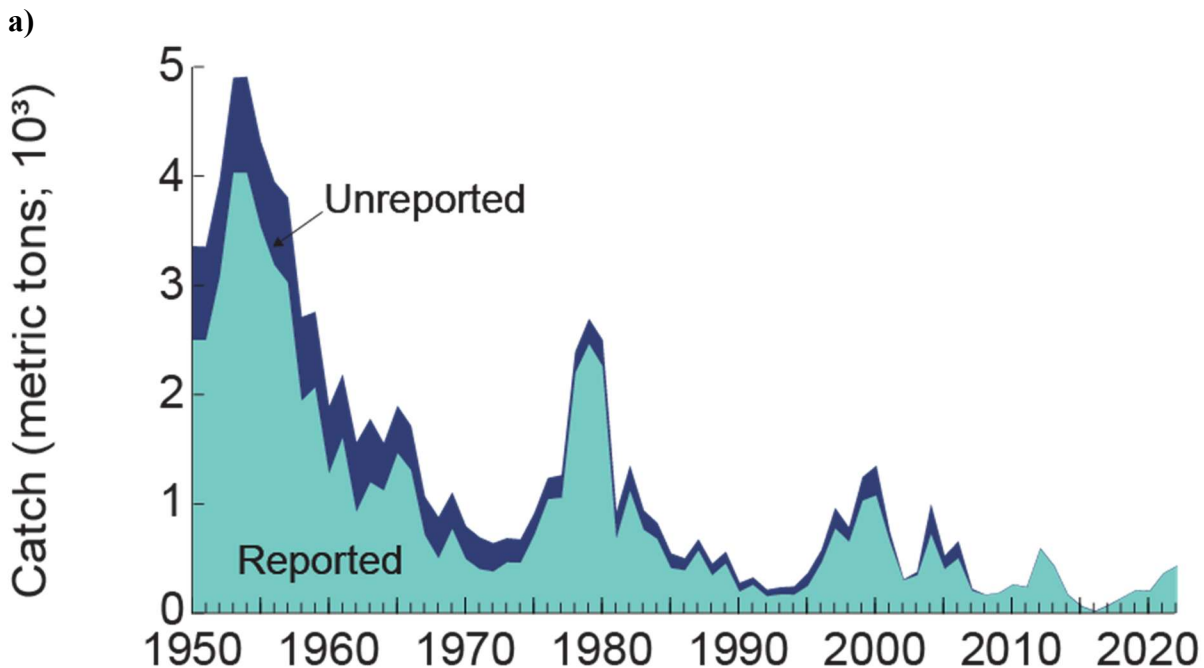
Artisanal discards were distinctively more variable than landings, as only two species were reported to have discards associated to their artisanal fishery: capelin and lumpfish. Artisanal discards were estimated to have experienced two major peaks in 2000 and 2004, of respectively 268 and 266 tonnes, separated by a sharp decrease in 2002 with only 3.5 tonnes of artisanal catch discarded at sea. These peaks correspond to peaks in lumpfish landings, as only females were

landed and males discarded at sea. Artisanal discards significantly decreased after 2007, being close to none today.

3.3.2.3 Bait

Four taxa were caught to be used as bait for the artisanal fisheries: capelin, waved whelk, softshell clam and shortfin squid. Capelin represents 39% of the total amount of bait needed from 1950 to 1992, waved whelk 22%, softshell clam 21% and shortfin squid 18%.

The amounts of bait required for the cod artisanal fishery decline steadily from 1950 to 1992, where no more bait was estimated to be caught as artisanal boats stopped targeting cod. Total amounts of bait were around 860 tonnes per year in the 1950s, declining to 460 in the 1960s, 230 in the 1970s, 140 in the 1980s until reaching a low 50 tonnes in the 1990s.



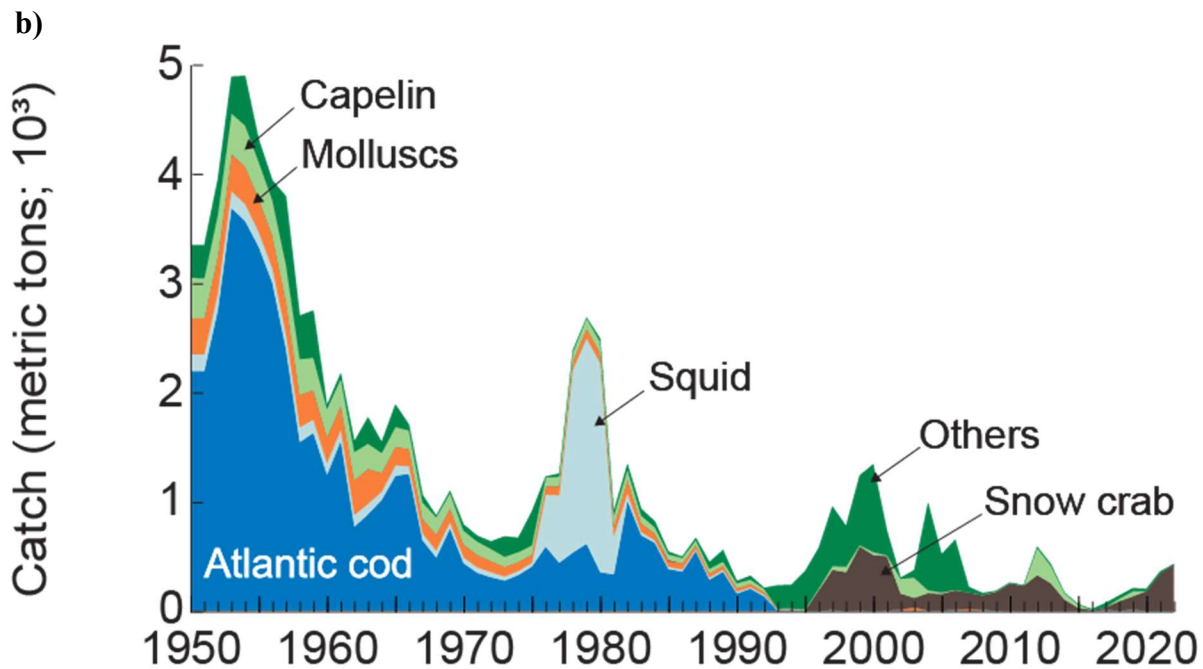


Figure 3.6. Reconstructed artisanal catch of the SPM fleet inside the SPM EEZ from 1950 to 2022, a) by reporting status and b) by taxa. ‘Others’ include 11 additional taxa.

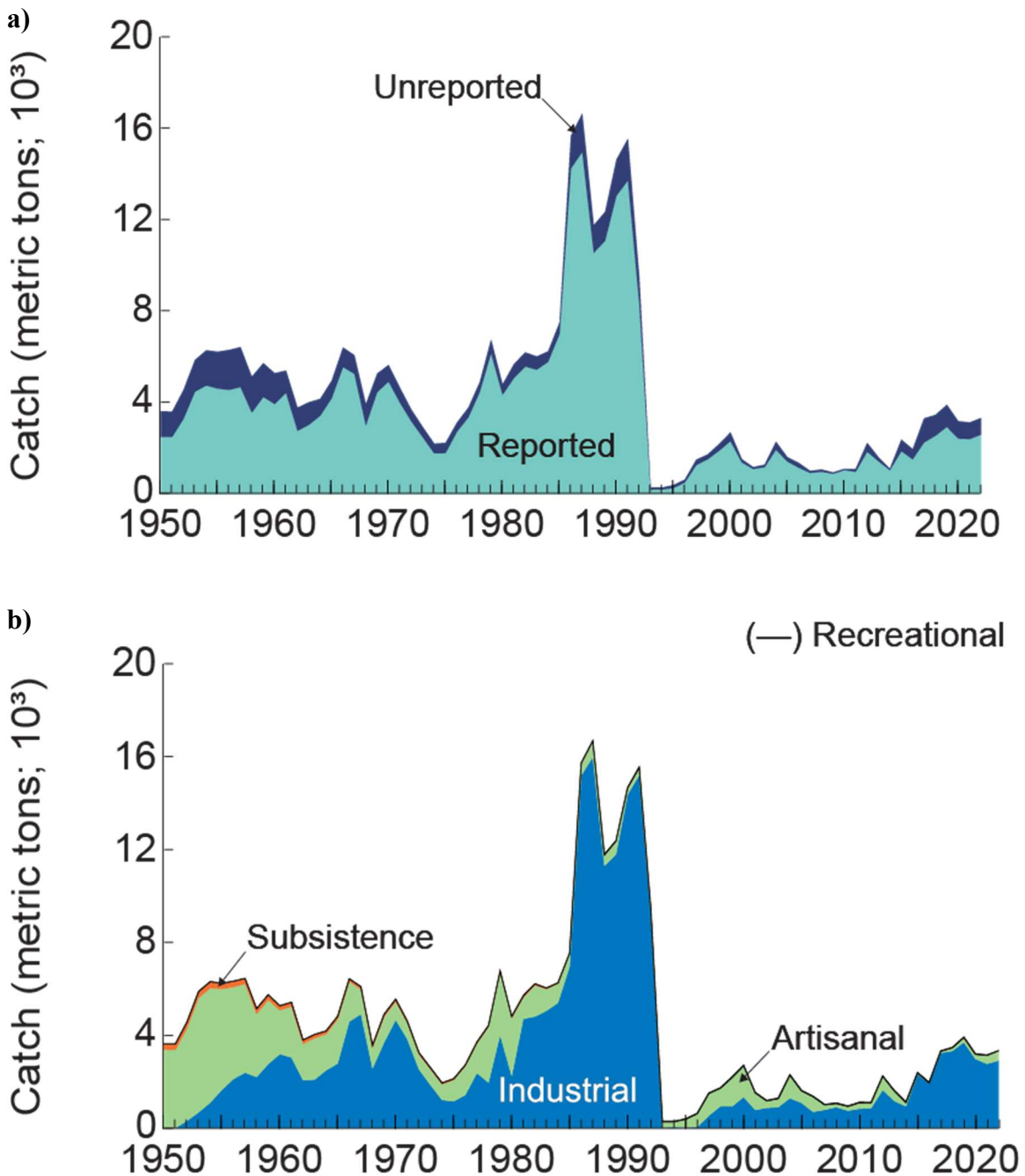
3.3.3 Subsistence catch

Subsistence catch was highest in the 1950s, with an average of 250 tonnes caught per year, then declined steadily until the 1990s where it was around 15 tonnes per year, with the exception of a slight peak between 1977 and 1982 (Figure 3.8). As most subsistence catch was derived from artisanal catch kept by the fishers instead of being landed, subsistence catch was shown to considerably decrease after 1992, following the collapse of the artisanal fleet. The main species caught for subsistence was cod (75%), followed by capelin (8%). Unidentified fish species made up 12% of the total subsistence catch, while the remaining 5% were split between skates, Atlantic mackerel, shortfin squid, American plaice, dogfish, lumpfish, mussels, American lobster, Atlantic salmon and snow crab.

3.3.4 Recreational catch

Recreational catch has been more or less constant throughout the years, and targets two species for which recreational licenses are issued: Atlantic salmon and American lobster.

American lobster recreational catch started in 1987 and experienced a sharp increase from 1987 to 1992, after which it stayed almost constant at around 15 tonnes per year. Atlantic salmon recreational catch has also been almost constant from 1987 to 2022, oscillating around 1.2 tonnes caught per year, with the exception of two peaks of 3 and 3.8 tonnes in 2013 and 2016. Total subsistence catch was a minimum of 3.3 tonnes in 1987 and a maximum of 18.6 tonnes in 2016.



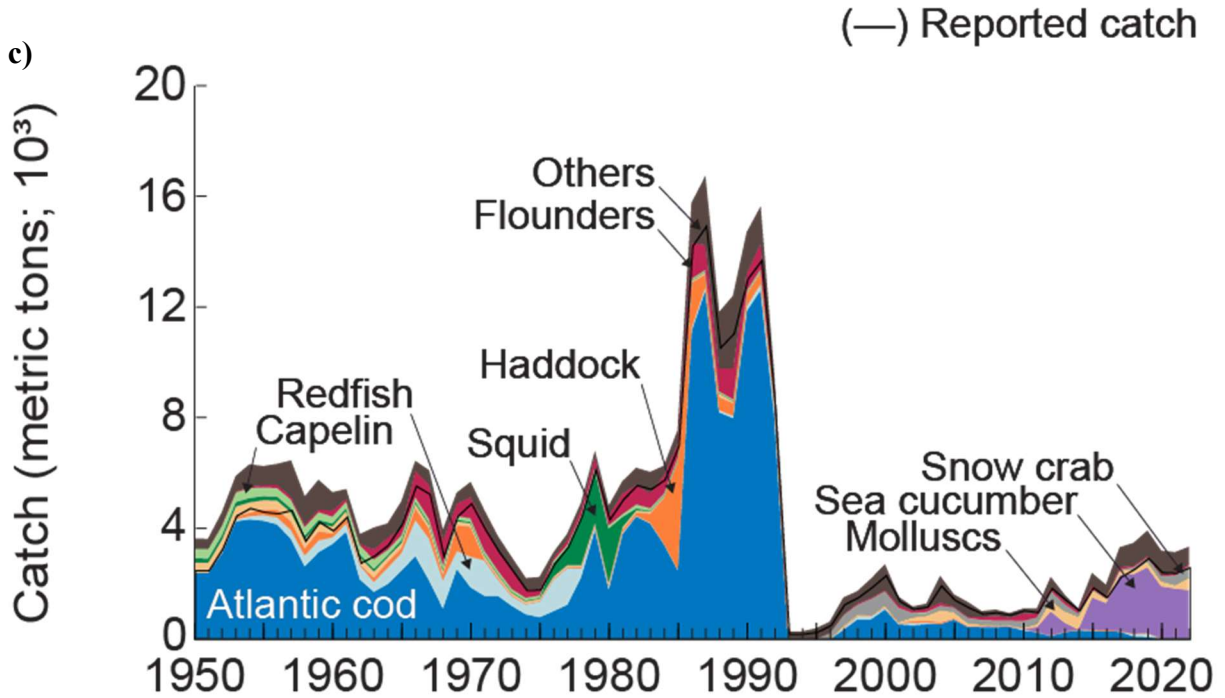


Figure 3.7. Total reconstructed catch of the SPM fleet within the SPM EEZ, from 1950 to 2022, a) by reporting status, b) by sector and c) by taxa. Total catch includes landings and discards. Recreational catch is represented by a black line on the graph. ‘Others’ include 28 other taxa.

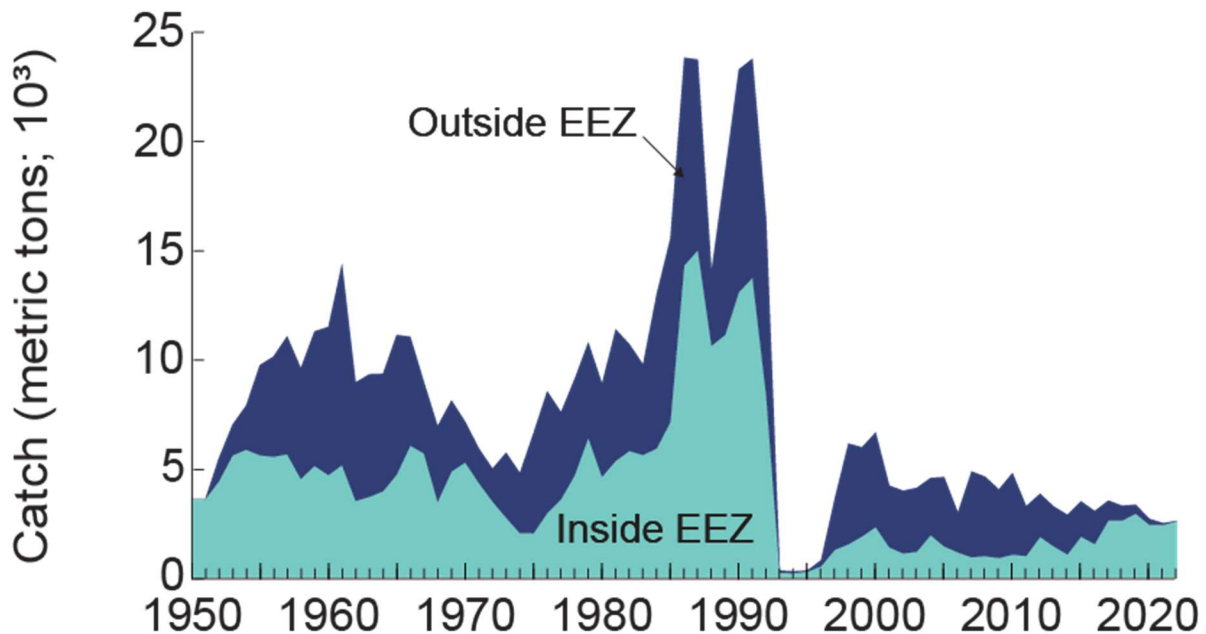


Figure 3.8. Total landings by SPM inside and outside of the SPM EEZ from 1950 to 2022. All landings from the four fishing sectors (industrial, artisanal, recreational and subsistence) are included.

3.3.5 Mean trophic level of the catch

The mean trophic level of the species making up the catch inside the SPM EEZ, and the total catch inside and outside the EEZ, have been declining since the 2000s, following a previously sharp decline matching with the 1992 cod collapse (Figure 3.9). Mean trophic level was highest in 1990, at 4.08 over all catches and 4.06 for catches exclusively inside the EEZ, and lowest in 2022, at 2.38 both over all catches and for catches exclusively inside the EEZ.

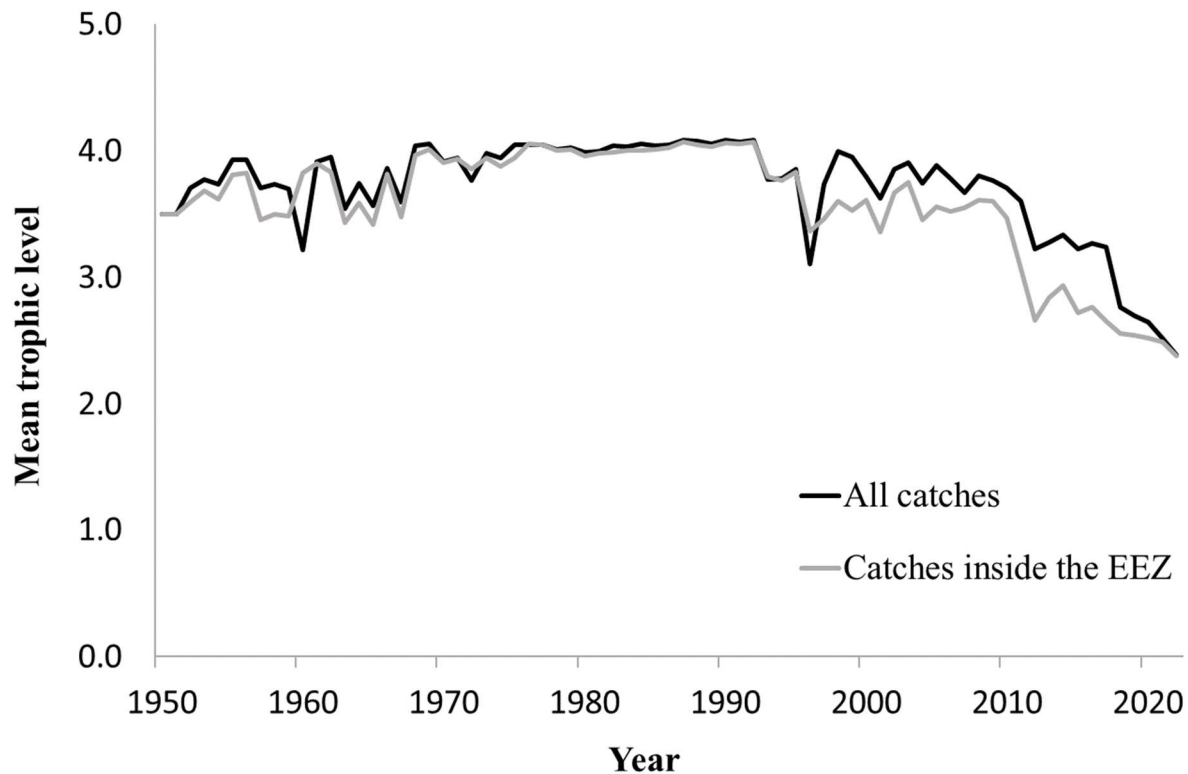


Figure 3.9. Mean trophic level of the species caught by SPM fleets from 1950 to 2022. The black line represents all catches within and outside the EEZ, while the grey line shows catches exclusively inside the EEZ.

3.3.6 Mean temperature of the catch

The mean temperature of the catch (in degrees Celsius) by SPM fleet inside the SPM EEZ, has been more-or-less constant between 1950-2004, succeeded by a sharp decline between 2004 and 2022 (Figure 3.10). When sea cucumber, which has dominated the catch since the late 2000s, is

excluded, the breakpoint and subsequent sharp decline in the trend disappear, revealing instead a gradual decline in mean catch temperature over the full period (Figure 3.10).

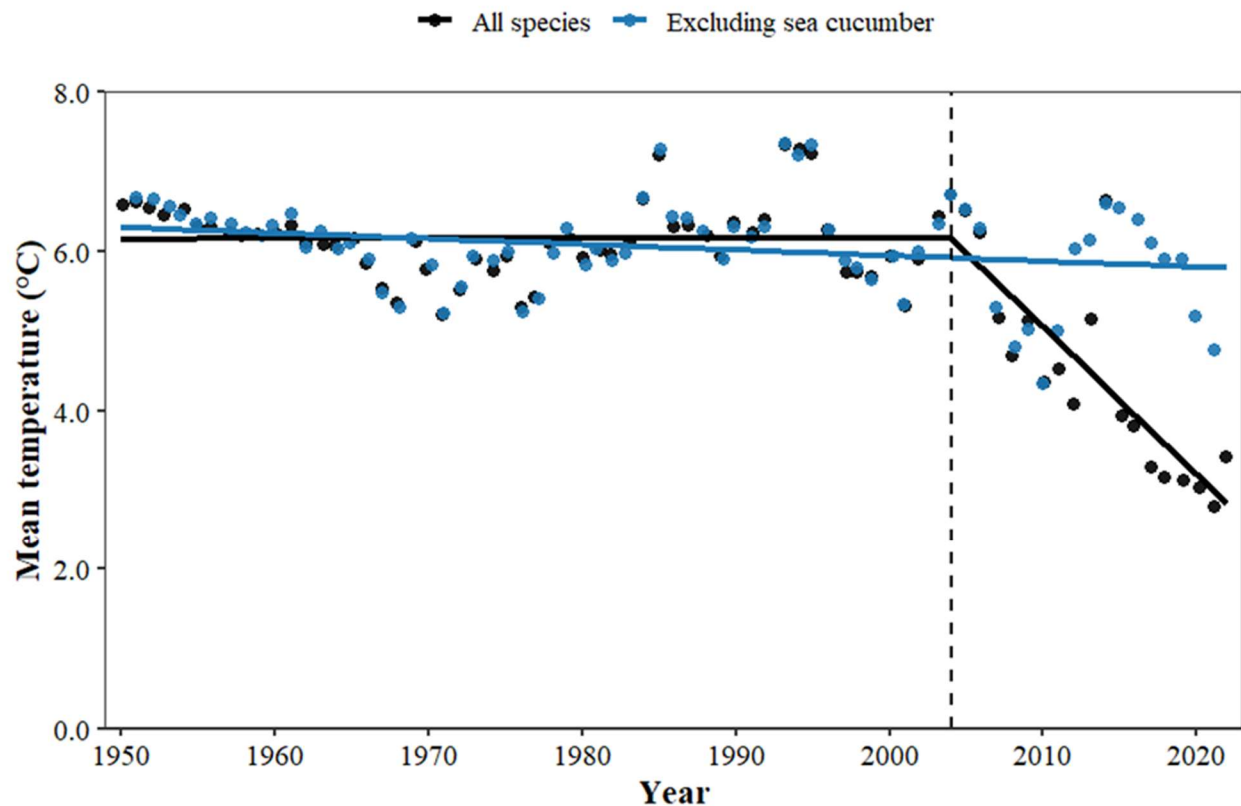


Figure 3.10. Mean temperature of the catch by SPM fleets from 1950 to 2022 inside the SPM EEZ. The black series includes all species caught by SPM fleets, whereas the blue series is adjusted to exclude sea cucumbers from the catch. The dash line represents the breakpoint in the mean temperature of the catch trend.

3.4 Discussion

This study showed an attempt at reconstructing the total amounts of seafood caught by Saint Pierre and Miquelon's fleets between 1950 and 2022, in their home EEZ as well as in the surrounding Eastern Canada EEZ. Total catches by SPM boats were estimated to be 1.2 times higher than the reported catch. In SPM's EEZ, reconstructed catches were as well 1.2 times higher than the reported catch. The unreported catch was mainly made up of domestic industrial discards in and outside of the home EEZ. In the 1950s-1960s, amounts of fish and seafood caught to bait the lines in the cod and groundfish fisheries constituted another significant part of the unreported

data. While subsistence and recreational fishing were small in SPM, they also contributed to the total seafood amounts that were not reported to official reporting bodies. In the home EEZ, unreported industrial catch represents 52.5% of the total unreported catch, unreported artisanal catch 36.5%, unreported subsistence catch 10%, and unreported recreational catch 1%.

3.4.1 Trends in catches from 1950 to 2022

Total catches inside and outside the home EEZ follow similar trends overall, categorized by a steady increase in the 1950s and 1960s, followed by a decrease in the mid-1970s and a sharp increase leading to peaking catches in the 1980s. This increase in the 1950s is due to the introduction of trawlers in SPM, replacing the formerly used schooners and promoting the rise of the industrial fishery sector. Historically, this period corresponds to a post-WWII country experiencing the new worldwide economic expansion commonly referred to as the *Trente Glorieuses* (i.e., ‘thirty glorious years’) in France. This expansion stretched until the mid-1970s and gave rise to major progress in technological advancement and mechanization across industries, resulting in increased industrial production and a rising gross domestic product (Allaya and Rucheton, 2008; Fourastié, 2014). In the fishing industry, this economic boom manifested through the development of freezer fishing trawlers, responding to the increased demand for fish and seafood. Trawlers – and particularly bottom-trawlers targeting groundfish by dragging large nets along the seabed – capable of exploiting soaring quantities of fish farther offshore were central to the expansion of fisheries. They prompted a rise in fishing effort and total catches, and with them the increase of bycatch and proportionally discarded seafood in the Northwest Atlantic (Pauly, 2002; Clark et al., 2015; Zeller et al., 2017).

The expansion of industrial trawlers persisted through the 1980s, with an increase in the subsidies allocated to the fishing industry by the French government, an incentive for fleet expansion, and a surging fishing effort (Wilson and Le Floch, 2016; Sumaila et al., 2019). By partly covering fuel costs and equipment, these subsidies decreased operational costs for the SPM fleets, foreshadowing a rise in profit for higher amounts of fish caught (Sumaila and Pauly, 2006; Wilson and Le Floch, 2016). Supplementary financial incentives were given to promote the hiring of additional fishers and to reward higher landings, contributing to the growing fishing effort in the 1980s. Subsidies applied to the artisanal sector as well, as small-scale fishers received bonuses

for those who would bring the highest tonnage of fish back to port (Wilson and Le Floch, 2016; M. Derible, local historian, 2024, personal communication). The surge in effort is reflected in the sharp increase in catches, as shown by the catch peak from 1985 to 1992, which was the highest throughout the entire study period. This peak can also be partly attributed to the extension of Canada's Exclusive Fishing Zone coupled with the Foreign Vessel Fishing Regulations in 1977, which prompted in the following years the reduced exploitation of local stocks by foreign vessels and an increase in stock access for SPM (Symmons, 1980). With this increased effort, stocks such as the Atlantic cod stock already overexploited were exposed to major pressure, which contributed to accelerating their depletion.

The development of industrial fisheries by all fishing nations in the Northwest Atlantic prompted an overfishing crisis leading to the severe depletion of cod stocks, and to related diplomatic disputes between France and Canada for fishing rights and access to stocks in the Northwest Atlantic (Marston, 1993; McDorman, 1994; Bavington, 2010). The year 1992 marked a turning point for the fisheries in SPM, with both the implementation of the Northwest Atlantic cod moratorium and the inception of an official EEZ with a surface area reduced by a factor of four from what France had originally claimed. This formerly claimed area was, however, not based upon international political agreement, and did not constitute a zone with formal exclusive fishing rights (with the exception of the 12 miles of "territorial waters") (Forest, 2022). Following the moratorium, quotas management strategies were adopted in 1994 (d'Aboville, 2007), laying the foundation for the relative rebound of the industrial sector in the late 1990s and almost steady industrial catches up to 2022.

While artisanal catches from 1950 to 2022 show an overall decreasing tendency, it is mainly marked by a "collapse" of the artisanal fisheries in 1992 following the cod moratorium, and the disappearance of doris as boats used in the artisanal sector (F. Teletchea, University of Lorraine, October 2024, personal communication). SPM was an archipelago relying on cod fished artisanally for decades before the introduction of the first trawlers, but the rise of a new industrial fleet shifted the trends. While most cod was caught industrially starting in 1952, artisanal boats continued to operate consistently until 1992. The new increase in artisanal fisheries in the early 2000s is categorized by mostly marine invertebrates (large crustaceans and molluscs) and to lumpfish, exploited for its roe.

This reconstruction allowed a more comprehensive understanding of fisheries spatial trends for shared stocks between SPM and Canada. While catches were substantially higher inside the home EEZ during the “golden age” of cod fisheries, the new increase in catches starting at the end of the 1990s throughout the 2020s shows a different tendency, with industrial catches being almost two times higher outside of the home EEZ than inside. These trends are due not only to the reduction in size of the EEZ, but also to the way quotas were allocated between SPM and Canada following a bilateral agreement signed in 1994 (d’Aboville, 2007). This agreement established joint Total Allowable Catches (TACs) in different NAFO divisions and subdivisions of which SPM has access to a certain percentage. Only five species have allocated quotas that are exclusively managed within the home EEZ since 1987, four of which are marine invertebrates. When looking at the 3Ps subdivision in which the SPM EEZ is located, joint TACs have been established for six commercially exploited groups: four of these groups have quotas of less than 15% of the TAC, and two of less than 5% (deBeauregard, 2013, Vigneau et al., 2013). Overall, the fractions of TACs granted to SPM are very small.

Reduced access to finfish quotas implies fewer opportunities to target high-value commercial fish species like cod and halibut, and lower economic return for local fisheries (Poos et al., 2010). This explains the strong historical declines in the economic value and efforts of the fishing industry in SPM, leading to a fishing sector weighing much less in the local economy today, and involving a much smaller fraction of the population (Wilson and Le Floc’h, 2016). As an archipelago with a significant portion of its fishing industry reliant on international exports, smaller quotas may hinder SPM's ability to compete with dominant fishing powers in the global seafood trade. Ultimately, a reduced share in TACs limits the growth potential of the fishing industry (Vigneau et al., 2013; Wilson and Le Floc’h, 2016).

3.4.2 The strength and limitations of reconstruction methods

Assessing major trends in different fisheries sectors, for different target species and different years is made possible through the methods of catch reconstructions. This aligns with the concerns on accounting with more precision for what is caught by whom to inform sustainable fisheries measures: the only way to paint a comprehensive historical portrait of local fisheries is to include all sectors and actors, including small-scale sectors that usually go ignored by official

reporting bodies (Pauly and Zeller, 2016). Despite some having minimal weight in comparison to the amplitude of industrial fisheries, sectors' contribution to the total catch has to weigh in for properly informed fisheries management efforts (Tesfamichael and Pauly, 2011). On top of this, describing the fisheries with additional layers of precision allows us to create a baseline that can be used for foregoing assessment of the impact and future of SPM's fisheries.

In spite of promoting greater accuracy in catch assessments, fisheries reconstructions have several limitations that prevent us from confidently asserting they are a fully accurate depiction of reality. One shows through the formal definition of fishing sectors: according to the *Sea Around Us* nomenclature standards, while both artisanal and industrial sectors have commercial outcomes whether on a local or larger scale, what sets the sector apart is mostly the gear amplitude, with larger vessels and more invasive fishing techniques such as trawling being characteristic of the industrial sector (Pauly and Zeller, 2016). In SPM, sector definition does not rest on this basis. Rather, it is established by vessel size, and both artisanal and industrial sectors defined according to SPM national standards are using trawling methods (Wilson and Le Floc'h, 2016). Nationally classifying trawling as an artisanal method conflicts with the defined scope and characteristics of the artisanal sector, which is considered in reconstruction guidelines to be limited to the inshore fishing area of a country (Pauly and Zeller, 2016). As a result, no formal distinction exists between small wooden boats fishing with handlines and larger vessels (up to 35 meters long) using pelagic or bottom trawls, and therefore having a much greater impact on the ecosystem. Moreover, it can create discrepancies in the data used to disaggregate catch by sector in a reconstruction. Creating this distinction is essential for comprehensive frameworks to implement ecosystem-based management measures.

Nonetheless, we can confidently argue that reconstructions are more accurate than official reports can be, by providing a picture far more detailed and comprehensive of the behavior of local fisheries. Limitations and sources of uncertainty are usually communicated through the reliability scores attributed to the data for periods of five years, for every sector. Based on evidence and agreement, these scores help assess the confidence of the data sources used in estimating historical and present trends (Zeller et al., 2016). In SPM, sources of uncertainty arise mostly when trying to quantify components of the fisheries that are poorly documented or assessed, such as discards and bait caught for the artisanal fisheries, as explored in the following sections of this chapter.

3.4.3 A challenge in fisheries: assessing and limiting discards

The rise of industrial fisheries in SPM and the persistence of trawlers as preferred fishing vessels led to large quantities of fish caught as bycatch. Bycatch arises mostly when fishing gear is poorly selective or highly destructive (e.g., bottom trawlers) (Jenkins and Garrison, 2013). For an archipelago like SPM targeting mainly one high-value species (here, cod), most bycatch had little commercial value and was discarded. Individuals of a target species of a sub-legal size in quota-managed fisheries constitute another important component of discards (Morizur et al., 1998). Discard mortality rates vary upon individual condition before release, and are species-specific: they tend to be higher for groundfish and lower for shellfish, such as lobsters and scallops (Benoit et al., 2012; Rudders et al., 2017; Mérillet et al., 2018). Benoit et al. (2012) estimated that discarded cod had a 5% average short-term survival rate in 1991-1992, and that this rate became higher in the 2000s (around 30% average) when fishing effort decreased following the moratorium. Nonetheless, a major portion of discarded fish does not survive, which justifies the concern to push for fishery practices minimizing discards (Bellido et al., 2011).

Quantifying discards remains a major challenge in catch reconstructions, mainly due to the scarcity of discard reports and the bias that calculating discards based on observer studies can represent. Indeed, studies have shown that despite being highly valuable sources of data, at-sea observer surveys tend to underestimate discards as fisher's behavior changes when observers are present on board (Liggins et al., 1997; Benoit and Allard, 2009). Furthermore, if estimating total quantities discarded is already challenging, identifying species discarded and species-specific rates of discard is even more complex (Benoît et al., 2012). Discards are still poorly monitored in many fisheries, or there are significant gaps in monitoring that make obtaining comprehensive and high-confidence discard reports difficult (Gavaris, 2010). Ultimately, it is challenging to accurately estimate which species are discarded in SPM and the magnitude of impacts on the ecosystem these discards represent, but we can infer from neighboring fisheries like the Newfoundland groundfish fisheries.

On top of increasing fishing impacts on marine populations, discards become an issue when management measures and quotas are structured in a way that forces fishers to discard portions of their catch that exceed the established limits (Turner, 1997). For a small archipelago like SPM, excess quantities discarded may appear minimal when compared to larger regions, but still

represented lost income for local fishers, particularly during the ‘golden age’ of the cod fisheries. Discarded quantities of sub-legal size or juvenile individuals that do not survive represent lost income for future-year fisheries, lost food sources, but also contribute to exacerbating the resource’s depletion rate (Morizur et al., 1998; Harrington et al., 2005; Heath et al., 2014). Lost economic value per fish matters more in a small quota system: fish discarded represent wasted economic opportunities, which has a stronger impact in a small archipelago lacking economic buffers (Turner, 1997; Harrington et al., 2005).

In a small EEZ such as SPM, localized discards may have a greater ecological impact as fish populations and local stocks, especially of marine invertebrates with a slow growth rate, have less space and fewer resources to recover within the EEZ (Alverson et al., 1994; Kaiser and DeGroot, 2000). Even small quantities of fish discarded, whether bycatch or sub-legal individuals, could alter predator-prey dynamics in the ecosystem, especially when undersized juveniles are making up most of the discarded catch, jeopardizing future population growth and stock recovery (Kaiser and DeGroot, 2000; Harrington et al., 2005). Since SPM already operates under tight quotas, reducing stock resilience and local replenishment could lead to further economic depletion and stricter fishing limits in shared stocks in the long term (Grafton et al., 2023). This is further impacted by the data gaps that discard unaccounted for create in fisheries assessments. Discarded juvenile fishes not counted in models can lead to the miscalculation of recruitment rates. Conservation measures and population stock assessments rely on the accuracy of mortality estimates to be effective and account for necessary adjustments (Morizur et al., 1998; Sharma et al., 2019). Complete data is essential in a small EEZ like SPM as there is less room for uncertainty and errors in management decisions. Contingently, a record of minimal discards and sustainable fishing practices could favor SPM in the negotiations for quota allocations, as shown in cases of responsible fisheries management (Cochrane, 2002).

3.4.4 Other sources of unreported data: the mystery around bait

Besides discards, amounts of fish caught as bait in SPM’s artisanal fisheries are also unaccounted for in official reports. Interestingly, bait seems to be easily omitted from reconstructions despite the enormous quantities required, especially for countries or territories where a single fishery plays a dominant role in the economy, as was the case with SPM in the past.

This can be largely attributed to the challenges of accurately quantifying bait catches. Since bait is typically not landed or reported as a distinct catch, but instead used immediately within the fishery, its true volume remains difficult to assess. This issue is especially prevalent in fisheries relying on locally-caught bait, as opposed to imported sources. The omission of bait from both official reports and reconstructed data contributes to the significant underestimation of the total fishing effort and depletion of resources in the ecosystem, which can lead to misinformed management decisions (Anticamara et al., 2011).

In SPM, most bait used in the cod artisanal fishery was made of small molluscs and small forage fish. Bivalves used as bait were mostly fished in the Grand Barachois (Ancellin, 1955), which led to the severe depletion of bivalves in the lagoon. Bivalves decline have severe consequences on the water turbidity and quality, and leads to ecosystem disruptions. As filter feeders, small bivalves contribute greatly to the biofiltration of nutrients in the ecosystem, further contributing to nutrient cycling and water clarity (Murphy and Kremer, 1985; Vaughn and Hoellein, 2018). Consequently, studies have shown that bivalves play an active role in the bioremediation of chemicals entering the water system (Dame and Kenneth, 2011; Vaughn and Hoellein, 2018).

As another species used as bait, the large quantities of capelin caught and unaccounted for in official reports contributed to the depletion of a forage species that used to have a central role in local fisheries and local culture (Dumont and Provost, 2008; Buren et al., 2014), without management strategies taking into account accurate fishing mortality data. Capelin's central role in the Northwest Atlantic ecosystem as a forage fish linking producers to large consumers at higher trophic levels was greatly triggered by extensive and continuous overfishing, particularly during the 1970-1990s (Montevecchi et al., 2007; Buren et al., 2014). Reducing the populations of forage species jeopardizes stable ecosystem functioning, and puts at risk the entire predator-prey dynamics of the food web, potentially leading to further reductions in prey density (Mills et al., 1993).

3.4.5 Fishing down the marine food web in SPM

Large-scale depletions of fish populations through overfishing have been widely observed across the world's fishing nations since the 1950s, translating into an overall decline of the world's

fisheries (Pauly and Zeller, 2016). While the population's demand for fish and seafood it is still high, many stocks have been fished to unsustainable levels and the demand cannot be met (Iudicello et al., 2012). The 1992 cod collapse historically reflected the imbalance between demand and availability, ultimately leading to stocks reaching critical depletion states. While the cod fisheries slowly emerged again in the 2000s, SPM will likely never be able to rely on cod the way it used to, and the quotas allocated for local fisheries are very low nowadays. Multiple larger fish stock depletions, among which was cod, the most fished species of the Northwest Atlantic (Morgan et al., 2016; Schijns et al., 2021), led to a shift in the trophic level (TL) of species targeted by SPM fisheries. Where cod, haddock, and redfish used to make up the greatest part of the catch, local fisheries rely today on species such as sea cucumber, snow crab, and scallops. Fishing marine macroinvertebrates is not new: the shortfin squid fishery was predominant in SPM's artisanal sector through the years (Ancellin, 1955). But SPM fisheries are today disproportionately reliant on invertebrate species. This shift from higher trophic levels (cod TL = 3.6-4.4, haddock TL = 3.7-4.2) to lower trophic levels (sea cucumber TL = 2.0-2.7, sea scallop TL = 2-2.1) (Froese and Pauly, 2010) is a prime example of Pauly et al.'s (1998) concept of fishing down the marine food web, stating an obvious decline in the mean trophic level of species targeted by global fisheries from the 1950s to the near present. Generally, 'fishing down the marine food web' threatens ecosystem resiliency by disrupting food web dynamics through the removal of predators, causing cascading effects on the rest of the food web and weakening the resilience of ecosystems (Pauly et al., 1998; Pauly and Palomares, 2001; Pauly, 2006).

Palomares and Pauly (2022) emphasized that this shift in SPM concerns species that have high commercial value but whose stocks are less abundant. This not only reflects unsustainable fishing practices where stocks of higher trophic level species have been overfished, but will prove to be unsustainable as extended fishing effort due to high economic yield can push these less abundant and lower trophic level stocks to further decline (Pauly et al., 1998). Moreover, fishing practices targeting invertebrates such as sea cucumbers are more destructive of the seafloor, with the use of bottom trawling methods threatening benthic communities and habitat structure (Pauly, 2006). Directing fishing effort toward species at the bottom of the food web, which are responsible for essential transfers of primary production to higher trophic levels, can have significant bottom-

up impacts on the ecosystem and its services, another invertebrate fisheries trade-off local management systems need to consider (Smith et al., 2011).

With a constrained and irregular EEZ surface area, coupled with the occasional absence of migratory stocks within its waters, SPM has limited space to bounce back from historical stock depletions and target diverse species in their fisheries (deBeauregard, 2013). Fishing down the marine food web is prone to happen with limited stock access. The resulting fisheries relying mostly on invertebrates tend to be unstable both ecologically and economically (Caddy and Seijo, 2005; Foley, 2013). With increased effort redirected to invertebrate species, pressure on their stocks increases, which has been proven to lead to stock overexploitation and potential collapse in Holothuroidea species (Eriksson et al., 2010; Anderson et al., 2011; Purcell et al., 2016). SPM faces the threat of significant economic challenges if these invertebrate stocks were to decline due to environmental pressures or overfishing (Perry et al., 1999).

SPM has recently been manifesting a renewed interest in the fisheries of Atlantic halibut (*Hippoglossus hippoglossus*; TL = 4.0; F. Teletchea, University of Lorraine, February 2025, personal communication; Froese and Pauly, 2010). At the end of 2024, a share of the Atlantic halibut TAC between Canada and SPM was agreed upon. If this share is very small, it is expected to promote the growth of SPM's halibut fishery (Paturel, 2024). It allows SPM to fish halibut in both their EEZ and the high seas, but not in the Eastern Canada's EEZ (DFO, 2024a). As the Northwest Atlantic stock of *H. hippoglossus* distributed over NAFO 3NOPs, 4VWX and 5Zc used to be under independent management by Canada and by SPM, like the sea cucumber stock in 3Ps (DFO, 2024b), this new development promises joint management between both parties. The stock has been increasing since the 2000s, and its spatial occurrence within the SPM range is projected to increase with increasing ocean temperatures (Boudreau et al., 2017; Czich et al., 2023). This developing fishery could be economically promising and help temper the ongoing shift to lower trophic-level species fisheries if managed sustainably.

3.4.6 Catching fish at colder temperatures

Reconstructed fisheries data additionally allowed to contextualize SPM within the broader framework of global warming and its influence on the distribution of fish and invertebrates, through the estimation of the mean temperature of the catch (MTC) by SPM fleets from 1950 to

2022. The MTC index was reported by Cheung *et al.* (2013) as a measure of the evolution of the preferred temperature of exploited species in a warming ocean. It highlights increases in the MTC of non-tropical areas, and general stabilization around the tropics, as a result of species moving poleward in relation to changes in sea surface temperatures (Cheung *et al.*, 2013). These increases have been observed around the world in both marine and freshwater habitats (Cheung *et al.*, 2013; Tsikliras *et al.*, 2015; Kangur *et al.*, 2021).

SPM presents a trend that differs from the rule established by Cheung *et al.* (2013), where MTC increases slightly until 2004, then presents a sharp decline. A similar ‘peculiar case’ has been observed in the Arabian-Persian Gulf, where the sharp decline in recent years was attributed to the increased and disproportioned effort on *Trichurus lepturus* (Alajmi *et al.*, 2023). However, when removing sea cucumber from SPM catches in an attempt of verifying of the observed decline in MTC could be attributed to the species for which effort has been in strong increase since 2008, the MTC still shows a slight decline over the time period. We can hypothesize that such exception to the rule would pertain to the fishery having gradually shifted to increased depths of exploitation, i.e., deep-sea species with a colder preferred temperature, and that this decline is linked to SPM being rather isolated, where fishes shifting poleward would not have yet reached the archipelago.

3.5 Conclusion

Reconstructing the catch of a small EEZ like SPM reveals the issues that reporting bodies not accounting for the whole picture bring to various areas of management including stock assessment, recruitment calculations, stock rebuilding measures, and effective sustainable fishing strategies. Fishing mortality unaccounted for through bait and discards being unreported greatly influences the way management measures can be effective in ensuring stock resiliency and populations’ natural replenishment, and hinders efforts to implement effective conservation strategies and resource allocations. This is why catch reconstructions are essential to produce data with increased accuracy that can then be used in comprehensive fisheries management plans. Small archipelagos with restricted shares in quotas and restricted exclusive fishing areas like SPM have fewer economic buffers and less room for errors in management decisions, underlying the strong need for management strategies that will consider all facets of local fisheries and their respective impact on ecosystem dynamics and resilience. The lack of transparency around bait fisheries and

discarded catch undermines the accurate and historical representation of local economic dependence on these practices, and how important they are – or have been – to local livelihoods.

This reconstruction supports the hypothesis that including unreported estimates of different fisheries sectors accounts for a higher tonnage caught by SPM from 1950 to 2022 than the reported baseline catch. Several uncertainties still surround some fishing sectors in SPM, such as the recreational fisheries catch and seafood amounts caught as subsistence, as a result of the lack of clear reporting rules. As catch reconstructions are an iterative process, further work will be needed to assess the extent of these sectors, with further uncovered information or with the help of new management strategies. Finally, the shift towards invertebrate species in recent years' fisheries illustrates the 'fishing down' phenomenon. If not comprehensively managed in consideration of the lower resilience of invertebrate species like sea cucumbers, these lower-trophic level fisheries will likely be unsustainable for the local economy and the SPM marine ecosystem.

Chapter 4: Ecopath with Ecosim modelling of the marine ecosystem surrounding Saint Pierre and Miquelon

4.1 Introduction

Complex marine ecosystems are characterized by an interplay of predator-prey relationships between different producers and consumers in the system, and a variety of behavioral and community patterns. Seasonal fluctuations in primary productivity influence abundance and vertical stratification of zooplankton, in turn determining temporal and spatial availability of food for secondary consumers, thus grouping and migration patterns. Abundance, distribution and feeding of preys influence predator abundance, distribution and feeding; and reciprocally. Predators' patterns and predation vulnerability define foraging behavior in preys in a way that optimizes both growth and survival chances (Ahrens *et al.*, 2011).

Where conservation planning and fisheries management used to be conducted using a single-species approach, the focus has shifted to a multi-species approach today defined as ecosystem-based management (EBFM) (Pikitch *et al.*, 2004). This approach reflects the desire to align with sustainability concerns in fisheries, and optimize ecological resilience for the persistence of exploitable stocks (Link, 2010). Managing a fishery within an ecosystem-based framework requires more than focusing on the target species alone. It involves, inter alia, assessing how the incidental capture of non-target species by this fishery affects the abundance and dynamics of other functional groups in the ecosystem. It also requires evaluating how the removal of the target species alters predator-prey relationships in the system, potentially affecting food web stability, and how fishing pressure may affect ecosystem resilience. Additionally, it takes into consideration how shifts in environmental parameters may affect species in the system, and thus certain fisheries (FAO, 2008).

4.1.1 Background and rationale for ecosystem modeling

Ecosystem models, developed as a complementary tool to single species models, include environmental factors and interactions at multiple levels within the ecosystem. They incorporate population dynamics and predator-prey relationships, but also a variety of biological, ecological

and economic variables. This added complexity allows to apprehend fisheries management within its full ecosystem context, to improve conceptual understanding and inform policy decisions (FAO, 2008; Howell *et al.*, 2021).

Ecopath, then Ecopath with Ecosim (EwE), has been developed since the 1980s as an ecosystem modeling software for food web analysis, relying on the principle of mass balance, where the energy inputs must balance the energy outputs of each functional group in a system (Polovina, 1984; Christensen and Pauly, 1992). EwE has evolved into a suite of three main modules: Ecopath, which constructs a mass-balanced, static snapshot of an ecosystem's trophic structure; Ecosim, which simulates dynamic changes in biomass and trophic flows over time; and Ecospace, which adds spatial and temporal variability. An Ecopath model requires the input of several core parameters for each functional group, including biomass, production, consumption, diet composition, and catch, and runs a routine of linear equations to solve for missing parameters, ensure mass balance and produce a picture of the energy flows in the system (Christensen and Walters, 2004). Ecopath helps visualize these flows, the transfer efficiencies between functional groups, the omnivory index (i.e., measuring how broadly consumers feed across different trophic levels; Pauly *et al.*, 1987), as well as the trophic levels of each species or group in the system (Christensen and Walters, 2004). By incorporating fleet and catch data in Ecopath models, fishing pressure on different functional groups can be modelled, and the ecosystem impacts of fisheries can be quantified (Pauly *et al.*, 2000).

4.1.2 Ecopath and Ecosim as complementary tools

Where Ecopath provides a static snapshot of the ecosystem at a certain period of time, Ecosim was developed, using differential equations, to incorporate dynamic temporal components to the ecosystem models. Ecosim relies on the foraging arena theory, a concept developed by Dr. Carl Walters to render Lotka Volterra dynamics more realistic (Ahrens *et al.*, 2012). The foraging arena theory describes how preys move between vulnerability states, and is used to represent how predator prey interactions are limited by both ecological and behavioral factors, rather than assuming predators can instantly consume all available prey. The idea is that preys are not always equally vulnerable, as some adopt behaviors making them unavailable to predators at any given time (Ahrens *et al.*, 2012). By incorporating the foraging arena theory, Ecosim is able to capture

density-dependent dynamics without the unrealistically strong oscillations generated by Lotka-Volterra dynamics.

The model framework allows the inclusion of additional parameters to account for environmental variability, human induced pressures, as well as seasonal dynamics in food web structure and productivity. These inputs can be used to replicate historical patterns in key drivers, e.g., fishing mortality and fishing effort, thereby enhancing the model's realism and explanatory power. Incorporating such environmental and physical drivers also extends the model's utility beyond hindcasting. It enables scenario testing, allowing to explore the potential outcomes of alternative fishing strategies, management measures, and policy options on ecosystem structure and function (Pauly et al., 2000). Ecosim facilitates retrospective analysis of how past fishing activity has shaped biomass trends and community structure, and prospective analysis on how future fishing activity has the potential to do so.

4.1.3 Ecological context of the Saint Pierre Bank Ecosystem and SPM's fisheries

EwE is a highly relevant tool when looking at the historical evolution and trajectory of fishing practices in small-scale archipelagos strongly reliant on fisheries, like Saint Pierre and Miquelon (SPM). SPM is the only French overseas territory located in the Northwest Atlantic. About 25 km south of the Canadian province of Newfoundland-and-Labrador, SPM is located north on the Saint Pierre Bank, a 50 to 100 meters average depth continental shelf part of the productive and biodiverse Grand Banks of Newfoundland (Cermakian *et al.*, 1970; Ruiz Diaz *et al.*, 2024). SPM's marine ecosystem is driven by the interaction between two oceanographic regimes which strongly influence thermal stratification, and nutrient-rich upwelling over the Saint Pierre Bank: the cold Labrador current and warmer currents west of the Bank (Jutras *et al.*, 2003; Bridier *et al.*, 2021). These conditions generate a high primary production, which in turn plays a role in determining species distribution and seasonal migration patterns: high productivity leads to rich fish and invertebrate diversity, while the temperature and depth clines create a distinct separation in benthic and pelagic species assemblages (Macpherson, 2003; Colbourne and Murphy, 2008; Briggs and Bowen, 2013).

Saint Pierre Bank is an ecosystem that has undergone considerable change over the last six decades, as presented in the previous chapters: groundfish fisheries started increasing in the 1960s

to reach peaks in the 1980s, before strongly declining following the Atlantic cod (*Gadus morhua*) collapse in the Northwest Atlantic in 1992 (Bultel and Zylich, 2015; Forest, 2022). The rise in abundance of several seal species, including grey seals and harp seals, had substantial top-down effects on the marine food web (Hammill *et al.*, 2007; Hammill and Stenson, 2005). Subsequently, the system experienced an increase in invertebrate biomass, which manifests itself in the diet composition of multiple species now feeding largely on shrimps, crustaceans and other benthic invertebrates (Carscadden *et al.*, 2001). These changes are mainly the result of shifting and unstable fishing pressures over the years, and are interesting to examine from a multi-species perspective to understand the resulting impacts on predator–prey relationships and biomasses in the ecosystem.

Most fishing activity in SPM takes place on the Saint Pierre Bank. The Exclusive Economic Zone (EEZ) of SPM, unique in its position as an enclave of the Eastern Canadian EEZ (Figure 3.1; c.f. *Chapter 3: Reconstructing what SPM has caught from 1950 to 2022*), falls mostly within the North Atlantic Fisheries Organization (NAFO) management subdivision 3Ps, which covers the entire Saint Pierre Banks as well as parts of Burgeo Banks and Green Banks (Palomares and Pauly, 2022). NAFO Subdivision 3Ps is thus a focal area for modeling the Saint Pierre Bank ecosystem and assessing the historical and projected development of SPM fisheries.

As explored in *Chapter 2*, while both fish and invertebrate communities have been historically targeted by fisheries in SPM, notable shifts in mean trophic level exploited over time can be observed (Bultel and Zylich, 2015). Prior to the 1992 cod collapse in the Northwest Atlantic, following years of overexploitation and stock depletion, cod fisheries were the main source of revenue in SPM (Forest, 2022). Being also the year when SPM saw its EEZ be reduced to less than one-third the area originally claimed before the official EEZ arbitration, 1992 thus marked a turning point in SPM’s fishing history (Forest, 2022). In the following years, quota management measures were established between both countries, and SPM received a small share of Total Allowable Catches (TACs) in NAFO 3Ps (Forest, 2022; Teletchea, 2022). Once an archipelago thriving from cod fisheries, SPM experienced a multi fishery sector collapse that led to a severely impacted fishing industry, and altered local cultural identity and economy (Ancellin, 1955; Shjins, 2021).

Following this collapse, SPM's fisheries are today mostly relying on invertebrate species, notably sea cucumber (*Cucumaria frondosa*) and deep-sea scallop (*Placopecten magellanicus*), with a renewed interest for Atlantic halibut (*Hippoglossus hippoglossus*) fisheries, though it is still small (Teletchea, 2022). Such a shift is a prime example of fishing down the marine food-web (Pauly *et al.*, 1998), where a shift in fishing target to lower trophic-level species occurs when higher trophic-level species have been depleted in the system, as highlighted in *Chapter 2*. Further concern arises in the light of such practices for maintaining balanced predator-prey relationships within the ecosystem (Caddy and Seijo, 2005; Smith *et al.*, 2011; Foley, 2012). Exploring ecosystem dynamics under past, present and future exploitation through modeling allows for better understanding on trophic structure, and the implications of shifts in fishing pressures on the food web.

4.1.4 Chapter overview and research objectives

Where other NAFO subdivisions have been modeled using the EwE software in the years succeeding the cod collapse (Bundy *et al.*, 2000; Morissette *et al.*, 2003; Bundy, 2004; Tam and Bundy, 2019), the 3Ps subdivision remains understudied, with fewer assessments conducted within its boundaries. No NAFO 3PS EwE model has been constructed before, despite being the major fishing grounds of a small-scale and politically complex fishing region like SPM, facing challenges in sustainably managing its marine resources under changing environmental and fishing pressures (Teletchea, 2022). In this context subject to ongoing management discussions, this study aims to provide better understanding on how fishing activities and ecosystem structure in NAFO subdivision 3Ps (i.e., the sea around SPM) have changed over time, and how future fishing scenarios may affect key species and ecosystem dynamics.

This will be done first by building two descriptive Ecopath models of the 3Ps ecosystem in 1960-1965, when groundfish fisheries were expanding, and in 2000-2009, after the collapse of cod and the rise of invertebrates' fisheries. These snapshots provide mass-balance representations of the system at different periods where different fishing pressures operated, and allow the comparison of ecosystem structure between the two periods. Using these Ecopath models as a baseline, an Ecosim model will be built to examine how varying fishing effort scenarios may affect

biomass trends in NAFO 3Ps. Specifically, these model addresses the following research questions:

1. How did historical fishing effort by SPM and other fleets shape the biomass and trophic structure of the 3Ps ecosystem, and could further impact it?
2. What are the relative contributions of fishing and predation to the mortality of key species in each period?
3. How may exponential increases in fishing effort from SPM fleets affect the biomass of target species over time?
4. How can ecosystem modeling inform sustainable management policies for a small-scale fishing region like SPM?

These research questions build on the following hypotheses: (1) the 3Ps ecosystem experienced a decrease in mean trophic level and a simplification of food web interactions from 1960–1969 to 2000–2009, reflecting the effects of intense fishing and the cod collapse, (2) fishing mortality has decreased for most fished species between the two periods, except for commercial invertebrates species where it replaced predation as the dominant source of mortality, (3) increasing fishing effort from SPM dredge and longline fleets will reduce the biomass of their target species (sea cucumber, Atlantic halibut and sea scallops) and may indirectly affect associated trophic groups.

This chapter builds on the biodiversity checklist conducted in Chapter 1 and integrates the catch reconstructed in Chapter 2, to provide an additional layer of realism to ecosystem modelling in SPM. This works provides the first food web model for SPM, and marks the first application of the EwE software for French waters in the Northwest Atlantic. It allows to evaluate how SPM's fishing activity interacts with broader regional dynamics, and contributes to methodological literature on applying EwE in data-limited or cross-jurisdictional marine systems.

4.2 Materials and methods

4.2.1 Study area

The Northwest Atlantic Fisheries Organization (NAFO) delimits the Northwest Atlantic (i.e., the NAFO Convention Area, which encompasses coastal state's EEZ and the NAFO

regulatory area falling outside of these EEZs) into several sub-areas, divisions and subdivisions, which serve as management units for fishery resources in the area (Koen-Alonso *et al.*, 2019). The NAFO subdivision 3Ps is part of the larger NAFO sub-area 3 and division 3P, and extends from Cape Saint Mary in the south-west of Newfoundland, to Burgeo Banks in the south-east. Approximately 93% of the Saint Pierre and Miquelon's EEZ is included in NAFO subdivision 3Ps. While the SPM EEZ makes up approximately 11% of 3Ps, the rest of the subdivision falls within the Eastern Canada EEZ, with the exception of an exceedingly small portion of the subdivision at its southernmost part lying within the High Seas. The total study area was estimated to be 86,956.12 km², through spatial data analysis from the Sea Around Us databases (www.seaaroundus.org).

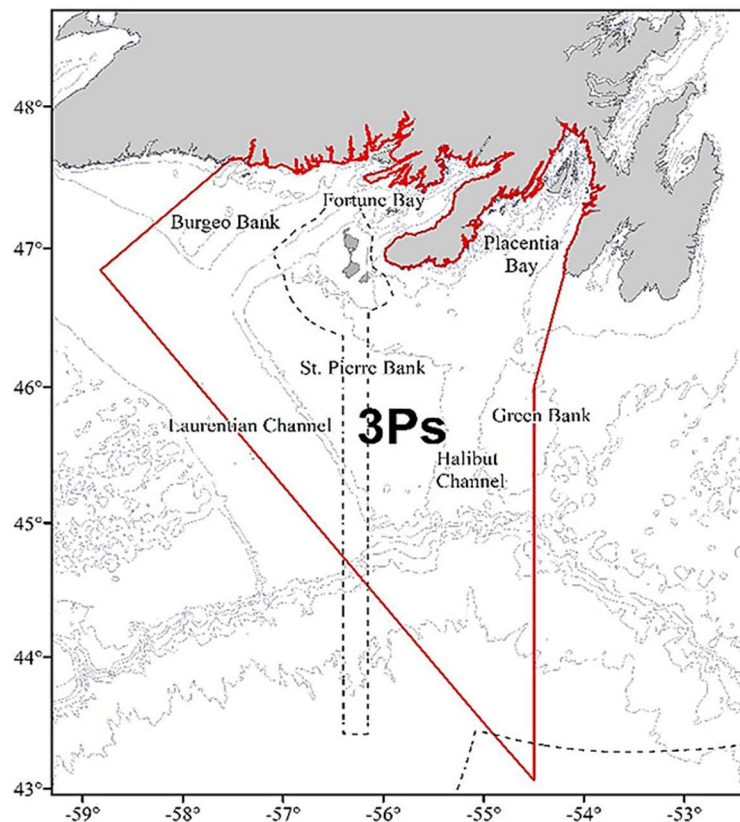


Figure 4.1. Map of NAFO Subdivision 3Ps in the south of Newfoundland. The dashed line limits the Exclusive Economic Zone of Saint Pierre and Miquelon (DFO, 2025).

4.2.2 Ecopath static model

Ecopath models are static representations of the ecosystem at a chosen period in time, during which they represent the trophic relationships between functional groups in a system, which can be one species or a group of species. Ecopath relies upon the principle of steady-state or mass-balance, which is defined by the input of the models, i.e., consumption, must balance the sum of the outputs, i.e., production, respiration and egestion (unassimilated food) (Christensen and Pauly, 1992). This principle is modelled by two equations, the first one ensuring energy balance of the flows between groups:

$$Q_i = P_i + R_i + U_i \quad (7)$$

where for a group i , Q is the consumption, P is the production, R is the respiration and U is the unassimilated food (Christensen and Pauly, 1992). The production in the previous equation can be defined by the following equation, which is ensuring mass balance between the groups in the system:

$$P_i = Y_i + M2_i \cdot B_i + E_i + BA_i + M0_i \cdot B_i \quad (8)$$

where for a group i , Y is the total fishery catch rate, $M2$ is the instantaneous predation rate, B is the biomass, E is the migration rate equal to the emigration minus the immigration, BA is the biomass accumulation rate and $M0$ is the ‘other mortality’ rate. This equation can also be expressed as:

$$P_i = \sum_{j=1}^n \left(\frac{Q}{B} \right)_j \cdot B_j \cdot DC_{ij} + Y_i + E_i + \left(\frac{P}{B} \right)_i \cdot B_i \cdot (1 - EE_i) \quad (9)$$

where for a group i , and a predator j , Q/B is the consumption/biomass ratio of the predator, which multiplied to the biomass B of the predator and the contribution of the group to the diet composition DC of the predator, represents the predation mortality of a group i . Y is the total fishery catch rate, which represents the fishing mortality, E is the net migration, BA is the biomass accumulation. The other mortality of a group i is the product of the production/biomass ratio P/B , the biomass B and the portion of mortality not explained by the model, as opposed to the portion explained by the model which is expressed as the ecotrophic efficiency EE (Christensen and Walters, 2004).

Each of the functional group in the model is dependent on the two aforementioned balanced equations. A minimum of five input parameters is required for each group (i.e., with the exception of primary producers and detritus, which require fewer input parameters) to parametrize the model:

the diet composition, the catch, and three of the four other parameters, i.e., biomass, P/B , Q/B and EE . Following these inputs, the ‘missing parameters’ are estimated by iterations from the algorithms included in the model’s parametrization routine. The most robust approach is to let the model estimate the EE , through the following equation (Christensen and Walters, 2004):

$$EE_i = \frac{Y_i + E_i + BA_i + B_i \times M2_i}{P_i} \quad (10)$$

where for a group i , Y is the total fishery catch rate, E is the net migration rate, BA is the biomass accumulation rate, B is the biomass, $M2$ is the instantaneous predation rate, and P is the production.

4.2.2.1 Biomass density

Species or group biomass, expressed in tonnes per surface unit ($t \cdot km^{-2}$) was estimated through trawl survey data, hydroacoustic data or population analysis in NAFO 3Ps or in adjacent areas when information in 3Ps was not available. Most trawl data in the Northwest Atlantic originated from two survey campaigns: the Engels otter trawl data dating up to spring 1995, and the Campelen shrimp trawl data, from fall 1995 onwards. The Campelen had a higher efficiency at sampling smaller fish species (Stansbury, 1996; Cadigan *et al.*, 2023).

4.2.2.2 Production rate

Production for a group is calculated as the product between the biomass and the production/biomass (P/B) ratio of this group. P/B ratio is expressed in $year^{-1}$, while production rate is expressed in $t \cdot km^{-2} \cdot year^{-1}$. When production rate or P/B estimates were not available for a group, it was assumed that production was equivalent to biomass multiplied by natural mortality and the catch added to the product (Allen, 1971; Pauly, 1997). In other terms, that the P/B of a group i is equivalent to the total mortality Z of this group, which is the addition of natural mortality M and fishing mortality F :

$$\left(\frac{P}{B}\right)_i = Z_i = M_i + F_i \quad (11)$$

Ultimately, production can be estimated for most groups by assuming a P/Q ratio of 0.15 (i.e., a gross efficiency of 15%) when no consumption or P/B estimate is available. This estimate was assumed to be ecologically reasonable (Christensen and Walters, 2024).

4.2.2.3 Consumption rate

Consumption, i.e., the utilization of food by a group, is expressed in biomass per surface unit per year ($\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$), while the Q/B ratio is expressed in year^{-1} . The international biological database FishBase (www.fishbase.org) includes information on growth parameters, diet composition and consumption, and a life-history tool developed to estimate the Q/B ratio of a species based on empirical relationships proposed by Palomares and Pauly (1998) using the surrounding temperature, asymptotic weight (i.e., the weight attained at a very old age), and the aspect ratio of the caudal fin of the species as an indicative of metabolic activity (Palomares and Pauly, 1998; Froese *et al.*, 2000). Consumption was either estimated from published consumption studies, daily rations from stomach content data, FishBase life-history tool, or by assuming a P/Q ratio of 0.15 (i.e., a gross efficiency of 15%) when no consumption or Q/B estimate was available.

4.2.2.4 Diet composition

Diet composition for each of the functional groups was estimated from published stomach content or diet studies. Stomach contents are best representative of a species diet as the latter is spatially and temporally variable; however, very few of these studies were available for the selected study area. Diets were studied in similar ecosystems in areas adjacent to or near NAFO 3Ps, and when temporal variations were not available, were adjusted to reflect significant changes in the post-1992 3Ps ecosystem, e.g., the sharp diminution of cod biomass or the sharp increase in shrimp biomass.

4.2.2.5 Landings and discards

All catch data (i.e., landings and discards for each exploited group) input in the models was derived from reconstructed catch time series extracted for NAFO 3Ps from the Sea Around Us databases (www.seaaroundus.org).

4.2.2.6 Balancing the models

Once input parameters are entered, most models will need additional adjustments to said parameters in order for the model to be mass-balanced. A model is unbalanced if $EE > 1$ for one or

multiple functional groups. To balance the models, changes to the diet matrix were explored first, to reduce predation mortality and be consistent with the biomasses of the model. If these changes did not reduce the *EE*, the parameters with the most uncertainty out of *B*, *P/B* and *Q/B* were re-evaluated, i.e., balancing the models was done based on the degree of confidence of each parameter. Ultimately, *EE* can be set to an assumed value to solve for biomass when data are lacking: as an example, the commonly used *EE* value of 0.95 reflects a near-complete use of a functional group's production while keeping a mathematically stable *EE*. As criteria for setting *EE* for groups where biomass is unavailable is that it should be ecologically reasonable (Christensen and Pauly, 1992; Christensen and Walters. 2024, p. 61-62).

Similarly, the gross food conversion efficiency (*GE*) equivalent to the ratio between production and consumption for each group, will generally be between 0.1 and 0.3 (i.e., 10% to 30%) for most species, with exceptions of marine mammals, seabirds and small invertebrates (Christensen and Walters, 2024, p.70-76). When *GE* was unrealistic, the production or consumption parameters input were revised and modified according to the sources available, or to ecologically reasonable assumptions. *GE* was set to a default value of 0.15 (i.e., unless another value was specified for a certain group in published studies) to obtain new estimates of *P/B* or *Q/B* when adjustments were not enough to lead to realistic *GE* values.

4.2.2.7 The NAFO 3Ps models

Two models of NAFO subdivision 3Ps were constructed for two different periods: 1960-1969 and 2000-2009. The periods were chosen to be representative of different states of the ecosystem, before the 1980s surge in effort, and after the 1992 cod-collapse. To build these models, 39 functional groups were considered (Table 4.1). Three commercially exploited were chosen to be multistanza groups, i.e., separated into two groups by age/size to account for differences in diet composition and in recruitment for fisheries: Atlantic cod (*Gadus morhua*), Greenland halibut (*Reinhardtius hippoglossoides*) and Atlantic halibut (*Hippoglossus hippoglossus*).

Few to no studies on marine mammals, seabirds and some fish and invertebrates have been done in the NAFO 3Ps subdivision. When data was not available specifically within the 3Ps area, data was used from Ecopath models constructed in neighboring areas. Models and area parameters were carefully reviewed with the additional expertise of Dr. Lyne Morissette (University of

Quebec at Rimouski) and classified in order of similarity to the NAFO 3Ps ecosystem as follows: the northern Gulf of Saint-Lawrence, i.e., NAFO 4RS (Morissette *et al.*, 2003), the Newfoundland-Labrador shelf, i.e., NAFO 2J3KLNO (Bundy *et al.*, 2000; Tam and Bundy, 2019), and the eastern Scotian Shelf (Bundy, 2004). Data was taken from methods used in these models in regards of ecosystem similarity, but also of period concordance and robustness of the methods.

Table 4.1. Functional groups defined for the 1960-1969 and 2000-2009 models in NAFO 3Ps. Species in bold are chosen to be representative species of their functional group, as the species of main commercial interest, higher abundance, or with the most data available in 3Ps.

Group Name	Main species
Piscivorous Cetaceans	<i>Balaenoptera physalus</i> , <i>Balaenoptera acutorostrata</i> , <i>Lagenorhynchus acutus</i> , <i>Lagenorhynchus albirostris</i> , <i>Megaptera novaeangliae</i> , <i>Phocoena phocoena</i> , <i>Delphinus delphi</i> , <i>Phyoster macrocephalus</i> , <i>Globicephala melas</i> , <i>Stenella coeruleoalba</i>
Planktivorous Cetaceans	<i>Balaenoptera borealis</i> , <i>Balaenoptera musculus</i>
Carnivorous Cetaceans	<i>Orcinus orca</i>
Harp seals	<i>Phoca groenlandica</i>
Hooded seals	<i>Cystophora cristata</i>
Grey seals	<i>Halichoerus grypus</i>
Harbour seals	<i>Phoca vitulina</i>
Piscivorous Seabirds	<i>Alca torda</i> , <i>Calonectris diomedea</i> , <i>Catharacta maccormicki</i> , <i>Cephus grylle</i> , <i>Chlidonias niger</i> , <i>Chroicocephalus ridibundus</i> , <i>C. Philadelphia</i> , <i>Fratercula arctica</i> , <i>Fulmarus glacialis</i> , <i>Larus argentatus</i> , <i>L. delewarensis</i> , <i>L. fiscus</i> , <i>L. marinus</i> , <i>L. hyperboreus</i> , <i>L. glaucoides</i> , <i>Leucophaeus atricilla</i> , <i>Morus bassanus</i> , <i>Oceanodroma leucorhoa</i> , <i>Oceanites oceanicus</i> , <i>Phalacrocorax auritus</i> , <i>P. carbo</i> , <i>Puffinus gravis</i> , <i>P. griseus</i> , <i>P. puffinus</i> , <i>Sternula antillarum</i> , <i>Sterna hirundo</i> , <i>S. paradisaea</i> , <i>S. caspia</i> , <i>Stercorarius longicaudus</i> , <i>S. parasiticus</i> , <i>S. pomarinus</i> , <i>S. skua</i> , <i>Rissa tridactyla</i> , <i>Uria aalge</i> , <i>U. lomvia</i> , <i>Xema sabini</i>
Planktivorous Seabirds	<i>Alle alle</i>
Benthivorous Seabirds	<i>Branta canadensis</i> , <i>Clangula hyemalis</i> , <i>Gavia immer</i> , <i>G. stellata</i> , <i>Histrionicus histrionicus</i> , <i>Melanitta fusca</i> , <i>M. negra</i> , <i>M. perspicillata</i> , <i>Mergus merganser</i> , <i>M. serrator</i> , <i>Phalaropus fulicarius</i> , <i>P. lobatus</i> , <i>Podiceps grisigena</i> , <i>Somateria mollissima</i> ,
Large Atlantic cod (> 35 cm)	<i>Gadus morhua</i>

Group Name	Main species
Small Atlantic cod (≤ 35 cm)	<i>Gadus morhua</i>
Large Greenland halibut (> 40 cm)	<i>Reinhardtius hippoglossoides</i>
Small Greenland halibut (≤ 40 cm)	<i>Reinhardtius hippoglossoides</i>
Large Atlantic halibut (> 81 cm)	<i>Hippoglossus hippoglossus</i>
Small Atlantic halibut (≤ 81 cm)	<i>Hippoglossus hippoglossus</i>
American plaice	<i>Hippoglossoides platessoides</i>
Flounders	<i>Glyptocephalus cynoglossus</i> , <i>Myzopsetta ferruginea</i> , <i>Paralichthys oblongus</i> , <i>Pseudopleuronectes americanus</i> , Pleuronectidae
Skates	<i>Raja laevis</i> , <i>R. ocellata</i> , <i>R. radiata</i> , <i>Malacoraja senta</i> , <i>R. spinicauda</i> ,
Redfish	<i>Sebastes fasciatus</i> , <i>S. mentella</i>
Large demersal feeders	<i>Anarhichas</i> spp., <i>Centroscyllium fabricii</i> , <i>Lophius americanus</i> , <i>Pollachius virens</i> , <i>Urophycis tenuis</i> , <i>Lycodes</i> spp., <i>Coryphaenoides rupestris</i> , Macrouridae, <i>Zoarces americanus</i> , <i>Brosme brosme</i> , Scorpaneiformes, Phycidae
Small demersal feeders	<i>Argentina</i> spp., <i>Myoxocephalus</i> spp., <i>Tautoglabrus adspersus</i> , Blenniidae, Cottidae, Zoarcidae, <i>Merluccius bilinearis</i>
Capelin	<i>Mallotus villosus</i>
Haddock	<i>Melanogrammus aeglefinus</i>
Sand lance	<i>Ammodytes americanus</i> , <i>A. dubius</i>
Arctic cod	<i>Boreogadus saida</i>
Large pelagic feeders	<i>Carcharodon carcharias</i> , <i>Cetorhinus maximus</i> , <i>Lamna nasus</i> , <i>Isurus oxyrinchus</i> , <i>Prionace glauca</i> , <i>Salmo salar</i> , <i>Somniosus microcephalus</i> , <i>Squalus acanthias</i> , Squalidae, <i>Thunnus thynnus</i> , <i>Thunnus alalunga</i> , other Gadiformes and piscivorous large pelagic feeders
Piscivorous small pelagic feeders	<i>Cyclopterus lumpus</i> , <i>Scomber scombrus</i> , other piscivorous mesopelagics
Planktivorous small pelagic feeders	<i>Clupea harengus</i> , <i>Gonatus</i> spp., <i>Scomberesox saurus</i> , <i>Alosa</i> , other planktivorous mesopelagics
Shrimp	<i>Pandalus borealis</i> , <i>Pandalus montagui</i>
Large crustaceans	<i>Chionoecetes opilio</i> , other non-commercial species (<i>Hyas</i> spp.)
Echinoderms	<i>Echinarachnius parma</i> , <i>Stronglyocentrotus doebrachiensis</i> , <i>Ophiura</i> spp., Echinodea and Holoturoidea
Sea cucumber	<i>Cucumaria frondosa</i>

Group Name	Main species
Lobster	<i>Homarus americanus</i>
Squid	<i>Illex illecebrosus</i> , Theutida
Molluscs	<i>Buccinum undatum</i> , <i>Placopecten magellanicus</i> , <i>Chlamys islandica</i> , <i>Cyrtodaria siliqua</i> , <i>Mytilus edulis</i> , <i>Crassostrea virginica</i> , other non-commercial bivalve and molluscs species
Polychaetes	<i>Parexogone hebes</i> , other polychaetes species
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians, tunicates > 5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly <i>Calanus finmarchicus</i> , <i>C. hyperboreus</i> , and <i>Oithona similis</i>), tunicates < 5 mm, meroplankton
Phytoplankton	Diatom species such as <i>Chaetoceros affinis</i> , <i>Chaetoceros</i> spp., <i>Fragilariopsis oceanica</i> , <i>F. cylindrus</i> , <i>Leptocylindrus minimus</i> , <i>Thalassiosira bioculata</i> , <i>T. nordenskioldii</i> , <i>T. pacifica</i> , <i>T. punctigera</i> , other autotrophic and mixotrophic organisms including dinoflagellates and mixotrophic <i>Stombidium</i> spp.
Detritus	----

4.2.3 Particle size distribution

Growth parameters were entered for each of the 41 functional groups of the model (excluding detritus): length at infinity or asymptotic size (L_{inf}), a and b in the length-weight relationship, and the growth coefficient K in the von Bertalanffy growth function (VBGF) were extracted from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org). When multiple estimates of growth parameters were available for a species, the ones originating from the Northwest Atlantic were chosen. The asymptotic weight (W_{inf}) was then estimated using the following equation:

$$W_{inf} = a \cdot L_{inf}^b \quad (12)$$

These growth parameters allowed to build a Particle Size Distribution (PSD) for the two balanced models through an EwE integrated routine, to produce a size spectrum of the groups' biomasses at two time-periods (Pauly and Christensen, 2002). This routine accounts for (1) multiple groups having ontogenies spanning several size classes and (2) the different growth rates of different size groups.

The growth of a species across different size classes is expressed by the combined following VBGFs:

$$L_t = L_{inf} [1 - e^{-K(t-t_0)}] \quad (13)$$

$$W_t = W_{inf} [1 - e^{-K(t-t_0)}]^b \quad (14)$$

where L_t is the mean length at age t of a species, t_0 is the age at size 0, and W_t is the mean weight at age t (Pauly and Christensen, 2002) .

4.2.4 Ecosim time-dynamic model

Ecosim is a module of EwE allowing the creation of a dynamic temporal simulation of how the ecosystem responds over time to changes in different parameters (e.g., fishing pressure, environmental conditions, management scenarios), reliant on the mass-balance results of the initial Ecopath model. Ecosim uses a set of differential equations accounting for predator–prey interactions through a foraging arena theory, which regulates consumption rates depending on prey availability and vulnerability, to track biomass fluctuations and energy flow across trophic levels (Ahrens *et al.*, 2012; Christensen and Walters, 2024). The basic version of these equations is:

$$\frac{dB_i}{dt} = g_i \sum_{j=1}^n Q_{ij} - \sum_{j=1}^n Q_{ji} + I_i - (F_i + e_i + M0_i)B_i \quad (13)$$

where for a group i , dB/dt is the growth rate during the time interval dt in terms of the group's biomass, g is the net growth efficiency, Q_{ij} and Q_{ji} are the consumption rates by group i on group j and by j on i , I is the immigration rate, F is the fishing mortality, e is the emigration rate, $M0$ is the other mortality rate, and B is the biomass.

4.2.4.1 Time-series and forcing functions

The 1960-1969 mass-balanced Ecopath model of NAFO 3Ps was chosen as a starting point for Ecosim time-dynamic simulations. Additional ‘reference’ data were entered in Ecosim in the form of time-series to improve temporal predictability. Catch time series were available through reconstructed catch data from the Sea Around Us (www.seaaroundus.org) from 1960 to 2015 for

most countries fishing in NAFO 3Ps, and from 1960 to 2022 for SPM (c.f. *Chapter 3: Reconstructing what SPM has caught from 1950 to 2022*) for all species of commercial interest. Relative biomass time series were available, covering limited periods for a few species and groups of species of the model. Only time series specific to NAFO 3Ps were input in the model, with the exception of seal species where biomass trends in the Northwest Atlantic were available (DFO, 2005, 2016, 2018a, 2018b, 2020; Hammill and Stenson, 2005, 2006; Hammill *et al.*, 2007; Simpson *et al.*, 2012; Dwyer *et al.*, 2016; Rideout *et al.*, 2016; Bourne *et al.*, 2023).

Additional drivers can be entered in the model in the form of forcing functions that are either seasonal or long-term and can be used to study the impact of physical or environmental factors on the groups in the system, thus acting as drivers of change over time. These external drivers are user-defined and allow for increased realism in the model by reproducing historical trends, or can help simulate scenarios and explore hypotheses about ecosystem responses, e.g., to fisheries through climate change with rising temperature, or seasonal primary productivity variations. Fishing effort and fishing mortality are drivers that can both be entered as historical time-series and used as forcing drivers to simulate different fishing scenarios (Christensen and Walters, 2024).

Fishing mortality was calculated for large cod, large Atlantic halibut, sea cucumber, large demersals, planktivorous small pelagics, haddock, American plaice, skates, founders, large crustacea and lobster. Fishing effort was calculated for SPM artisanal boats (i.e., changes in the number of artisanal boats; Eynaud, 1986; F. Teletchea, University of Lorraine, personal communication, 2024), SPM trawlers (i.e., changes in the number of SPM-flagged industrial trawlers, Bertrand and Mahe, 1988; J. Vigneau, IFREMER, personal communication, 2025) and Canadian fleets (i.e., using CPUE data in NAFO 3Ps; Forest *et al.*, 1979; Bishop, 1988; Parsons and Stead, 2011), as SPM and Canada are the two main countries exploiting marine species in NAFO 3Ps. For the gears of interest where effort time series were not available (i.e., SPM dredges and SPM longlines), fishing mortality was input as a time series for the species targeted by these gears (i.e., respectively sea cucumber and Atlantic halibut). For species without fishing mortality time series as drivers, the weight of their catch and/or biomass time series was halved, to avoid overfitting from the model.

4.2.4.2 Fitting to time series

Once time-series are entered in the Ecosim model, the model must be calibrated so that its predictions align as closely as possible with observed data over time. This process, known as *fitting to time-series*, was done through the estimation of vulnerability multipliers and by conducting sensitivity searches. Vulnerability multipliers are key determinants of the model's behavior, describing how strongly prey populations are impacted by an increase in predator populations toward carrying capacity, where predator production depends on prey productivity (Bentley *et al.*, 2024). Ecosim includes an automated statistical calibration routine which allows for estimation of vulnerability multipliers using a sum of squares (SS) minimization approach and the Akaike Information Criteria (AIC) to evaluate and identify the statistically 'best fit' model, i.e., the lowest AIC reached by the routine runs (Scott *et al.*, 2016). To avoid overfitting, the number of parameters estimated was limited by the number of independent time series (following best practice recommendations, Heymans *et al.* 2016). Parameter selection was informed by sensitivity analyses, which identified multipliers with the greatest impact on model fit, and automated stepwise fitting routines that explore multiple parameter combinations efficiently (Christensen and Walters, 2016). Combined searches of vulnerability and anomaly parameters were compared using SS and AIC to evaluate optimal parameterization.

4.2.4.3 Projections of fishing effort

Three different effort scenarios were created to observe potential impacts on species' biomasses: a 50%, 100% and 200% exponential increase of fishing effort, over a period of 75 years from 2025 to 2100. The increases were projected on three of SPM's major fishing fleets, which target economically important species: the dredges (i.e., targeting sea cucumber), longlines (i.e., targeting Atlantic halibut) and scallop dredges (i.e., targeting deep-sea scallops and Iceland scallops). Fishing effort was kept constant for the other fleets in order to isolate potential effects. This approach reflects effort increases that have already been observed in the past, i.e., with strong exponential increases in SPM dredges effort between 2000 and 2020. As these years mark the faster development of a deep-sea scallop and sea cucumber fishery (hence a strong effort increase over a 20 years period), a similar increase over 75 years was estimated to be realistic.

4.2.5 Ecospace spatial model

The Ecospace module uses the parametrization of the mass-balanced Ecopath model and the fitted Ecosim model to create spatial and time-dynamic simulations. This added spatial component relies on the same set of differential equations as in Ecosim, as well as on group or species-specific habitat and movement preferences, spatial grid characteristics and spatial patterns of fishing or environmental forcing (Christensen *et al.*, 2014; de Mutsert *et al.*, 2023). Ecospace allows the exploration of ecosystem dynamics across a defined spatial grid, incorporating habitat preferences, environmental gradients (e.g., depth, temperature), and species interactions (Christensen *et al.*, 2014; de Mutsert *et al.*, 2023).

The NAFO 3Ps 1960-1969 Ecopath model was used to parametrize the Ecosim and Ecospace modules, to obtain a first attempt at species distributions maps for the area. The 3Ps area is represented in the model by a (xx by yy) grid of cells, defined as land or water, where the immigration rate within each cell is the sum of the emigration in the four surrounding cells, represented by the following equation:

$$B_{out,rci} = \sum_{d=1}^4 m_{id} \cdot B_{rci} \quad (14)$$

where for group i , $B_{out,rci}$ are the emigration flows, d is movement direction, m are the instantaneous movement rates and B_{rci} is the biomass density in the cell.

The bathymetry of NAFO 3Ps was extracted from GEBCO (www.gebco.net) depth maps data in R studio to get a depth base map of the area, added on the grid of cells. Habitat suitability maps were built for each functional group based on habitat preference (e.g., shallow shelf, slope or offshore deep) and depth ranges defined as group-specific environmental response functions, which determined the maximum biomass each cell could support. Movement of functional groups was modeled using foraging responses.

4.3 Results

4.3.1 Input parameters for the 1960-1969 and 2000-2009 Ecopath models

The present section describes the inputs for each functional group of the NAFO subdivision 3Ps and the Saint-Pierre and Miquelon archipelago used to parametrize and balance two Ecopath models, respectively representing a static picture of the ecosystem in 1960-1969 and 2000-2009.

4.3.1.1 Cetaceans

Background

Cetaceans were divided into three independent groups according to feeding habits. Piscivorous cetaceans are defined as cetaceans primarily feeding on fish. In the region, they are represented by 10 species, including the fin whale (*Balaenoptera physalus*), the common minke whale (*Balaenoptera acutorostrata*), the humpback whale (*Megaptera novaengliae*) and the Atlantic white-sided dolphin (*Lagenorhynchus acutus*).

Planktivorous cetaceans are defined as cetaceans that are primarily suspension feeders, as they feed on planktonic organisms. In 3Ps, they are represented by two species: the blue whale (*Balaenoptera musculus*) and the sei whale (*Balaenoptera borealis*).

Carnivorous cetaceans are defined as whales that primarily feed on other marine mammals, and are represented by one species in the region: the killer whale (*Orcinus orca*). Killer whales are known to be transient in the waters of NAFO 3Ps, thus not frequenting the area year-round (L. Morissette, marine ecologist, 2024, personal communication). As no marine survey has estimated the time cetaceans spend in the 3Ps area, their approximate residency time was assumed to be 180 days per year.

Catch

None of the aforementioned groups are commercially caught in the NAFO 3Ps subdivision, nor on the adjacent Newfoundland Shelf. There were no records of bycatch either.

Biomass

Biomass estimates for piscivorous and planktivorous cetaceans were taken from Tam and Bundy's (2019) estimates for the Newfoundland Shelf and assumed to be representative of the Saint Pierre Bank area. Estimates from Bundy *et al.* (2000) back calculated from Northwest Atlantic total population sizes between 1974-1993 were used for the 1960-1969 model, while estimates from Lawson and Gosselin (2018) in eastern Canada in 2007-2016 were used for the 2000-2009 model. Biomass was adjusted for the number of days spent in the area, assuming it corresponds to half a year, to reflect the highly migratory nature of cetaceans. Biomass was estimated to be respectively $B = 0.221 \text{ t}\cdot\text{km}^{-2}$ and $B = 0.028 \text{ t}\cdot\text{km}^{-2}$ for piscivorous and planktivorous cetaceans in 1960-1969. For the 2000-2009 model, it was estimated to be $B = 0.145 \text{ t}\cdot\text{km}^{-2}$ for piscivorous cetaceans and $B = 0.025 \text{ t}\cdot\text{km}^{-2}$ for planktivorous cetaceans.

Killer whales' biomass was taken from personal communications with Dr. L. Morissette (marine ecologist, 2024) and estimated to be 50 individuals per year around the SPM archipelago, present an average of six months per year, giving a biomass of $0.001 \text{ t}\cdot\text{km}^{-2}$, for a mean body weight of 3.8 t. This biomass was used for both periods.

Production:Biomass

P/B ratios for piscivorous, planktivorous and carnivorous cetaceans were calculated according to the methods proposed by Tam and Bundy (2019), with Hoenig's (1983) equation to derive the mortality Z using maximum age estimates from Trites and Pauly (1998). P/B ratio was estimated to be 0.110 year^{-1} for piscivorous cetaceans, and 0.055 year^{-1} for planktivorous cetaceans. These P/B ratios were used for both the 1960-1969 and 2000-2009 models (Table 4.2). For killer whales, the value $Z = P/B = 0.084 \text{ year}^{-1}$, using a maximum age of 50 years, was also used for both models (Table 4.3).

Table 4.2. Production to biomass ratio estimates for piscivorous cetaceans. The P/B ratio calculated for the group was used for both the 1960-1969 and 2000-2009 models.

Species	Maximum age (years)	Mortality (Z ; year ⁻¹)
Humpback whale	75	0.059
Fin whale	98	0.047
Harbour porpoise	13	0.273
White beaked dolphin	30	0.132
White sided dolphin	30	0.132
Common dolphin	30	0.132
Sperm whale	69	0.064
Pilot whale	45	0.092
Minke whale	47	0.089
Mean P/B for group	--	0.110

Table 4.3. Production to biomass ratio estimates for planktivorous cetaceans. The P/B ratio calculated for the group was used for both the 1960-1969 and 2000-2009 models.

	Maximum age (year)	Mortality (Z ; year ⁻¹)
Blue whale	100	0.046
Sei whale	69	0.064
Mean P/B for group	--	0.055

Consumption: Biomass

The Q/B ratios for piscivorous, planktivorous and carnivorous were taken from Tam and Bundy's (2019) model on NAFO 2J3KLNO, and assumed to be representative of 3Ps. Q/B ratios for piscivorous cetaceans were assumed to be 5.387 year⁻¹ for the 1960-1969 model and 5.394 year⁻¹ for the 2000-2009 model. These values are derived from Tam and Bundy's calculations integrating residency time (i.e., around 180 days per year) and consumption rates. Q/B ratios for planktivorous cetaceans were assumed to be 3.468 year⁻¹ for both models, while Q/B ratios for killer whales was assumed to be 8.1 year⁻¹ for both models. High Q/B values reflect the high metabolic rates of marine mammals.

Diet composition

Diet breakdown and estimates for carnivorous cetaceans were given by L. Morissette (marine ecologist, 2024, personal communication) based on surveys done on the Saint Pierre Bank. Killer whales feed mainly on small piscivorous cetaceans (30%), small planktivorous cetaceans (13%), and seals (55%). Fishes make up approximately 5% of their diet.

Piscivorous cetaceans' diet was estimated using estimates for humpback whale, fin whale, and harbour porpoise on the Newfoundland Shelf from Bundy *et al.* (2000) and for white beaked dolphin and common dolphin from isotopes comparison and literature reviews done by Pauly *et al.* (1998), since little to no data is available for the 3Ps zone. It was adapted to include sperm and pilot whales (squid-eating whales), which also occur in the area. Diet composition was weighted by the estimated biomass of respective species in the area. Piscivorous cetaceans' diet is over 50% made up of capelin in the area of study. Planktivorous cetaceans' diet was estimated from stomach content analysis of sei and blue whales in the Northwest Atlantic from Mitchell (1975). Planktivorous whales' diet is composed at 90% of large zooplankton, almost entirely made up of euphausiids (krill), but also copepods and small fish like capelin (Table 4.4).

Table 4.4. Diet compositions of cetaceans as input in both models. Values with an asterisk (*) mean that a group is present in the diet composition, but only in very small amounts.

<i>Prey</i>	Piscivorous cetacea	Planktivorous cetacea	Carnivorous cetacea
Piscivorous cetacea	—	—	0.400
Planktivorous cetacea	—	—	0.128
Harp seals	—	—	0.250
Hooded seals	—	—	0.020
Grey seals	—	—	0.008
Harbour seals	—	—	0.100
Small cod	0.001	--	—
Large Greenland halibut	—	—	0.055
Large Atlantic halibut	—	—	0.005
American plaice	0.010	—	—
Flounders	0.050	—	—
Skates	0.010	—	—
Small demersals	0.001	—	—
Capelin	0.572	0.050	—
Sand lance	0.083	0.050	—
Pisc. small pelagics	—	—	0.034
Plank. small pelagics	0.060	—	0.000*
Squid	0.130	—	—
Large zooplankton	0.083	0.900	—

Balancing the model

Piscivorous cetaceans' diet was adjusted in the 2000-2009 model to reflect the decline of cod in the system, while killer whales' diet was adjusted to reflect the increase in seals in the area.

4.3.1.2 Seals

Background

Four species of seals (*Pinnipedia*) can be found around Saint Pierre Bank, though in larger abundances in the neighboring Gulf of Saint Lawrence, Labrador Shelf and Scotian Shelf areas: the harp seal (*Pagophilus groenlandicus*), hooded seal (*Cystophora cristata*), grey seal (*Halichoerus grypus*) and harbour seal (*Phoca vitulina*). Harp and hooded seals are distributed mostly around the Northwest Atlantic and the Arctic Ocean, ranging all the way to the Barents Sea, and are dependent on ice coverage for their breeding season. Hooded seals are, however, much less abundant than harp seals in the study area. Grey seals are largely distributed across the North Atlantic Ocean and the Baltic Sea. Harbour seal distribution encompasses a much larger area, including the North Atlantic, Arctic and North Pacific oceans.

Out of these four species, only harbour and grey seals have regular feeding grounds on the Saint Pierre Bank, and are almost yearlong residents around the SPM archipelago, while harp and hooded seals have seasonal occurrences. The study area does not, however, encompass any of these species' breeding, whelping or molting sites, but corresponds to migration zones between molting and breeding areas.

Biomass

Harp and hooded seal biomass was available for 2013-2015 on the Newfoundland shelf, and not for earlier periods than the 1980s. Seal biomass for the 1960-1969 model was therefore calculated using abundance estimates and mean mass at age, and adjusted according to the Northwest Atlantic general trends, as these trends show an increase in pinniped's population abundance (Table 4.5).

For harp seals, Hammill and Stenson's (2005) study shows an increase of 295% in total population from 1960 to 2005 in the Northwest Atlantic. The average number of individuals was 2 million in 1960-69 and 5.5 million in 2000-09 for the FAO statistical area 21. Using an average weight of 130 kg (0.13 t) entails a population biomass of $0.042 \text{ t} \cdot \text{km}^{-2}$ for 1960-69 and $0.114 \text{ t} \cdot \text{km}^{-2}$ for 2000-2009. Knowing the breeding grounds of this species are not located in 3Ps, this biomass was divided per 2 to reflect the time spent in 3Ps giving estimates of respectively $B = 0.020 \text{ t} \cdot \text{km}^{-2}$ and $B = 0.057 \text{ t} \cdot \text{km}^{-2}$.

For hooded seals, Hammill and Stenson (2006) estimated that the North Atlantic population was around 380,000 individuals in 1965, and increased to 550,000 individuals in 2005, showing an increase of 145%. Using an average weight of 180 kg (0.28 t), $B = 0.017 \text{ t} \cdot \text{km}^{-2}$ and $B = 0.025 \text{ t} \cdot \text{km}^{-2}$ were calculated. Hooded seals' range extends to 3Ps but neither their breeding, molting nor foraging areas overlap with 3Ps. Biomass was divided in half to reflect an approximate time spent in 3Ps. The final biomass estimates were $B = 0.008 \text{ t} \cdot \text{km}^{-2}$ for the 1960s and $B = 0.012 \text{ t} \cdot \text{km}^{-2}$ for the 2000s.

Abundance of grey seals through pup production has increased 10 times between 1977 and 1993, and total population has increased from around 4,000 individuals to 204,000 individuals from 1969 to 1999 (Hammill *et al.*, 2023). Grey seals population estimates were available only for the combined Scotian Shelf and Gulf of Saint Lawrence where they are most abundant and breed. Population abundance was multiplied by the average weight of 0.29 t and divided by the total FAO Area 21 surface area, to be conservative and representative of the absence of grey seals breeding and molting grounds in 3Ps. This allowed to obtain $B = 0.0009 \text{ t} \cdot \text{km}^{-2}$ for the 1960s and $B = 0.016 \text{ t} \cdot \text{km}^{-2}$ for the 2000s.

For harbour seals, no population estimate was available for the Northwest Atlantic, so no trend could be observed. The closest estimates available were from Tam and Bundy (2019) for the Newfoundland shelf in 1980 and 2013, and were used in our model. Biomass was therefore assumed to be respectively $B = 0.01 \text{ t} \cdot \text{km}^{-2}$ and $B = 0.015 \text{ t} \cdot \text{km}^{-2}$.

Table 4.5. Biomass estimates for harp, hooded and grey seals in NAFO 3Ps, used in the 1960-1969 and in the 2000-2009 models.

Seal species	Period	Average number of individuals (million)	Mean body weight (t)	Biomass ($\text{t} \cdot \text{km}^{-2}$)	Days spent in 3Ps	Adjustment for time spent in 3Ps
Harp seals	1960-1969	2.0	0.13	0.0415	~180	0.0207
	2000-2009	5.5	0.13	0.1142	~180	0.0571
Hooded seals	1960-1969	0.38	0.28	0.0169	~180	0.0085
	2000-2009	0.55	0.28	0.0246	~180	0.0123
Grey seals	1960-1969	0.004	0.29	0.0009	N/A	N/A
	2000-2009	0.20	0.29	0.0162	N/A	N/A

Production:Biomass

P/B ratios for harp, hooded, grey and harbour seals were calculated using Hoenig's (1983) mortality equation and maximum age estimates from Trites and Pauly (1998). The calculated P/B values were used for the two Ecopath models (Table 4.6).

Table 4.6. Production to biomass ratio estimates for seals. The P/B ratio calculated for the group was used for both the 1960-1969 and 2000-2009 models.

Seal species	Maximum age (years)	Mortality (Z ; year ⁻¹)
Harp seals	26	0.149
Hooded seals	35	0.115
Grey seals	39	0.105
Harbour seals	31	0.128

Consumption:Biomass

Q/B ratios values for harp, hooded and harbour seals were taken from Tam and Bundy (2019)'s model of the Newfoundland Shelf, derived from mean annual consumption estimates, and were respectively $Q/B = 16.78 \text{ year}^{-1}$, $Q/B = 18.23 \text{ year}^{-1}$, and $Q/B = 13.00 \text{ year}^{-1}$ for the 1960-1969 model (estimates taken from Tam and Bundy's (2019) 1980-1985 model), and $Q/B = 17.64 \text{ year}^{-1}$, $Q/B = 18.33 \text{ year}^{-1}$, and $Q/B = 13.00 \text{ year}^{-1}$ for the 2000-2009 model (estimates taken from Tam and Bundy's (2019) 2013-2015 model).

For grey seals, Q/B ratio was taken from Bundy's (2004) model of the Eastern Scotian Shelf and estimated to be $Q/B = 11.80 \text{ year}^{-1}$, a value input in both models.

Diet composition

Harp seals diet was estimated for the Northwest Atlantic in 1900-1995 (Lawson *et al.*, 1997), in 2J3KL during 1991-1993 (Lawson *et al.*, 1993) and for the St Lawrence Estuary (Hammill and Stenson 2000; Lawson *et al.*, 1995). Prey consumption variations in time were studied through Lawson and Stenson (1995) to obtain a representative diet for the 1960-1969 model, since the nearshore collections zone included Saint Pierre and Miquelon. It was adjusted for the 2000-2009 to reflect the diminution of cod biomass in the system. Major prey for harp seals include redfish (40%), capelin (43%), Atlantic cod (7%), and sand lance (5%).

Hooded seals' diet was estimated through data from Ross (1993) and Hammill and Stenson (2000). It was adjusted for the 2000-2009 to reflect the diminution of cod biomass in the system.

Hooded seals' diet is primarily composed of Greenland halibut (26%), Atlantic cod (22%), flounders (15%), and redfish (13%).

Grey seals diet composition estimates were available from Benoit and Bowen (1990), and were compared with diets studies from Hammill and Stenson (2000) and Murie and Lavigne (1992), as well as a supplementary diet study from Hammill and Stenson (2007) in Southern Newfoundland, with a study area adjacent to the SPM archipelago. Other diet estimates available from Bundy's (2004) model of the Scotian Shelf for 1995-2000 were used to adjust diet composition to reflect post 1990s ecosystem changes for the 2000-2009 model. Estimates show that the main species preyed on are Atlantic cod (51%), small demersal fish (12%), capelin (8%) and flounders (7%).

Harbour seals diet was estimated from stomach content analysis in the Bay of Fundy and the Eastern Scotian Shelf between 1988 and 1992 (Bowen and Harrison, 1996) and from the 2J3KL area with data from Hammill and Stenson (2000), estimating diet was primarily composed of herring and other small planktivorous pelagic fish (43%), mackerel and other small piscivorous pelagic fish (20%), Atlantic cod (8%) and capelin (6%) (Table 4.7). It was adjusted for the 2000-2009 model to reflect the lower cod biomass in the system.

Table 4.7. Diet composition for the four species of seals as input in the 1960-1969 model. Values with an asterisk (*) mean group is present in the diet composition in very small amounts. Changes in composition in the 2000-2009 model were minimal.

<i>Prey</i>	Harp seals	Hooded seals	Grey seals	Harbour seals
Large cod	0.016	0.111	0.205	0.019
Small cod	0.048	0.107	0.310	0.056
Large Green. halibut	–	0.017	–	–
Small Green. halibut	–	0.235	0.001	–
Large Atlantic halibut	–	0.005	0.001	–
Small Atlantic halibut	–	–	0.004	0.001
American plaice	–	–	0.022	–
Flounders	0.001	0.146	0.074	0.018
Skates	–	–	0.013	0.001
Redfish	0.400	0.131	0.003	0.004
Large demersals	0.005	0.012	0.045	0.027
Small demersals	0.003	0.057	0.120	0.030
Capelin	0.434	0.005	0.085	0.059
Haddock	–	–	0.010	–
Sand lance	0.057	–	0.037	–
Arctic cod	0.000*	0.020	0.005	–
Large pelagics	–	–	–	0.087
Pisci. small pelagics	–	0.064	0.005	0.198
Plank. small pelagics	0.031	0.090	0.054	0.435
Shrimp	0.000*	–	0.000*	0.059
Large crustacea	–	–	0.001	0.004
Squid	0.000*	–	0.005	0.002
Large zooplankton	0.002	–	–	0.001

Balancing the models

In the 1960-1969 model, the proportion of grey seals in the diet of killer whales and large pelagic fish was lowered, and the remaining proportion distributed among other species making up the diet of large pelagic fish and carnivorous cetaceans, to balance the *EE* of grey seals. Additionally, to balance the *EE* of harp seals and hooded seals, the proportion of both species was lowered in the diet of large pelagic fish, and in the diet of carnivorous cetaceans, as the evidence relative to the proportion of seals in orca's diet in SPM is based on recent observations. The diet of carnivorous cetaceans was consequently adjusted according to diet studies for killer whale in the North Atlantic (Lawson and Snow, 2008; Matthews *et al.*, 2021). Ultimately, as the impact of hooded seal on its preys was too large, biomass was divided by two in the 1960-1969 model to be more representative of the high mobility of the species within NAFO 3Ps.

In the 2000-2009 model, the *EE* of grey seals was balanced by lowering their proportion in the diet of killer whales and large pelagic fish, while the remaining proportion was distributed among other species making up the diet of both groups.

4.3.1.3 Seabirds

Background

Seabirds found around Southern Newfoundland and the Saint Pierre Bank can be divided in three groups according to their feeding behavior: piscivorous, planktivorous and benthivorous seabirds. Piscivorous seabird species occurring in the area include both inshore (i.e., whose habitat and feeding grounds includes coastal and wetland areas) and offshore (i.e., whose life cycle is spent mostly at sea, coming to land only to breed) bird species such as the Atlantic puffin (*Fratercula arctica*) razorbill (*Alca torda*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), great cormorant (*Phalacrocorax carbo*), Leach's storm petrel (*Hydrobates leucorhous*), and common tern (*Sterna hirundo*).

Planktivorous seabirds are represented by one species, the little auk or dovekie (*Alle alle*), a Holarctic species which occurs in 3Ps mostly in the winter, when they move southwards to feed on zooplankton (Abraham and Etcheberry, 2014).

Benthivorous seabirds are represented mostly by Holarctic and highly migrating species of ducks, geese and eiders whose winter-feeding grounds encompass 3Ps, such as the Canadian goose (*Branta canadensis*), red-throated loon (*Gavia stellata*), common eider (*Somateria mollissima*), common loon (*Gavia immer*), and surf scoter (*Melanitta perspicillata*). Benthivorous seabirds feed mostly on small benthic invertebrates, including bivalves and small crustaceans, as well as fish larvae.

Biomass

While SPM's biodiversity monitoring includes breeding pairs assessments on the Grand Colombier island, the limited sampling did not provide estimates robust enough for inferences on seabird biomass in NAFO 3Ps. Generally, there is not sufficient knowledge on breeding colonies counts in NAFO 3Ps to use as population estimates. Assuming breeding and wintering areas are similar between NAFO 3Ps and NAFO 2J3KLNO, seabirds biomass estimates were taken from

Bundy *et al.*, (2000) and Tam and Bundy's (2019) models of the Newfoundland shelf. Estimates for the 1985-1987 models were used for the 1960-1969 3Ps model, while estimates for the 2013-2015 model were used for the 2000-2009 model. Most biomass estimates were derived from abundance estimates from bird census surveys in NAFO 2GHJ3KLNO by the Canadian Wildlife Services and individual biomass estimates by Bundy *et al.* (2000) and Warkentin and Newton (2013).

Piscivorous seabirds biomass was assumed to be $0.012 \text{ t} \cdot \text{km}^{-2}$ for 1960-1969 and $0.0071 \text{ t} \cdot \text{km}^{-2}$ for 2000-2009. Benthivorous seabirds biomass was assumed to be $0.0002 \text{ t} \cdot \text{km}^{-2}$ for 1960-1969 and $0.0017 \text{ t} \cdot \text{km}^{-2}$ for 2000-2009, while planktivorous seabirds biomass was assumed to be $0.0022 \text{ t} \cdot \text{km}^{-2}$ for 1960-1969 and $0.0056 \text{ t} \cdot \text{km}^{-2}$ for 2000-2009.

Production:Biomass

The P/B ratio of piscivorous seabirds was assumed to be 0.25 year^{-1} as estimated by Bundy *et al.* (2000) for the Newfoundland Shelf. The P/B ratio of planktivorous seabirds was assumed to be 0.15 year^{-1} as estimated by Tam and Bundy (2013) from Gabrielsen *et al.* (1991) reporting low production per breeding pair. The P/B ratio of benthivorous seabirds was taken from Mawhinney *et al.*'s (1999) estimates of common eiders mortality in the Bay of Fundy, and assumed to be 0.13 year^{-1} . These values were used for both models.

Consumption:Biomass

The Q/B ratios of piscivorous seabirds was taken from prey consumption estimates by Barrett *et al.* (2006) for NAFO 2GHJ, and NAFO 3LKNMO, of 119.41 year^{-1} , and was used for both the 1960-1969 and 2000-2009 models. For planktivorous seabirds, Q/B was taken from Tam and Bundy (2019), derived from dovekie consumption estimates in British Columbia by Vermeer (1984), estimating a 17.7% consumption rate per year. Q/B was assumed to be 64.605 year^{-1} for both models. Q/B for benthivorous seabirds was similarly taken from Tam and Bundy (2019, and derived from consumption studies of common eiders wintering in the Gulf of Saint Lawrence by Guillemette *et al.* (2003). Q/B was assumed to be 45.291 year^{-1} for both models.

Diet composition

Piscivorous seabirds diet was adapted from Bundy *et al.* (2000), and is mostly represented by Atlantic pelagic species such as herring and mackerel, as well as forage fish like capelin. Planktivorous seabirds diet was adapted from Burke *et al.* (2014) from diet studies in coastal Newfoundland, where it was estimated that copepods (*Calanus* spp. and other copepods), amphipods, and jellyfish were making up the highest part of dovekie's diet. The diet of benthivorous seabirds was estimated through lipids and stable isotopes analysis of common eiders in the Arctic, and includes bivalves, polychaetes, and copepods (Dahl *et al.*, 2003). These diet composition estimates were used for both the 1960-1969 and 2000-2009 models, and adapted to the 2000-2009 model to reflect the diminution of cod biomass and increase of capelin biomass in the system for piscivorous seabirds (Table 4.8).

Table 4.8. Diet composition of piscivorous, planktivorous and benthivorous seabirds as input in both the 1960-1969 and 2000-2009 models.

<i>Prey</i>	Piscivorous seabirds	Planktivorous seabirds	Benthivorous seabirds
Small cod	0.020	—	—
Small Green. halibut	0.004	—	—
American plaice	0.004	—	—
Flounders	0.004	—	—
Skates	0.004	—	—
Small demersals	0.020	—	—
Capelin	0.700	—	—
Sand lance	0.200	—	—
Arctic cod	0.005	—	—
Large pelagics	0.002	—	—
Pisci. small pelagics	0.025	—	—
Plank. small pelagics	0.012	—	0.100
Molluscs	—	—	0.200
Polychaetes	—	—	0.030
Other benthic invertebrates	—	0.011	0.420
Large zooplankton	—	0.537	0.250
Small zooplankton	—	0.202	—

Balancing the model

No adjustments to the input parameters were necessary to balance the two models.

4.3.1.4 Atlantic cod (multistanza group)

Background

Atlantic cod (*Gadus morhua*) is a demersal gadoid species widely distributed across the North Atlantic and Arctic Oceans. In 3Ps, cod is a transboundary stock, characterized by offshore and inshore components with complex and various migration patterns. Spawning is extensively distributed all over 3Ps and seasonally variable (DFO, 2024). In the Northwest Atlantic, cod has been a dominant predatory fish species of the ecosystem, and the primary targeted species by industrial and artisanal fisheries before the stock collapse and subsequent cod fishing moratorium of 1992. Commercial landings in 3Ps increased largely through the 1950s to the 1960s, and decreased sharply in the 1990s (Divovich *et al.*, 2015).

For both models constructed and to better represent the species' life history stages, Atlantic cod was divided into two stanza: small cod (i.e., size less or equal to 45 cm, 0 to 4 years old) and large cod (i.e., size larger than 45 cm, 4 years old onwards), with a threshold determined by the minimum size of capture in Eastern Canada set at 45 cm according to DFO, as well as by notable diet composition dissimilarities between juvenile and adult cod (see *Diet composition*).

Catch

Catch data for large cod in NAFO 3Ps was available through the Sea Around Us database (www.seaaroundus.org): reconstructed catch data of all countries fishing in 3Ps was used to obtain a yearly catch estimate of $0.813 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 1960-1969 period, and of $0.0174 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 2000-2009 period. Additionally, catch data reconstructed in this study (c.f. *Chapter 2: Reconstructing what SPM has caught from 1950 to 2022*) for the Saint-Pierre and Miquelon fleet was input in the models as a separate fleet. The yearly catch estimate by SPM was of $0.032 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 1960-1969 period, and of $\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 2000-2009 period. Small cod was assumed to not have any catch, while cod discards were split between small (80%) and large (20%) cod assuming small cod are more likely to be discarded as they do not meet the minimal authorized landing size. Total discards were of $0.101 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 1960-1969 period, and of $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 2000-2009 period.

Biomass

Annual cod biomass estimates were available from RV surveys in NAFO 3Ps between 1960 and 1969 (Bratley *et al.*, 2000), where it was estimated to be an average of 196,500 t, giving a biomass of $2.260 \text{ t} \cdot \text{km}^{-2}$, and between 2000 and 2009 (Ings *et al.*, 2019) where it was estimated to be an average of 66,550 t, giving a biomass of $0.765 \text{ t} \cdot \text{km}^{-2}$. Large cod was the ‘leading’ stanza for both models. Small cod biomass was estimated through the model to be $B = 1.872 \text{ t} \cdot \text{km}^{-2}$ for 1960-1969, and $B = 0.998 \text{ t} \cdot \text{km}^{-2}$ for 2000-2009 (Table 4.10).

Production:Biomass

Large cod mortality Z was calculated using the average natural mortality $M = 0.3 \text{ year}^{-1}$ inferred from estimates in the Southern Gulf of Saint Lawrence by Sinclair (2001) and Swain *et al.* (2011), and the fishing mortality rate $F = 0.383 \text{ year}^{-1}$ from the 1960-1969 model, and $F = 0.265 \text{ year}^{-1}$ for the 2000-2009 model. These values respectively allowed to obtain $Z = P/B = 0.683 \text{ year}^{-1}$ and $Z = P/B = 0.565 \text{ year}^{-1}$.

Small cod mortality Z was taken from Tam and Bundy (2019) for the 1960-1969 and estimated to be $Z = P/B = 0.600 \text{ year}^{-1}$, lower than large cod biomass as a representation of the intense fishing pressure on cod larger than 45 cm. For the 2000-2009 model $Z = P/B = 1.10 \text{ year}^{-1}$ (Table 4.10).

Consumption:Biomass

Q/B for large cod was estimated from food consumption studies in a range of regions by Palomares and Pauly (1989), Pauly (1989) and Waiwood *et al.* (1980) ranging from 1.41 to 4.55 year^{-1} (Table 4.9). The average Q/B of 2.79 year^{-1} is concordant with the 2.58 year^{-1} estimate from the life-history tool in FishBase (Froese and Pauly, 2002). For small cod, the 1960-1969 model estimated a Q/B of 5.22 year^{-1} and the 2000-2009 model estimated a Q/B of 6.37 year^{-1} .

Table 4.9. Q/B values for large cod extracted from the literature for various regions of the North Atlantic and Arctic Oceans. The average Q/B calculated was used for both the 1960-1969 and 2000-2009 models.

Region	Q/B (year ⁻¹)	Source
Norway	1.41	Pauly (1989)
Denmark	1.94	Pauly (1989)
Gulf of Saint Lawrence	2.14	Waiwood <i>et al.</i> , 1980
Baltic Sea	2.17	Pauly (1989)
Georges Bank	2.19	Pauly (1989)
North Sea	2.26	Palomares and Pauly (1989)
North Sea	2.29	Palomares and Pauly (1989)
Barentss Sea	2.34	Pauly (1989)
Baltic Sea	2.58	Palomares and Pauly (1989)
Baltic Sea	2.70	Palomares and Pauly (1989)
Northwest Atlantic	3.43	Pauly (1989)
Iceland	4.08	Pauly (1989)
Faroe Islands	4.36	Pauly (1989)
Scotland	4.55	Pauly (1989)
Average Q/B	2.79	This study

Table 4.10. Input parameters for the Atlantic cod (*Gadus morhua*) multistanza group for the 1960-1969 and 2000-2009 models.

Period	Cod sizes	Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	Landings	$W_{\text{maturity}}/$ W_{inf}	K (year ⁻¹)
1960-1969	Cod > 45 cm	2.26	0.68	2.79	0.84	0.09	0.17
	Cod ≤ 45 cm	1.87	0.60	5.22	0.00	–	–
2000-2009	Cod > 45 cm	0.76	0.56	2.79	0.04	0.09	0.17
	Cod ≤ 45 cm	0.99	1.10	6.37	0.00	–	–

Diet composition

For the 1960-1969 model, large cod diet composition estimates were taken from stomach content surveys in southern Newfoundland in NAFO 3Ps by Krumsick and Rose (2012), and compared to DFO surveys in the 1960s on the Scotian Shelf and in the Bay of Fundy (Laurinolli *et al.*, 2004) to obtain more precision in the prey categorized as ‘other fish’ in Krumsick and Rose (2012). For the 2000-2009 model, diet composition taken from Krumsick and Rose (2012) was adjusted to reflect changes in the Northwest Atlantic ecosystem according to spring and summer RV surveys on the Scotian shelf in 1999 and 2000 (Bundy, 2004). Cod predation on sea cucumber,

a key fishery species in SPM, was added to the total diet composition through estimates from Francour (1997). Large cod diet is mainly composed of capelin, crabs, small planktivorous pelagic fish, and other benthic invertebrates, while the most important prey items of small cod are large zooplankton, shrimp, sand lance, and other small benthic invertebrates (Table 4.11).

Table 4.11. Diet composition for large and small cod as input in the two models. Values with an asterisk (*) mean group is present in the diet composition in very small amounts.

<i>Prey</i>	Cod > 35 cm		Cod ≤ 35 cm	
<i>Period</i>	<i>1960-1969</i>	<i>2000-2009</i>	<i>1960-1969</i>	<i>2000-2009</i>
Small cod	0.004	0.044	0.000*	0.002
American plaice	0.009	0.053	0.000*	–
Flounders	0.003	0.009	–	–
Redfish	0.004	0.004	0.001	0.005
Large demersals	0.005	0.021	–	–
Small demersals	0.019	0.016	0.004	0.016
Capelin	0.265	0.335	0.039	0.054
Haddock	0.003	0.004	–	–
Sand lance	0.075	0.067	0.120	0.194
Plank. small pelagics	0.029	0.080	0.001	0.045
Shrimp	0.077	0.052	0.113	0.170
Large crustacea	0.140	0.144	–	0.005
Sea cucumber	0.000*	0.000*	–	–
Echinoderms	0.026	0.013	–	–
Molluscs	0.058	0.020	0.045	0.000*
Squid	0.010	0.005	0.001	–
Polychaetes	0.028	–	0.057	0.034
Other benthic invert.	0.103	0.082	0.091	0.090
Large zooplankton	0.140	0.069	0.507	0.378
Small zooplankton	–	–	0.019	0.006

Balancing the model

No adjustments to the input parameters were necessary to balance the two models.

4.3.1.5 Greenland halibut (multistanza group)

Background

Greenland halibut (*Reinhardtus hippoglossoides*) is a predatory cold-water flatfish (order Pleuronectiformes) largely distributed across the North Atlantic, and living in depths ranging from

400 to 2200m (Dwyer *et al.*, 2010). The Northwest Atlantic Greenland halibut stock is assessed and managed as a single offshore population, for the entire NAFO Subarea 0+1. As an economically important species, commercial landings of Greenland halibut in 3Ps have been between 500 and 2500 tonnes per year between 1965 and 2010, peaking at the end of the 1970s and at the end of the 1990s, and steadily decreasing ever since. In SPM, commercial landings of Greenland Halibut have been consistently low through the years at less than 10 tonnes landed per year.

For both models constructed and to better represent the species' life history stages, Greenland halibut were made into a multistanza group and divided into two stanza: small Greenland halibut (i.e., size less or equal to 40 cm, 0 to 6 years old) and large Greenland halibut (i.e., size larger than 40 cm, 6 years old onwards), with a threshold corresponding to the minimum size where Greenland halibut are recruited to the fishery.

Catch

Large Greenland Halibut catch in NAFO 3Ps was available through the Sea Around Us database (www.seaaroundus.org): reconstructed catch data of all countries fishing in 3Ps was used to obtain a yearly catch estimate of $0.012 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 1960-1969 period, and of $0.016 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 2000-2009 period. There are no recorded catches by SPM fleet before 1971, while the yearly average for the 2000-2009 period is only $0.00032 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. There were no records of discards in reconstructed catch for either large or small Greenland halibut.

Biomass

Large Greenland halibut biomass was not assessed for 3PS, therefore was taken from Bundy *et al.* (2000), derived from assessments in the NAFO 2J3KLNO divisions in the early to mid-1970s, and estimated to be $B = 0.348 \text{ t} \cdot \text{km}^{-2}$ for the 1960-1969 model. For the 2000-2009 model, the estimate $B = 0.690 \text{ t} \cdot \text{km}^{-2}$ from Tam and Bundy's (2019) 2013-2015 model of the Newfoundland shelf was used, as there was no estimate closer in time and area (Table 4.12).

Biomass was calculated for large Greenland halibut, as it is the leading stanza of the multistanza group, while the model estimated small Greenland halibut biomass to be $0.089 \text{ t} \cdot \text{km}^{-2}$ for the 1960-1969 period, and $0.464 \text{ t} \cdot \text{km}^{-2}$ for the 2000-2009 period.

Production:Biomass

Large Greenland halibut mortality Z was calculated using a natural mortality M of 0.12 year⁻¹ calculated through FishBase's Life History Tool with an average temperature of 3.5°C and an asymptotic length of 114.5 cm. With the fishing mortality $F = 0.034$ year⁻¹ in the 1960-1969 model, $Z = P/B = 0.154$ year⁻¹, which means a production of 0.0535 t·km⁻²·year⁻¹. In the 2000-2009 model, Z was calculated using $M = 0.12$ year⁻¹ and $F = 0.024$ year⁻¹, leading to $Z = P/B = 0.144$ year⁻¹, which means a production of 0.994 t·km⁻²·year⁻¹. As these estimates seemed low in comparison to other models, the averaged value of 0.337 year⁻¹ in 1960-1969 and 0.332 year⁻¹ in 2000-2009 were calculated using a total mortality estimate of 0.52 year⁻¹ for older age class halibut from Tam and Bundy's (2019). P/B for small Greenland halibut was assumed to be 0.918 year⁻¹ for both models according to estimates from Tam and Bundy (2019) (Table 4.12).

Consumption:Biomass

Q/B ratio for Greenland halibut was calculated to be 1.30 year⁻¹ from FishBase's life history tool, for a preferred temperature of 3.5°C, and this value was used in both models. For small Greenland halibut, the 1960-1969 model estimated a Q/B of 3.76 year⁻¹ and the 2000-2009 model a Q/B of 3.51 year⁻¹.

Table 4.12. Input parameters for the Greenland halibut (*Reinhardtus hippoglossoides*) multistanza group for the 1960-1969 and 2000-2009 models.

Period	Size	Biomass (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	Landings	$W_{\text{maturity}}/W_{\text{inf}}$	K (year ⁻¹)
1960-1969	G. halibut > 40 cm	0.35	0.34	1.30	0.01	0.09	0.09
	G. halibut ≤ 40 cm	0.09	0.92	3.76	0.00	—	—
2000-2009	G. halibut > 40 cm	0.69	0.33	1.30	—	0.09	0.09
	G. halibut ≤ 40 cm	0.46	0.92	3.51	0.00	—	—

Diet composition

For the 1960-1969 model, large Greenland halibut diet was taken from RV surveys conducted on the Scotian Shelf between 1958 and 1969, while small Greenland halibut diet was

taken from surveys conducted on the Scotian shelf between 1960 and 1967, as estimated by Bundy (2004).

Diet composition for large and small Greenland halibut was adjusted to the 2000-2009 model with stomach content analysis conducted in the Northwest Atlantic between 1998 and 2003 by Dwyer *et al.* (2010), and data collected in NAFO zone 4RS between 1997 and 2002, as extracted by Morissette *et al* (2003) in their Ecopath model of the Northern Gulf of Saint Lawrence.

Large Greenland halibut diet is mostly composed of capelin, small demersal fishes such as silver hake, and sand lance, with a notable diminution in time of the proportion of sand lance in their diet. Small Greenland halibut mostly feed on shrimps, capelin, euphausiids and other large zooplankton (Table 4.13)

Table 4.13. Diet composition for large and small Greenland halibut as input in the two models.

<i>Prey</i> <i>Period</i>	G. halibut > 35 cm		G. halibut ≤ 35 cm	
	<i>1960-1969</i>	<i>2000-2009</i>	<i>1960-1969</i>	<i>2000-2009</i>
Small cod	0.031	0.011	—	—
American plaice	0.140	0.111	0.016	0.014
Flounders	0.031	0.031	0.007	0.007
Skates	0.028	0.028	—	—
Small demersals	0.156	0.156	0.038	0.038
Capelin	0.100	0.200	0.290	0.269
Haddock	0.094	0.094	0.005	0.054
Sand lance	0.150	0.050	0.050	0.004
Pisci. small pelagics	0.014	0.014	—	—
Plank. small pelagics	0.044	0.094	—	—
Shrimp	0.094	0.094	0.350	0.400
Echinoderms	0.003	0.003	0.007	0.007
Molluscs	—	—	0.007	0.007
Squid	0.031	0.031	0.019	0.019
Polychaetes	—	—	0.018	0.018
Other benthic invert.	0.062	0.062	0.062	0.033
Large zooplankton	0.021	0.021	0.130	0.130

Balancing the model

No adjustments to the input parameters were necessary to balance the two models.

4.3.1.6 Atlantic halibut (multistanza group)

Background

Atlantic halibut (*Hippoglossus hippoglossus*) is the largest species of cold-water flatfish (order Pleuronectiformes) largely distributed across the Northwest Atlantic through northern Greenland, and spawning on continental slopes. Atlantic halibut are demersal and slow growing, and can reach a maximum size of 3m, presenting sexual dimorphism with females being able to reach 1.5 times the size of males (den Heyer *et al.*, 2015). The Atlantic halibut stock is divided into two management units across the Southern Grand Banks and the Scotian Shelf (NAFO 3NOPS, NAFO 4VWX and NAFO 5Zc), and in the Gulf of Saint Lawrence (4RST). In SPM, Atlantic Halibut is a valuable species for local fisheries.

For both models constructed and to better represent the species' life history stages, i.e., the change between juvenile and adult stages, Atlantic halibut was made into a multistanza group and divided into two stanza: small Atlantic halibut (i.e., size less or equal to 65 cm, 0 to 6 years old) and large Atlantic halibut (i.e., size larger than 65 cm, 6 years old onwards), with a threshold corresponding to age at maturity and the size halibut are selected for the trawl gear fisheries, and hoping to account for changes in diet, as Atlantic halibut larger than 65 cm shift to a mostly piscivorous diet. This threshold is approximative, as accounting for sexual dimorphism and temporal evolutions in length at 50% maturity can present a challenge (Bundy, 2004; den Heyer *et al.*, 2015).

Catch

Total landings of Atlantic halibut by all fleets fishing in NAFO 3Ps between 1960 and 1969 amounted to 3,478 t, which corresponds to a yearly average of $0.004 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. In SPM, average annual landings are low, at $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. Between 2000 and 2009, total landings amounted to 1,739 t, which corresponds to a yearly average of $0.002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. No landings were recorded by SPM's fleet during this period. All catch were allocated to the large Atlantic halibut stanza, as small Atlantic halibut are too small to be landed according to the fishery's regulations. Discards were split between small (80%) and large (20%) Atlantic halibut assuming small halibut are more likely to be discarded as they do not meet the minimal authorized catch size. Average yearly discards for small Atlantic halibut were $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969, and $0.0002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$

¹ in 2000-2009, while average yearly discards for large Atlantic halibut were less than $0.0005 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for both periods.

Biomass

As Atlantic halibut is assessed as one large stock over the Grand Banks, annual biomass estimates were not available for NAFO 3Ps. Biomass estimates for the 1960-1969 model were therefore taken from Bundy (2004) model of the Scotian Shelf, as they were available for both stanza and were adjusted for catchability. The closest estimates in time from Bundy (2004) were between 1980 and 1985 and were an average of $B = 0.054 \text{ t} \cdot \text{km}^{-2}$ for large halibut. The model estimated a biomass of $0.011 \text{ t} \cdot \text{km}^{-2}$ for small halibut.

For the 2000-2009 model, biomass estimates were derived from longline surveys and tagging in NAFO 3NOPS, NAFO 4VWX, and NAFO 5Zc between 2000 and 2008 by Trzcinski *et al.* (2009). Average annual biomass was $0.022 \text{ t} \cdot \text{km}^{-2}$ for large halibut, and the model estimated a biomass of $0.004 \text{ t} \cdot \text{km}^{-2}$ for small halibut (Table 4.14).

Production:Biomass

Trzcinski *et al.* (2016) estimated natural Atlantic halibut mortality to be 0.10 year^{-1} , while Heyer *et al.* (2013) estimated the average natural mortality to be 0.22 year^{-1} through tagging studies. As this aforementioned average included both stanzas, and since indirect estimates through a range of studies review by Heyer *et al.* (2013) were ranging from 0.02 to 0.34 year^{-1} , natural mortality was assumed to be 0.10 year^{-1} for large halibut and 0.30 year^{-1} for small halibut. In the 1960-1969 model, total mortality Z for large Atlantic halibut was estimated using the natural mortality $M = 0.10 \text{ year}^{-1}$ and the fishing mortality $F = 0.088 \text{ year}^{-1}$ given by the model, to get $Z = P/B = 0.188 \text{ year}^{-1}$. For small Atlantic halibut, mortality was calculated using $M = 0.30 \text{ year}^{-1}$ and $F = 0.117 \text{ year}^{-1}$ to get $Z = P/B = 0.417 \text{ year}^{-1}$.

In the 2000-2009 model, large halibut mortality was estimated to be $Z = P/B = 0.191 \text{ year}^{-1}$ using $M = 0.01 \text{ year}^{-1}$ and $F = 0.091 \text{ year}^{-1}$ given by the model. For small halibut, it was estimated to be $Z = P/B = 0.333 \text{ year}^{-1}$ using $M = 0.30 \text{ year}^{-1}$ and $F = 0.033 \text{ year}^{-1}$ given by the model (Table 4.14).

Consumption: Biomass

Q/B ratio for large halibut was estimated assuming that $P/Q = 0.15$, with a production of $0.011 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for 1960-1969 and of $0.004 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for 2000-2009. This led to consumption values of respectively $0.070 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ and $0.028 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. Q/B was estimated to be 1.36 year^{-1} in the 1960-1969 model and 1.27 year^{-1} in the 2000-2009 model. For small halibut, the model calculated a Q/B of 3.18 year^{-1} for 1960-1969, and 2.85 year^{-1} for 2000-2009 (Table 4.14).

Table 4.14. Input parameters for the Atlantic halibut (*Hippoglossus hippoglossus*) multistanza group for the 1960-1969 and 2000-2009 models.

Period	Size	Biomass ($\text{t} \cdot \text{km}^{-2}$)	P/B (year^{-1})	Q/B (year^{-1})	Landings	$W_{\text{maturity}}/W_{\text{inf}}$	K (year^{-1})
1960-1969	A. halibut > 40 cm	0.05	0.18	1.36	0.004	0.09	0.10
	A. halibut $\leq$ 40 cm	0.01	0.42	3.18	0.000	—	—
2000-2009	A. halibut > 40 cm	0.02	0.19	1.27	0.002	0.09	0.10
	A. halibut $\leq$ 40 cm	0.01	0.33	2.85	0.000	—	—

Diet composition

Diet composition for both large and small Atlantic halibut in 1960-1969 was estimated through seasonal trawl surveys conducted between 1958 and 1969 by Kohler (1967). Diet was adjusted to the 2000-2009 model, through diet information gathered by Cargnelli *et al.* (1999) and from seasonal surveys conducted in 1999 and 2000 on the Scotian Shelf (Bundy, 2004). Large Atlantic halibut primarily feed on flatfishes, small demersals and shrimps, while small Atlantic halibut primarily feed on small cods, shrimps and other small crustaceans (Table 4.15).

Table 4.15. Diet composition for large and small Greenland halibut as input in the two models.

<i>Prey</i> <i>Period</i>	A. halibut > 35 cm		A. halibut ≤ 35 cm	
	<i>1960-1969</i>	<i>2000-2009</i>	<i>1960-1969</i>	<i>2000-2009</i>
Small cod	0.039	0.018	0.100	0.040
American plaice	0.136	0.130	–	–
Flounders	0.136	0.130	–	–
Redfish	0.039	0.030	–	–
Small demersals	0.195	0.121	0.050	0.040
Shrimp	0.323	0.323	0.160	0.140
Large crustacea	0.094	0.094	0.025	0.025
Echinoderms	0.008	0.008	–	–
Molluscs	0.017	0.026	0.065	0.045
Polychaetes	0.013	0.014	–	–
Other benthic invert.	–	0.106	0.550	0.660
Large zooplankton	–	–	0.050	0.050

Balancing the model

No adjustments to the input parameters were necessary to balance the two models.

4.3.1.7 American plaice*Background*

American plaice (*Hippoglossoides platessoides*) is a demersal flatfish (order Pleuronectiformes) distributed across continental shelves in the North Atlantic Ocean. Similar as other flatfish of the same order, American plaice is a slow growing cold-water species where the females have a faster growth rate than the males, and exhibits opportunistic feeding behaviors. Stock assessments and management for American Plaice are divided by specific NAFO divisions. In NAFO 3Ps, spawning is widespread across the subdivision (Morgan *et al.*, 2020).

Catch

Between 1960-1969, total reconstructed landings of American plaice by all fleets fishing in NAFO 3Ps amounted to approximately 50,347 t landed, giving an average of $0.059 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. SPM fleet landed an average of $0.003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ of American plaice. Between 2000-2009, total reconstructed landings of American plaice by all fleets fishing in NAFO 3Ps amounted to approximately 2,870 t landed, giving an average of $0.003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, while SPM fleet landed an average of $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$.

Reconstructed discards were especially high between 1960-1969, with an average of $0.386 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ of American plaice discarded, while discards were minimal between 2000-2009 with an average of $0.00005 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ discarded. This high tonnage of discards in the past can be linked back to the extensive discarding habits during the cod fisheries between 1950 and 1992.

Biomass

In NAFO 3Ps, American plaice biomass was declining from the mid-1980s to 1995 and showed some increase in the early 2000s. Biomass was available through DFO stock assessment surveys in 3PS. The oldest available data point was in 1983, and an average biomass was calculated from 1983 to 1985 knowing the stock decline happened after 1985 and that no tendency in biomass could be observed between 1983 and 1985 (Morgan *et al.*, 2002). As no other estimate was available for 3Ps, the average biomass estimate for 1960-1969 was $B = 1.169 \text{ t} \cdot \text{km}^{-2}$. DFO biomass surveys in 3Ps were available for the 2000-2009 period, and the average biomass estimated was $B = 0.277 \text{ t} \cdot \text{km}^{-2}$.

Production:Biomass

P/B ratio was calculated through total mortality estimates, using a natural mortality value of 0.315 year^{-1} averaged from two natural mortality estimates for the Northwest Atlantic available in FishBase (www.fishbase.org), of 0.40 year^{-1} for NAFO division 3N and 0.23 year^{-1} for NAFO division 3L. Both values were originally provided by Pitt's (1975) study of American plaice biology on Grand Banks. For the 1960-1969 model, the fishing mortality given by the model was $F = 0.383 \text{ year}^{-1}$, which led to an estimated $Z = P/B = 0.698 \text{ year}^{-1}$. For the 2000-2009 model, the fishing mortality given by the model was $F = 0.132 \text{ year}^{-1}$, which led to an estimated $Z = P/B = 0.328 \text{ year}^{-1}$.

Consumption:Biomass

Three different estimates of consumption were available for American plaice. The first one from daily ration surveys in the Grand Banks of Newfoundland from Zamarro (1992), using models from Elliott and Persson (1978), estimated a mean daily consumption of 0.34% of body mass per day, which would lead to a Q/B ratio of 1.241 year^{-1} with a mean consumption of $1.451 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969 and $0.344 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. The second estimate was

available from consumption studies in New Brunswick by MacDonald and Waiwood (1987) where mean daily consumption was estimated to be 1.28% of body mass per day, which would lead to a Q/B ratio of 4.672 year^{-1} with a mean consumption of $5.458 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 1960-1969 and $1.294 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 2000-2009. The third estimate of $Q/B = 1.700 \text{ year}^{-1}$ was given by FishBase for a temperature of 3°C , and would entail a mean consumption of $1.987 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 1960-1969 and $0.471 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 2000-2009. As no study was conducted to encompass the scope of 3Ps, these three values were averaged to obtain a mean Q/B of 2.538 year^{-1} which could reflect the fewer constraints on feeding in the 1960s due to higher prey availability, seen through the general higher biomass of the system. For the 2000-2009 model, the FishBase value of 1.700 year^{-1} was used.

Diet composition

For the 1960-1969 model, diet composition was extracted from stomach content studies in Western Nova Scotia from 1969 to 1972 by Langton and Bowman (1980), as it was the closest available estimate in time and area. For the 2000-2009 model, two stomach content studies were used to estimate diet composition: one in Georges Banks and the Scotian Shelf in the 1980s (Bowman *et al.*, 2000), and the other in the Flemish Cap Bank in 1993 (Rodriguez Marin *et al.*, 1994). Principle prey items include echinoderms such as brittle stars, large and small crustaceans, hyperiids and shrimp (Table 4.16).

Table 4.16. Diet composition of American plaice as input in the two models. Values with an asterisk (*) indicate that the group is present in the diet composition in very small amounts.

<i>Prey</i> <i>Period</i>	American plaice	
	<i>1960-1969</i>	<i>2000-2009</i>
Small cod	0.002	–
Flounders	–	0.001
Redfish	–	0.000*
Small demersals	0.006	0.002
Capelin	0.000*	0.090
Sand lance	–	0.058
Plank. small pelagics	–	0.003
Large crustacea	0.050	0.050
Shrimp	0.030	0.166
Echinoderms	0.746	0.350
Molluscs	0.046	0.013
Squid	–	0.001
Polychaetes	0.028	0.070
Other benthic invertebrates	0.045	0.169
Large zooplankton	0.047	0.134

Balancing the model

No adjustments to the input parameters were necessary to balance the 1960-1969 model. In the 2000-2009 model, the proportion of American plaice in the diet of large cod, large Greenland halibut and large pelagics was lowered to reflect the post-1980s decline in American plaice availability as a prey and balance the group's *EE* that was too high.

4.3.1.8 Flounders

Background

Three main species of flounders can be found in NAFO 3Ps: winter flounder (*Pseudopleuronectes americanus*), witch flounder (*Glyptocephalus cynoglossus*), and yellowtail flounder (*Myxopsetta ferruginea*). Flounders are adapted for benthic living through their flattened shape and the position of their eyes on the top of their body, allowing them to swim along the bottom of the ocean and to feed on a variety of benthic preys, usually preferring shallower waters where they spawn (Link *et al.*, 2002). In NAFO 3Ps, only the witch flounder stock is assessed and managed as a separate unit within the subdivision, being a key species for fisheries. Witch founder

is found in highest abundance on the edge of Saint Pierre Bank, and spawning occurs from January to April in deeper offshore areas of 3Ps (Bowering, 1989). Winter flounder ranges from Labrador to Georgia, and spawning occurs in the late winter to late spring (McCracken, 1963), while yellowtail flounder is found in higher abundance on the shelf of Saint Pierre and Grand Bank, with spawning occurring in late spring to early summer (Pitt, 1970).

Catch

Total reconstructed landings for the three species of flounders caught by all countries fishing in NAFO 3Ps amounted to 33,913 t between 1960-1969, implying an average catch of $0.039 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ and to 14,348 t between 2000-2009, implying an average catch of $0.0165 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. SPM landed an average of $0.002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969 and of $0.003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 2000-2009. Flounders reconstructed discards were an average of $0.115 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969 and $0.0004 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009.

Biomass

Witch flounder biomass was available from DFO surveys in 3Ps with the earliest data point in 1983. As no significant trend in biomass could be observed, an average was calculated over five years between 1983 and 1987 to get $B = 0.129 \text{ t} \cdot \text{km}^{-2}$ which was used as the biomass reference for the 1960-1969 model. Since no estimate was available for other flounder species in 3Ps, this value was conservatively doubled to get a biomass estimate of $0.257 \text{ t} \cdot \text{km}^{-2}$.

Witch flounder biomass was available from DFO surveys for 2000-2009 in 3Ps and estimated to be $B = 0.114 \text{ t} \cdot \text{km}^{-2}$. Bundy (2004) estimated total flounders' biomass to be $0.668 \text{ t} \cdot \text{km}^{-2}$ in 1995-2000 from the Newfoundland Shelf RV survey data, and as this value is adjusted for catchability and no biomass estimate was available in 3Ps for other flounder species, this value was used for the model.

Production:Biomass

P/B ratio for the 1960-1969 model was estimated using $M = 0.20 \text{ year}^{-1}$, averaged from two natural mortality of 0.15 year^{-1} in Southern New England (Lux, 1969) for yellowtail flounder and 0.3 year^{-1} on the east coast of Canada for winter flounder (Beverton *et al*, 1959), and the fishing

mortality $F = 0.261 \text{ year}^{-1}$ given by the model to get $Z = P/B = 0.461 \text{ year}^{-1}$. For the 2000-2009 model, total mortality was estimated using $M = 0.20 \text{ year}^{-1}$ and the fishing mortality from the model $F = 0.029 \text{ year}^{-1}$ to get $Z = P/B = 0.229 \text{ year}^{-1}$.

Consumption: Biomass

A Q/B of 4.60 year^{-1} was estimated by Grosslein *et al.* (1980) from consumption studies between 1963 and 1972 on Georges Bank. Stomach content analysis conducted between 1995 and 2000 on the Scotian Shelf gave Q/B estimates of 4.70 year^{-1} for yellowtail flounder, 2.40 year^{-1} for witch flounder and 1.70 year^{-1} for winter flounder (Bundy, 2004), giving an average of 2.933 year^{-1} for the flounders group. As no biomass estimate was available for each group, this average was used in lieu of a biomass weighted average. FishBase calculated values of 2.30 year^{-1} for yellowtail flounder, 2.00 year^{-1} for witch flounder and 1.80 year^{-1} for winter flounder at a temperature of 3°C . The final value averaged from all sources was 2.258 year^{-1} , and was used for both models, as no prior consumption assessments were available for all three species.

Diet composition

Diet composition for the 1960-1969 model was estimated from yellowtail flounder stomach content sampling conducted between 1968 and 1973 on Grand Bank (Pitt, 1976), and from witch flounder sampling in the eastern Atlantic (Rae, 1969). Diet composition for the 2000-2009 was taken from yellowtail and witch flounder stomach content surveys conducted in the Newfoundland Grand Banks between 2010 and 2015 (Tam and Bundy, 2019), and DFO stomach content samples from the Scotian Shelf in 1999 and 2000 (Bundy, 2004). Benthic invertebrates, including annelids and small crustaceans, small fish, and large zooplankton make up the most part of flounders diet (Table 4.17).

Table 4.17. Diet composition of flounders as input in the two models. Values with an asterisk (*) indicate that the group is present in the diet composition in very small amounts.

<i>Prey</i> <i>Period</i>	Flounders	
	1960-1969	2000-2009
Redfish	—	0.003
Small demersals	0.007	0.002
Capelin	0.025	0.011
Sand lance	0.025	0.036
Shrimp	0.007	0.019
Large crustacea	0.000*	0.000*
Echinoderms	0.053	0.000*
Molluscs	0.035	0.035
Polychaetes	0.470	0.208
Other benthic invertebrates	0.351	0.507
Large zooplankton	0.027	0.209

Balancing the model

As biomass was an estimate with high uncertainty and *EE* was too high in the 1960-1969 model, flounders' *EE* was set to the textbook value of 0.95 to obtain a new biomass estimate of 0.885 t·km⁻². No adjustments to the input parameters were necessary to balance the 2000-2009 model.

4.3.1.9 Skates

Background

Around ten species of skates (Family: Rajidae) are found around Newfoundland and in 3Ps, with the most common species being thorny skate (*Amblyraja radiata*), smooth skate (*Malacoraja senta*) and spinytail skate (*Bathyraja spinicauda*). Other species include Barndoor's, winter and Bigelow's skates. Thorny skate is assessed and managed as one stock on Grand Banks (NAFO divisions 3LNOPs), and has a widespread distribution across Saint Pierre Bank and 3Ps on a wide range of depths, but mostly concentrated between 50 to 150 meters. Reproductive events occur all year long on the Banks, with winter migrations on the edge of the shelf (Kulka and Miri, 2003). Skates make up a considerable part of commercial bycatch, while Canada's interest in skate fisheries mainly developed post 1990s following declines in other commercially exploited fish stocks. SPM skate fisheries in 3Ps were high from the 1970s to 1992, and increased again after 2000.

Catch

Total reconstructed landings for all fleets fishing in NAFO 3Ps amounted to 435 t between 1960-1969, implying an average catch of $0.0005 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, while the only landings recorded between 2000-2009 were from SPM boats. Average yearly catch by SPM's fleet was $0.0005 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969 and $0.002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 2000-2009. Average yearly discards were of $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969, with half of this amount being discarded by SPM's fleet, and of $0.027 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 2000-2009, the entire amount discarded by SPM.

Biomass

Thorny skate's biomass, the representative species of this group, was available from DFO assessments starting in 1972 in 3Ps (DFO, 2022), and a five-year average was calculated between 1972 and 1976 to get $B = 0.202 \text{ t} \cdot \text{km}^{-2}$, which was used as a reference biomass for the 1960-1969 model. As thorny skate is said to make up over 90% of the skates' biomass in Grand Banks surveys (DFO, 1998), this amount was assumed to be representative of the group, though likely to be an underestimate. Similarly, thorny skate biomass available between 2000 and 2009 from 3Ps DFO surveys (DFO, 2022) was used to calculate the yearly average $B = 0.395 \text{ t} \cdot \text{km}^{-2}$ for the skates group in the later model.

Production:Biomass

No production estimate was available for skates in 3Ps. Several natural mortality estimates were available in the literature, of $M = 0.214 \text{ year}^{-1}$ (Simon and Frank, 1996), 0.280 year^{-1} for thorny skate in FishBase, and 0.170 year^{-1} for smooth skate in FishBase (Froese and Pauly, 2002). In the 1960-1969 model, P/B was calculated using a natural mortality estimate of $M = 0.220 \text{ year}^{-1}$, averaged from the aforementioned values, and the fishing mortality $F = 0.011 \text{ year}^{-1}$ to get $P/B = Z = 0.231 \text{ year}^{-1}$, which is equal to a production of $0.043 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. In the 2000-2009 model, P/B was calculated using $M = 0.22 \text{ year}^{-1}$ and the $F = 0.01 \text{ year}^{-1}$ from the model to get $P/B = Z = 0.233 \text{ year}^{-1}$, which is equal to a production of $0.116 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$.

Consumption:Biomass

Bundy (2004) estimated a Q/B of 1.888 year^{-1} for the 1995-2000 model of the Scotian Shelf, and FishBase estimates a Q/B of 1.60 year^{-1} for thorny skates, 2.30 year^{-1} for smooth skates and 1.10 year^{-1} for spinytail skates at a temperature of 5° C . Skates consumption estimates from Link and Sosebee (2008) calculated for the Northeastern US for 2000 to 2005 calculated a mean consumption of $0.295 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ giving a Q/B estimate of 1.460 year^{-1} for the 1960-1969 model. However, we assume that this species would eat at least as much as its biomass, so the lower consumption limit would be $0.395 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 2000-2009 model, giving a Q/B estimate of 1.000 year^{-1} . Another consumption estimate for thorny skates of $0.395 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ was given by Dolgov (1997), giving Q/B estimates of 1.955 year^{-1} for the 1960-1969 model and 1.00 year^{-1} for the 2000-2009 model. A study of thorny $\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ which would lead to a Q/B of 2.361 year^{-1} for the 1960-1969 model and of $1.208 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for the 2000-2009 model. The averaged values of 1.860 year^{-1} and 1.352 year^{-1} were used respectively for the first and second models.

Diet composition

Thorny skates exhibit opportunistic bottom feeding behaviors (Kulka and Miri, 2003). For the 1960-1969 model, seasonal diet samples were available for the years 1969 and 1970 by McEachran et al. (1976) from the mid-Atlantic Bight, Georges Bank, and the Scotian Shelf. Data sampled was averaged for the four periods of the year sampled. For the 2000-2009 model, diet composition was taken from surveys for three skate species (i.e., thorny, winter and smooth skate) on the Scotian Shelf in 1999 and 2000 (Bundy, 2004) as it was the closest representative time period, and compared with data from seasonal stomach content sampling between 2002-2005 from five species of skates in the 3NO NAFO divisions from Gonzales Iglesias (2006) (Table 4.18).

Table 4.18. Diet composition of skates as input in the two models.

<i>Prey</i> <i>Period</i>	<i>Skates</i>	
	<i>1960-1969</i>	<i>2000-2009</i>
Flounders	0.010	–
Skates	0.010	–
Redfish	0.010	0.002
Large demersals	0.005	–
Small demersals	0.015	0.005
Capelin	–	0.004
Sand lance	0.010	0.100
Pisci. small pelagics	–	0.001
Plank. small pelagics	0.010	0.003
Shrimp	0.148	0.086
Large crustacea	0.099	0.002
Molluscs	0.064	–
Squid	–	0.001
Polychaetes	0.206	0.141
Other benthic invertebrates	0.102	0.162
Large zooplankton	0.310	0.493

Balancing the model

As skates *EE* was too high in the 1960-1969 model, and biomass was the parameter with the most uncertainty, *EE* was set to 0.95 to obtain a new biomass estimate of $B = 0.345 \text{ t} \cdot \text{km}^{-2}$. No adjustments to the input parameters were necessary to balance the 2000-2009 model.

4.3.1.10 Redfish*Background*

The group redfish (subfamily: Sebastinae) is represented by three species, the beaked redfish (*Sebastes mentella*), the Acadian redfish (*Sebastes fasciatus*) and the golden redfish (*Sebastes marinus*). Redfish are slow-growing and long-living fishes distributed largely through the Atlantic and Pacific Oceans. In the Atlantic Northwest, their south range limit is southern New Jersey while their north range limit is northern Labrador to Greenland, and they are assessed as three different management units (i.e., NAFO units 1, 2, 3) (DFO, 1999). Female redfish have the particularity to be viviparous, with live young released during the spawning season in spring. Redfish are found in the bottom of the water column, as well as in mid waters, usually described as a semi pelagic species (DFO, 1995).

Catch

Total reconstructed landings for all fleets catching redfish in NAFO 3Ps amounted to 91,304 t between 1960-1969, implying an average catch of $0.105 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, and to 15,652 t between 2000-2009, implying an average catch of $0.018 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. Average yearly catch by SPM's fleet was $0.008 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969 and $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 2000-2009. Average yearly discards were of $0.754 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969, and $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ by SPM's fleets. Between 2000-2009, discards were of $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ and $0.0002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ by SPM's fleets.

Biomass

For the 1960-1969 model, biomass was calculated from acoustic surveys conducted in the NAFO 3P zone (i.e., made up of subdivisions 3Ps and 3Pn) from 1973 to 1985 (Atkinson and Power, 1987). The average biomass of 36,381 tonnes was calculated over a five-year average, leading to $B = 0.419 \text{ t} \cdot \text{km}^{-2}$. As this estimate seemed considerably lower than other estimates for adjacent areas and only accounted for trawlable biomass, DFO's (1995) estimates on redfish status in NAFO unit 2 (i.e., including NAFO 3Ps, 3Pn, 4Vs and 4Vn) were used to calculate a biomass of $B = 0.881 \text{ t} \cdot \text{km}^{-2}$ in the 1970s, which was used for the first model.

For the 2000-2009 model, DFO's (1995) surveys estimates in NAFO 3Ps were only available until 1993. Instead, biomass estimated by Bundy (2004) for the Scotian Shelf for 1995 to 2000 was used with a q adjusted $B = 2.556 \text{ t} \cdot \text{km}^{-2}$, as this estimate was deemed more representative of the period of the model.

Production:Biomass

P/B was obtained using a natural mortality estimate of $M = 0.24 \text{ year}^{-1}$, average from two values given by FishBase of 0.16 year^{-1} for *Sebastes mentella* and 0.30 for *Sebastes fasciatus*, for an average temperature of 5°C . Fishing mortality from the models was $F = 0.391 \text{ year}^{-1}$ in 1960-1969 and $F = 0.008 \text{ year}^{-1}$ in 2000-2009. The resulting P/B were 0.631 year^{-1} for the 1960-1969 model, and 0.248 year^{-1} for the 2000-2009 model.

Consumption: Biomass

Dolgov and Drevetnyak (1990) estimated redfish consumption to biomass ratios to vary between 1.30 year⁻¹ and 6.00 year⁻¹ in the Barentss Sea. FishBase gave Q/B estimates of 2.60 year⁻¹ for *S. mentella* and 2.90 year⁻¹ for *S. fasciatus*. The average value of 2.75 year⁻¹ was used for both models.

Diet composition

Redfish diet composition was taken from Bundy (2004) estimates from the Scotian Shelf in the 1970, and from 1995-2000, as these two periods were the closest available estimates for the two models. As only spring and summer stomach content samples were collected in the 1990s surveys on the Scotian Shelf, diet composition was compared with 1993 to 1999 survey estimates for the Northern Gulf of Saint Lawrence (Morissette *et al.*, 2003) to include winter samples in the diet composition estimates for the 2000-2009 model. Redfish mostly feed on shrimps, krill and other small crustaceans (Table 4.19).

Table 4.19. Diet composition of redfish as input in the two models. Values with an asterisk (*) indicate that the group is present in the diet composition in very small amounts.

<i>Prey</i> <i>Period</i>	Redfish	
	<i>1960-1969</i>	<i>2000-2009</i>
Small cod	—	0.000*
Redfish	—	0.006
Small demersals	—	0.007
Capelin	—	0.051
Sand lance	—	0.004
Pisci. small pelagics	—	0.001
Plank. small pelagics	0.000*	0.073
Shrimp	0.279	0.440
Squid	—	0.002
Other benthic invertebrates	0.008	0.059
Large zooplankton	0.673	0.315
Small zooplankton	0.040	0.041

Balancing the model

Redfish are known to not be well sampled by bottom trawl surveys in relation to their semi pelagic nature (Bundy, 2004). As the biomass estimates for the 1960-1969 model were low and the EE of redfish too high, EE was set to the value of 0.95 to obtain a new biomass estimate $B =$

2.195 t·km⁻². This estimate seems to match the general Northwest Atlantic trends, where redfish biomass peaked in the 1970s and declined in the 1990s (Bundy, 2004). In the 2000-2009 model, Q/B was decreased to 2.40 year⁻¹ as GE was too low (i.e., < 10%), which is consistent with Q/B estimates for the Newfoundland Shelf by Bundy *et al.* (2000).

4.3.1.11 Other demersal fishes

Background

Demersal fishes are usually deep-water fishes feeding along the bottom of the water column. Demersal fishes have been split into two groups: small and large demersals. Large demersal fishes include species like white hake (*Urophycis tenuis*), cusk (*Brosme brosme*), American anglerfish or monkfish (*Lophius americanus*), Atlantic wolffish (*Anarhichas lupus*), pollock (*Pollachius virens*) and other species of the Gadidae and Lotidae families. In this group, white hake, monkfish and pollock are assessed as independent management units in NAFO 3Ps. Wolffish is assessed for NAFO division 3P (i.e., including subdivisions 3Ps and 3Pn). Pollock is found mostly along the slopes of the Saint Pierre and Grand Banks, and though the fishery is existent, it is not major commercial species. Small demersal fishes include silver hake (*Merluccius bilinearis*), as well as small eelpouts (family: Zoarcidae), sculpins (family: Cottidae) and blennies (family: Blenniidae). Though silver hake is commercially fished in NAFO 3Ps, very little information was available for this group in the study area.

Catch

Large demersal fishes total landings by all fleets fishing in NAFO 3Ps were mainly made of white hake and pollock catches, and amounted to a yearly average of 0.090 t·km⁻²·year⁻¹ landed between 1960-1969, and of 0.011 t·km⁻²·year⁻¹ between 2000-2009. Average yearly landings by SPM's fleet were around 0.001 t·km⁻²·year⁻¹ for both periods. Average yearly discards were 0.176 t·km⁻²·year⁻¹ between 1960-1969, and 0.001 t·km⁻²·year⁻¹ by SPM's fleets. Between 2000-2009, discards were 0.003 t·km⁻²·year⁻¹ and 0.0003 t·km⁻²·year⁻¹ by SPM's fleets.

Small demersal fishes total landings by all fleets fishing in NAFO 3Ps were entirely made of silver hake catches and amounted to a yearly average of 0.026 t·km⁻²·year⁻¹ landed between 1960-1969, and of 0.018 t·km⁻²·year⁻¹ between 2000-2009. There were no recorded landings of

silver hake by SPM for both periods. Average yearly discards were of $0.723 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969, and $0.0002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ by SPM's fleets. Between 2000-2009, discards were of $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for all fleets with almost no discards by SPM.

Biomass

Large demersal fishes biomass was available from surveys conducted in NAFO 3Ps for white hake, wolffish (*Anarhichas lupus* and *Anarhichas minor*) and monkfish for the years 1986 to 1990 (Kulka, 1996). The average biomass calculated was $B = 0.122 \text{ t} \cdot \text{km}^{-2}$. Additional assessments in NAFO 3Ps were available for pollock starting in 1977 (Murphy, 1999) and for white hake starting in 1972 (DFO, 2018). The adjusted biomass for the 1960-1969 model was $0.136 \text{ t} \cdot \text{km}^{-2}$. DFO surveys in NAFO 3Ps gave biomass estimates for white hake (DFO, 2018), wolffish (DFO, 2024) and monkfish (DFO, 2003). The group biomass estimated for the 2000-2009 model was $0.122 \text{ t} \cdot \text{km}^{-2}$. These estimates were both very low, and likely an underestimation of the biomass of the whole group, as no information was available for other species of large demersals. These two estimates were conservatively doubled to obtain new estimates of $B = 0.272 \text{ t} \cdot \text{km}^{-2}$ in 1960-1969 and $B = 0.244 \text{ t} \cdot \text{km}^{-2}$ in 2000-2009.

Small demersal fishes biomass estimates were available for silver hake from spring and fall surveys in the Scotian Shelf (NAFO 4VsW) and was $5.0 \text{ t} \cdot \text{km}^{-2}$ in 1980-1985 and $4.2 \text{ t} \cdot \text{km}^{-2}$ in 1995-1999 (Bundy, 2004). Bundy (2004) also estimated a biomass of $0.086 \text{ t} \cdot \text{km}^{-2}$ for small demersal piscivore feeders and of $0.032 \text{ t} \cdot \text{km}^{-2}$ for other small demersal fishes in 1980-1985, and of respectively $0.078 \text{ t} \cdot \text{km}^{-2}$ and $0.119 \text{ t} \cdot \text{km}^{-2}$ in 1995-1999. The total biomass $B = 5.118 \text{ t} \cdot \text{km}^{-2}$ was used for the 1960-1969 model and $B = 4.397 \text{ t} \cdot \text{km}^{-2}$ was used for the model 2000-2009, as no precise estimate was available for NAFO 3Ps.

Production:Biomass

For large demersals, P/B ratio was calculated using a natural mortality estimate $M = 0.15 \text{ year}^{-1}$ (i.e., averaged from three mortality estimates from FishBase of 0.22 year^{-1} for pollock, 0.12 year^{-1} for monkfish, 0.13 year^{-1} for white hake and 0.14 year^{-1} for wolffish) and the fishing mortalities of the two models, to get $Z = P/B = 0.654 \text{ year}^{-1}$ in 1960-1969 and $Z = P/B = 0.208 \text{ year}^{-1}$ in 2000-2009.

For small demersals, the natural mortality estimate $M = 0.4 \text{ year}^{-1}$ in the Northwest Atlantic for silver hake (Caddy and Defeo, 1996) and the fishing mortalities of the two models were used, to get $Z = P/B = 0.546 \text{ year}^{-1}$ in 1960-1969 and $Z = P/B = 0.404 \text{ year}^{-1}$ in 2000-2009.

Consumption: Biomass

FishBase was used to estimate the Q/B ratio of both groups with assumption of a temperature of 3°C (Froese and Pauly, 2002). The resulting estimates for large demersals were 4.76 year^{-1} for pollock, 1.0 year^{-1} for monkfish, 3.10 year^{-1} for white hake and 1.30 year^{-1} for wolffish. The average Q/B value of 2.54 year^{-1} was chosen for both models, resulting in consumption estimates of $1.661 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 1960-1969 and $0.711 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 2000-2009. For small demersals, the resulting Q/B was 4.26 year^{-1} , with a consumption of $21.803 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 1960-1969 and $18.731 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 2000-2009.

Diet composition

Demersal fishes diets are diverse, reflecting the large number of species making up these groups, and poorly studied in 3Ps. Large demersals diet was only available for pollock in 3Ps through stomach content analysis by Rockwood (2016) in 2012-2014. On the Scotian shelf, winter surveys of pollock stomach contents by Laurinolli *et al.* (2004) from 1983 to 1988 gave an additional estimate. Pollock diet composition was compared to Bundy *et al.*'s (2000) composite diet estimates derived from eight large demersal fish species and weighted by the relative biomass of each. This diet composition was used for both models.

Small demersals diet was estimated using silver hake stomach content data from DFO surveys in the Scotian Shelf (Bundy, 2004) and from Rockwood (2016) in NAFO 3Ps. The aforementioned study was used in addition to Scotian shelf data in 1981-1986 for the 1960-1969 model, and in addition to Scotian shelf data in 1999-2000 for the 2000-2009 model (Table 4.20).

Table 4.20. Diet composition of large and small demersal fish as input in the two models. Values with an asterisk (*) indicate that the group is present in the diet composition in very small amounts.

<i>Prey</i>	Large demersals	Small demersals	
<i>Period</i>		<i>1960-1969</i>	<i>2000-2009</i>
Small cod	0.019	0.001	0.005
American plaice	0.004	–	–
Flounders	0.003	–	–
Skates	0.024	–	–
Redfish	0.024	–	–
Small demersals	0.103	0.010	0.045
Capelin	0.101	0.020	0.190
Haddock	–	0.000*	0.030
Sand lance	0.114	0.010	0.100
Arctic cod	0.017	0.004	–
Pisci. small pelagics	0.087	0.002	0.024
Plank. small pelagics	0.044	0.003	0.012
Shrimp	0.054	0.020	0.120
Large crustacea	0.024	0.009	–
Lobster	0.002	0.000*	–
Echinoderms	0.050	0.110	0.050
Molluscs	0.017	0.050	0.050
Squid	0.004	–	0.001
Polychaetes	0.027	0.210	0.001
Other benthic invertebrates	0.037	0.300	0.002
Large zooplankton	0.230	0.200	0.320
Small zooplankton	0.015	0.050	0.050

Balancing the model

To balance the *EE* of large demersal fishes in the 1960-1969 model, and because few biomass surveys were conducted for this group in the 3Ps zone and none for the 1960-1969 period chosen for our model, biomass was assumed to be the parameter with the more uncertainty, and *EE* was set at a fixed value of 0.95 in order to obtain a biomass estimate accurate relatively to the fishing pressure on this group. The new biomass estimate was $B = 1.798 \text{ t} \cdot \text{km}^{-2}$. The same was done in the 2000-2009 model, to obtain a new estimate of $0.312 \text{ t} \cdot \text{km}^{-2}$. As *GE* was low for both groups of demersals in the 2000-2009 model, Q/B was lowered to 2.00 year^{-1} for large demersals and 4.00 year^{-1} for small demersals.

4.3.1.12 Capelin

Background

Capelin (*Mallotus villosus*) is a small forage fish of the Osmeridae family (i.e., smelt). As a pelagic fish, capelin is distributed through the water column, and has a widespread distribution in the North Atlantic and North Pacific oceans, with high concentration in the Atlantic Northwest. In NAFO 3Ps, the capelin stock is managed as an independent management unit (DFO, 2022). Capelin are short-lived fish, which are an important prey for many higher trophic level species in the ecosystem. Spawning happens mostly in the early summer (DFO, 2022). Capelin has historically always been a commercially important species in NAFO 3Ps, especially in SPM where it used to make up a considerable part of artisanal and subsistence fisheries, and was an important symbol, alongside Atlantic cod, of the importance of fisheries for local livelihoods (Bultel and Zylich, 2015; Forest, 2022). The Northwest Atlantic stock experienced a notable decline in the early 1990s due primarily to intense fishing pressures, and shows signs of recovery since the mid-2000s.

Catch

Capelin total landings by all fleets fishing in NAFO 3Ps amounted to 1,739 t landed between 1960-1969, implying a yearly average of $0.090 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, and to 9,565 t landed between 2000-2009, with a yearly average of $0.002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. Average yearly landings by SPM's fleet were around $0.003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969, and less than $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Average yearly discards were $0.003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969, and lower than $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Discards by SPM fleets were less than $0.00001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for both periods.

Biomass

There were no available biomass assessments in NAFO 3Ps for the two periods of the study. Capelin stocks general tendency shown a decline in 1975 followed by an increase in the early 1980s, and another noticeable decline in the 1990s in the Northwest Atlantic (Carscadden, 1984; Tam and Bundy, 2019). As groundfish RV surveys generally do not cover pelagic species, acoustic surveys by Miller (1992, 1993) in NAFO 3L and 3NO between 1982 and 1988 and the

methodology used by Bundy *et al.* (2000) to integrate juvenile capelin in the biomass calculations were used to obtain a yearly biomass average of $13.770 \text{ t}\cdot\text{km}^{-2}$ used in the 1960-1969 model. Acoustic surveys were also available in NAFO 3L from 2013 to 2015 by Tam and Bundy (2019). The biomass estimate of $4.97 \text{ t}\cdot\text{km}^{-2}$ was used for the 2000-2009 model.

Production:Biomass

P/B ratios were calculated using a natural mortality of 0.70 year^{-1} , averaged from natural mortality estimates of 0.60 year^{-1} in the Northern Gulf of Saint Lawrence (Morissette *et al.*, 2003), 0.62 , 0.77 and 0.82 year^{-1} (Chamberland *et al.*, 2021), and the fishing mortalities of the models $F = 0.0006 \text{ year}^{-1}$ in 1960-1969 and $F = 0.002 \text{ year}^{-1}$ in 2000-2009. Respective P/B ratios were $Z = P/B = 0.700 \text{ year}^{-1}$ and $F = 0.702 \text{ year}^{-1}$.

Consumption:Biomass

Consumption to biomass estimates ranged from 4.3 year^{-1} to 8.5 year^{-1} on the Newfoundland Shelf (Bundy *et al.*, 2000). FishBase estimated a Q/B of 3.8 year^{-1} for capelin (Froese and Pauly, 2002). Several other consumption estimates were available: Vesin *et al.* (1981) estimated daily consumption to be between 2.50 and 5.00% of body mass in the Saint Lawrence Estuary, giving an average Q/B of 13.688 year^{-1} , and Ajiad and Pushaeva (1991) between 1.47 and 2.00% of body mass in the Barentss Sea, giving an average Q/B of 6.330 year^{-1} . The average consumption to biomass ratio derived from these estimates is 7.940 year^{-1} , consistent with the range estimated by Bundy *et al.* (2000). This value was used for both models.

Diet composition

Capelin diet composition was available from stomach contents collected at 2 time periods on Grand Banks, in March-June 1972 (Kovalyov and Kudrin, 1973) and in April-May 1987-1990 Gerasimova (1994). The 1990 diet was compared to the 1999-2000 diet collected on the eastern Scotian Shelf from Bundy (2004), as well as diet composition estimates from Placentia Bay in Southern Newfoundland in 1999 by O'Driscoll (2001) to obtain a representative average for the 2000-2009 model. Capelin mostly feeds on large and small zooplankton species, including copepods and euphausiids (Table 4.21).

Table 4.21. Diet composition of capelin as input in the two models.

<i>Prey</i>	Capelin	
	<i>1960-1969</i>	<i>2000-2009</i>
Capelin	0.013	0.022
Sand lance	0.013	0.005
Shrimp	–	0.180
Polychaetes	–	0.147
Large zooplankton	0.599	0.371
Small zooplankton	0.375	0.275

Balancing the model

To balance the *EE* of capelin, Q/B was lowered in both models to the value of 4.3 year^{-1} as estimated for the Newfoundland Shelf by Bundy *et al.* (2000), as it was unlikely to be significantly higher than the Q/B value of other small pelagic fishes. In the 2000-2009 model, the proportion of capelin was lowered in the diet of harp seals and large cod, as these two groups had the highest predation rate on capelin. Ultimately, as *EE* was still uncharacteristically high, it was set to 0.95 to obtain a new biomass estimate of $7.648 \text{ t} \cdot \text{km}^{-2}$ in 2000-2009, as biomass was an input parameter of high uncertainty.

4.3.1.13 Haddock*Background*

Haddock (*Melanogrammus aeglefinus*) is a benthic fish of the Gadidae family feeding primarily in the bottom of the water column and ranging from Greenland to Cape Hatteras in the Northwest Atlantic (Dwyers *et al.*, 2020). The haddock stock on Saint Pierre Bank (NAFO 3Ps) is assessed as an independent management unit, and is showing faster growth than the Grand Banks Stock (Wheeland *et al.*, 2020). Haddock fisheries are under a moratorium in the Northwest Atlantic since 1993 due to critical stock depletion.

Catch

Total landings by all fleets fishing in NAFO 3Ps amounted to $0.078 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969, and $0.018 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 2000-2009. Average yearly landings by SPM's fleet were around $0.003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969, and $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Average

yearly discards were $0.072 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969, and lower than $0.002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Discards by SPM fleets were less than $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for both periods.

Biomass

Biomass estimates were available for the 1960s and the 2000s from RV surveys in NAFO 3Ps (Dwyers *et al.*, 2020). Biomass was an average of $0.034 \text{ t} \cdot \text{km}^{-2}$ and $0.038 \text{ t} \cdot \text{km}^{-2}$ in 2000-2009.

Production:Biomass

As the fishing mortality in the models was very high and biomass uncertain, P/B ratios were taken from Bundy (2004) estimates for NAFO divisions 4TVW. The 1980-1985 value of 0.450 year^{-1} was used in the 1960-1969 model, and the 1995-2000 value of 0.510 year^{-1} was used in the 2000-2009 model.

Consumption:Biomass

FishBase gave a Q/B value of 4.96 year^{-1} (Froese and Pauly, 2002), while Pauly (1989) estimated a ratio of 3.00 year^{-1} for Georges Bank. Consumption analysis of haddock stomach data in 1999 and 2000 in the Scotian Shelf estimated a Q/B of 5.19 year^{-1} (Bundy, 2004). The average value of $Q/B = 4.38 \text{ year}^{-1}$ was used for both models.

Diet composition

Haddock diet composition was taken from Rockwood (2016) stomach content analysis in 2012-2014 and as no other estimate was available for the species in NAFO 3Ps, it was assumed to be the reference for both time periods and used for both models (Table 4.22).

Table 4.22. Diet composition of haddock as input in the two models.

<i>Prey</i>	Haddock
Small cod	0.009
American plaice	0.001
Flounders	0.001
Redfish	0.004
Capelin	0.001
Sand lance	0.004
Pisci. small pelagics	0.002
Plank. Small pelagics	0.002
Echinoderms	0.360
Molluscs	0.031
Polychaetes	0.230
Large zooplankton	0.014
Small zooplankton	0.003

Balancing the model

As predation mortality for haddock was especially high, haddock proportion in the diet of large cod, large Greenland halibut and small demersals was lowered to be more representative of prey availability in the system. Additionally, biomass estimates seemed considerable low, particularly considering fishing pressure on this species. Biomass was therefore deemed to be the most uncertain input, with estimates rising from 7,000 t in 1984 to 32,000 t in 1985. Though haddock is a rapid growing fish, such rapid stock changes seem unlikely, and since catchability of smaller fish was said to be lower prior to trawl survey gear changes in 1996 (DFO, 2001), *EE* was set to the value of 0.95 to obtain new biomass estimates of 0.432 t·km⁻² in 1960-1969 and 0.441 t·km⁻² in 2000-2009.

4.3.1.14 Other forage fish*Background*

Sand lances (*Ammodytes* spp.), also called sand eels, are mostly represented by the American sand lance (*Ammodytes americanus*) and the northern sand lance (*Ammodytes dubius*) in the Northwest Atlantic, with a widespread distribution from the coast of Delaware, USA, to Greenland. The main difference between both species lies in their distribution through the water columns: *A. dubius* can be found in colder waters, up to 80 meters deep, while *A. americanus*

prefers shallower waters less than 20 m deep. They are small semi-demersal forage fishes and an important prey for many higher trophic level species in the ecosystem (Staudinger *et al.*, 2020).

Arctic cod (*Boreogadus saida*), also referred to as polar cod, is a pelagic species of Gadidae with a circumpolar range. Though mostly abundant in the Arctic Ocean, it is an important prey in the Northwest Atlantic ecosystem, ranging from Labrador to the Gulf of Saint Lawrence. Arctic cod are cold-water adapted gadoids that can be found in depths up to 900 m (Lear, 1983).

Catch

There were no recorded landings of either species between 1960 and 1969, while total reconstructed landings of sand lance between 2000 and 2009 were less than $0.0001 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$. There were no recorded discards of either species in either of the two periods of study.

Biomass

Very little information on biomass was available for sand lance or arctic cod. Sand lance biomass estimated were available for the Scotian shelf (Bundy, 2004), were a catchability adjusted range of 7.31 to $22.38 \text{ t}\cdot\text{km}^{-2}$, giving an average of $B = 14.840 \text{ t}\cdot\text{km}^{-2}$ for the 1995 to 2000 model, which was used for the 2000-2009 model. For the 1960-1969 model, sand lance ecotrophic efficiency was set to 0.95 to obtain a biomass estimate of $3.800 \text{ t}\cdot\text{km}^{-2}$. These biomass estimates are reflective of the large increase in sand lance biomass described at the end of the 1990s (Bundy, 2004).

For Arctic cod, Morissette *et al.* (2003) estimated an Atlantic cod to Arctic cod ratio of $700:1$. Using this ratio and the cod biomass in the NAFO 3Ps gives biomass estimates of $0.003 \text{ t}\cdot\text{km}^{-2}$ in 1960-1969 and $0.002 \text{ t}\cdot\text{km}^{-2}$ in 2000-2009. However, these estimates seem low in comparison to Arctic cod biomass estimates in the Newfoundland Shelf of $2.793 \text{ t}\cdot\text{km}^{-2}$ by Tam and Bundy (2019) and $2.805 \text{ t}\cdot\text{km}^{-2}$ by Bundy *et al.* (2000).

Production:Biomass

Winters (1983) estimated sand lance total mortality on Grand Banks using catch curve analysis and highlighted the predator role of Atlantic cod on sand lance mortality. Total mortality Z was 1.15 year^{-1} in 1968-1974, and this value was used for the first model. As cod biomass was

considerably lower in 2000-2009, therefore predation pressure on sand lance lower, P/B was estimated to be 0.62 year^{-1} as calculated by Winters (1983) for the late 1970s.

Bradstreet (1986) estimated Arctic cod total mortality from catch curve analysis to be 0.409 year^{-1} for 1 to 2 years old cod, and 0.380 year^{-1} for 2 to 3 years old cod. The average value of 0.395 year^{-1} was used for both models.

Consumption: Biomass

Q/B ratios for northern sand lance (*A. dubius*) was 3.50 year^{-1} and 5.30 year^{-1} for American sand lance (*A. americanus*) in FishBase for a temperature of 5°C (Froese and Pauly, 2002). A study on daily rations in Georges Bank between 1977 and 1986 by Gilman (1994) estimated a Q/B of 8.16 year^{-1} and Bundy (2004) estimated a Q/B of 4.07 year^{-1} from stomach analysis on the Scotian Shelf in 1995-2000. Assuming a P/Q of 0.15 year^{-1} would give a Q/B ratio of 7.670 year^{-1} in 1960-1969 and 4.133 year^{-1} in 2000-2009. Average Q/B values with the other Q/B gives estimates available were 6.157 year^{-1} in 1960-1969 and 4.250 year^{-1} in 2000-2009.

Q/B ratio for Arctic cod was given by FishBase for temperature of 1.5°C and was 2.70 (Froese and Pauly, 2002). As biomass was uncertain, and no consumption estimates were available for NAFO 3Ps or other adjacent areas, this estimate was used for both models.

Diet composition

Sand lance diet was taken from Scott (1973) content analysis of 130 stomachs in the Scotian Shelf and was used for both models. Sand lance primarily feed on polychaetes larvae, copepods and other small zooplankton. Arctic cod diet was available for the Newfoundland Shelf (Bundy *et al*, 2000) and was used for both models. Arctic cod feed primarily on large zooplankton such as copepods and amphipods (Table 4.23).

Table 4.23. Diet composition for sand lance and arctic cod as input in the two models. Values with an asterisk (*) indicate that the group is present in the diet composition in very small amounts.

<i>Prey</i>	Sand lance	Arctic cod
Capelin	–	0.038
Arctic cod	–	0.002
Polychaetes	0.000*	0.000*
Large zooplankton	0.350	0.640
Small zooplankton	0.649	0.320
Phytoplankton	0.000*	–

Balancing the model

Arctic cod *EE* was too high in both models. As biomass was uncertain for NAFO 3Ps, *EE* was set to 0.95 to obtain new biomass estimates of 0.355 t·km⁻² in 1960-1969 and 0.180 t·km⁻² in 2000-2009.

4.3.1.15 Pelagic fishes

Background

Pelagic fishes are distributed through the water column, as opposed to demersal fish feeding primarily at the bottom of the ocean. Pelagic fishes are important for local fisheries in NAFO 3Ps, were split into three groups for the models: large pelagics, piscivorous small pelagics, and planktivorous small pelagics. The large pelagic fishes group is composed of larger predatory fish such as Atlantic salmon (*Salmo salar*), Atlantic bluefin tuna (*Thunnus thynnus*), as well as species of sharks such as blue shark (*Prionace glauca*), spiny dogfish (*Squalus acanthias*) (i.e., a benthopelagic species), basking shark (*Carcharodon carcharias*), porbeagle (*Lamna nasus*), and shortfin mako shark (*Isurus oxyrinchus*). The piscivorous small pelagic fishes group is mainly represented by Atlantic mackerel (*Scomber scombrus*) and lumpfish (*Cyclopterus lumpus*) (i.e., a benthopelagic species), while planktivorous small pelagic fishes are mainly represented by Atlantic herring (*Clupea harengus*).

Spiny dogfish is one of the most widespread shark species in the Northwest Atlantic. Though mostly abundant on the Scotian Shelf, it is transient in NAFO 3Ps. Mackerel is a transient species in 3Ps, and the northern portion of the Northwest Atlantic stock spawns mainly in the summer in the Gulf of Saint Lawrence (DFO, 2024c). Lumpfish in 3PS and in SPM's EEZ is primarily harvested for its roe, and spawns in the spring off the coast of Newfoundland (Briand,

1995). The 3Ps herring population spawns in southern Newfoundland, mostly in the fall (i.e., northern part of the 3Ps division) (DFO, 2022).

Catch

In 1960-1969, total landings of large pelagic fishes by all fleets fishing in NAFO 3Ps were mostly made up of dogfish and salmon and amounted to $0.012 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$. Total landings of small piscivorous pelagic fishes were mostly made up of mackerel and amounted to $0.012 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$, while total landings of small planktivorous pelagic fishes were mostly made up of herring and amounted to $0.379 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$. Average yearly landings by SPM's fleet were less than $0.0001 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for large pelagic fishes, 0.001 for piscivorous small pelagic fishes, while there were none for planktivorous small pelagic fishes. Average yearly discards were $0.072 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for large pelagics, $0.064 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for small piscivorous pelagic fishes and $0.0004 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for small planktivorous pelagic fishes.

In 2000-2009, total landings of large pelagics amounted to $0.009 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$, $0.011 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for small piscivorous pelagic fishes, and $0.039 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for small planktivorous pelagic fishes. Average yearly landings by SPM's fleet were less than $0.0001 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for the three groups. Average yearly discards were $0.001 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for large pelagic fishes and for small piscivorous pelagic fishes, and less than $0.0001 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for small planktivorous pelagic fishes.

Biomass

As spiny dogfish was considered to be the representative species of the large pelagic fishes group (i.e., being the species mostly targeted by local fisheries, as well as abundant in the area), dogfish biomass estimates were used as a reference for the group. Biomass was not available in NAFO 3ps, but RV surveys in the Scotian Shelf (Bundy, 2004) allowed the calculation of an average over 5 years between 1980 to 1985 to obtain $B = 0.241 \text{ t}\cdot\text{km}^{-2}$. Additionally, estimates of transient pelagic biomass including tuna and shark species were available in the Scotian Shelf for the same period (Bundy, 2004), and the $0.018 \text{ t}\cdot\text{km}^{-2}$ was added to dogfish biomass to obtain $B = 0.259 \text{ t}\cdot\text{km}^{-2}$ for the group. For the 2000-2009, dogfish biomass estimates on the Scotian Shelf (Bundy, 2004) between 1995 and 2000 were used to obtain $B = 0.105 \text{ t}\cdot\text{km}^{-2}$. Additionally,

estimates of transient pelagic biomass in the Scotian Shelf for the same period (Bundy, 2004) of $0.009 \text{ t} \cdot \text{km}^{-2}$ were added to dogfish biomass to obtain $B = 0.114 \text{ t} \cdot \text{km}^{-2}$ for the group. As no biomass estimates were available for the area for other species making up the large pelagic fishes group, these estimate were kept as they are to be conservative: this is taking into account the fact that while dogfish is considered to not be well sampled by RV surveys (Bundy, 2004), the species is usually mostly abundant in the Scotian Shelf and only transient over Saint Pierre Bank. Therefore, the biomass estimate kept was estimated to be somewhat representative of NAFO 3Ps.

Small piscivorous pelagic fishes biomass estimates were not available for the study area at either of the two periods. Morissette *et al.* (2003) estimated Atlantic mackerel biomass in the Gulf of Saint Lawrence from an egg production index. As mackerel is a transient species in 3Ps that migrates from the Scotian shelf to the Gulf of St Lawrence, biomass should be divided by two to make up for the migratory nature of the species, as well as to reflect the decline in biomass that can be observed through Bundy (2004) model of the Scotian shelf between 1980-85 and 1995-2000. Biomasses input in the model where is $B = 2.456 \text{ t} \cdot \text{km}^{-2}$ in 1960-1969 and $1.231 \text{ t} \cdot \text{km}^{-2}$ in 2000-2009.

Small planktivorous pelagic fishes biomass was available for herring in Newfoundland, and biomass was shown to be relatively higher in the 1990s than it was before 1980 in Fortune bay in 3Ps. Historical population estimates from research vessel catch show a biomass of $2.534 \text{ t} \cdot \text{km}^{-2}$ between 1983-1987, which was used for the 1960-1969 model, and $3.596 \text{ t} \cdot \text{km}^{-2}$ between 2000-2009 (Bourne *et al.*, 2023).

Production:Biomass

P/B ratio for large pelagic fishes were calculated using the natural mortality estimate $M = 0.10 \text{ year}^{-1}$, as species in this group are mostly large, long living fish with low mortality (Lorenzen, 2022), and the fishing mortalities in the model $F = 0.325 \text{ year}^{-1}$ in 1960-1969 and $F = 0.223 \text{ year}^{-1}$ in 2000-2009, to get the respective P/B ratios of 0.425 year^{-1} and 0.323 year^{-1} .

P/B ratio was estimated to be 0.290 year^{-1} in the North Sea (Christensen, 1992) for small piscivorous pelagic fishes, which was also used by Bundy (2004) for models of the Scotian Shelf. Other values were calculated using a mortality M of 0.20 year^{-1} (Morissette, 2003), and the fishing mortalities $F = 0.030 \text{ year}^{-1}$ in 1960-1969 and $F = 0.010 \text{ year}^{-1}$ in 2000-2009. Averaged P/B with

the aforementioned value were respectively 0.260 year^{-1} and 0.250 year^{-1} . Several M values were available through Pauly (1989) for Atlantic herring, and the average value of $M = 0.264$ was used to calculate $Z = P/B$, along with the models' fishing mortalities $F = 0.150$ in 1960-1969 and $F = 0.018$ in 2000-2009. The resulting P/B for small planktivorous pelagic fishes were 0.414 year^{-1} and 0.282 year^{-1} .

Consumption: Biomass

Q/B values estimated in various studies for spiny dogfish were 2.70 year^{-1} (Tanasichuk *et al.*, 1991) in British Columbia, 4.77 year^{-1} on the New England Coast (Pauly, 1989) and 4.77 year^{-1} estimated by FishBase (Froese and Pauly, 2002). Stillwell and Kohler (1985) estimated swordfish Q/B to range from 3.4 to 5.8 year^{-1} . The value of 4.77 year^{-1} was used for both models. FishBase gave a Q/B value of 4.40 year^{-1} for Atlantic mackerel (Froese and Pauly, 2002), the same value given by Pauly (1989) on Georges Bank, and a value of 1.80 year^{-1} for lumpfish at a temperature of 5°C (Froese and Pauly, 2002). Additionally, consumption estimates were available for mackerel in the North Sea and estimated to be 6% of body mass per day (Mehl and Westgard, 1983), which would lead to a Q/B of 2.19 year^{-1} . However, it is assumed that mackerel would eat at least as much food as its biomass, giving a Q/B estimate of 2.50 year^{-1} . The average estimate of 3.45 year^{-1} was chosen for both models.

Pauly (1989) calculated Q/B values of 8.62 year^{-1} for alewife (*Alosa pseudoharengus*) and 4.59 year^{-1} for herring. FishBase gave a Q/B value of 10.10 year^{-1} (Froese and Pauly, 2002). As the FishBase value seem high, the average of 6.61 year^{-1} was used for the small planktivorous pelagic fishes group, giving consumption estimates of $16.750 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 1960-1969 and $23.770 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ in 2000-2009.

Diet composition

Large pelagic fishes diet was estimated through consumption estimates of swordfish on Georges Bank (Stillwell and Kohler, 1985), blue shark on Georges Banks and southern Nova Scotia (Laurinolli *et al.*, 2002) and spiny dogfish on Georges Bank in the 1980s (Bundy, 2004). Diet was adjusted on the basis of the presence of great white shark in the area, feeding on seal species (L. Morissette, marine ecologist, 2024, personal communication). It was adjusted for the

second model using spiny dogfish stomach sampling in the spring and summer of 1999-2000 on the Scotian Shelf and additional consumption data from Bundy (2004) on transient pelagics on the Scotian shelf in 1999-2000. Main prey items were sand lance, small piscivorous pelagic fishes, squid and large zooplankton (Table 4.24).

Small piscivorous pelagic fishes diet was estimated through mackerel stomach content analysis on the Scotian Shelf and Georges Bank (Kulka and Stobo, 1981), as well as in the Gulf of Saint Lawrence (Gregoire and Castonguay, 1989). To adjust to the most recent model, diet composition was compared with a diet study from Suca *et al.* (2018) on small pelagic fishes feeding behavior in the Northwest Atlantic. Mackerel's main preys include amphipods, copepods and fish larvae. Small planktivorous pelagic fishes diet was estimated through herring stomach content collected in the Gulf of Saint Lawrence and adjacent waters between 1970 and 1973 (Messieh *et al.*, 1979). Assumptions from Gartner *et al.* (1997) on other small pelagic fishes diet as well as feeding behavior analysis from Suca *et al.* (2018) were used to adjust the diet composition to the 2000-2009 period. Herring feed primarily on large and small zooplankton (Table 4.25).

Table 4.24. Diet composition of large pelagic fishes as input in the two models. Values with an asterisk (*) indicate that the group is present in the diet composition in very small amounts.

<i>Prey</i>	Large pelagics	
	<i>1960-1969</i>	<i>2000-2009</i>
Harp seals	0.001	0.001
Hooded seals	0.000*	0.000*
Grey seals	—	0.000*
Harbour seals	0.000*	0.000*
Large cod	0.003	0.003
Small cod	0.011	—
American plaice	0.001	0.070
Flounders	0.042	0.023
Skates	0.004	0.004
Redfish	0.030	0.036
Large demersals	0.044	0.036
Small demersals	0.107	0.110
Capelin	0.005	0.020
Haddock	—	0.008
Sand lance	0.110	0.020
Large pelagics	0.015	0.020
Pisci. small pelagics	0.107	0.165
Plank. small pelagics	0.072	0.093
Shrimp	0.008	0.046
Large crustacea	0.002	0.002
Echinoderms	0.000*	—
Molluscs	0.016	—
Squid	0.251	0.216
Polychaetes	0.004	—
Other benthic invertebrates	0.015	0.093
Large zooplankton	0.143	0.033

Table 4.26. Diet composition for piscivorous and planktivorous small pelagic fishes as input in the two models.

	Pisci. small pelagics		Plank. small pelagics	
	<i>1960-1969</i>	<i>2000-2009</i>	<i>1960-1969</i>	<i>2000-2009</i>
Sand lance	0.002	0.005	—	—
Plank. small pelagics	0.004	0.001	—	—
Shrimp	0.002	0.002	0.063	0.080
Molluscs	0.002	0.002	—	—
Other benthic invertebrates	—	—	0.046	0.029
Large zooplankton	0.540	0.540	0.431	0.410
Small zooplankton	0.450	0.450	0.460	0.481

Balancing the model

As *EE* was too high for large pelagics in 1960-1969 and biomass was the most uncertain estimate, *EE* was set to 0.95 to balance the model by obtaining a new biomass estimate of $0.281 \text{ t} \cdot \text{km}^{-2}$. To balance the *EE* of piscivorous and planktivorous small pelagics in the 1960-1969 model, their proportion in the diet of large demersal, their main predator, was lowered. Ultimately, and as gross efficiency was too low for these two groups, *P/Q* was set to 0.15 as a reasonable assumption to obtain new *P/B* estimates of 0.517 year^{-1} for piscivorous small pelagics and 0.688 year^{-1} for planktivorous small pelagics (where the *Q/B* value of 4.59 year^{-1} from Pauly (1989) was used). These values are concordant with *P/B* values estimated for the same species in areas adjacent to 3Ps (Bundy, 2004; Morissette *et al.*, 2003).

4.3.1.16 Crustaceans

Background

Crustaceans have been divided into three groups for the purpose of the models; shrimps, large crustaceans and lobster. The most abundant shrimp species in NAFO 3Ps is the northern or pink shrimp (*Pandalus borealis*), which is of commercial interest for industrial fisheries. Northern shrimps are distributed from Davis Strait to the Gulf of Maine, preferring the bottom range of the water column. They are known for their nocturnal vertical migration, following zooplankton gradients (DFO, 2004).

The large crustaceans group is mostly represented by snow crab (*Chionoecetes opilio*) and other larger crabs (e.g., *Hyas coarctatus* and *Hyas* spp.). Snow crab is distributed from Labrador to western Nova Scotia, preferring colder temperatures on muddy or sandy bottoms. Individuals are usually recruited for commercial fisheries at around 10 years (DFO, 2022). The snow crab fishery have increased considerably after the 1990s, and is the largest on the Newfoundland Shelf (Mullowney *et al.*, 2014). American lobster (*Homarus americanus*) is a crustacean species of high economic interest for commercial fisheries in NAFO 3Ps, as well as for pots and traps and recreational fisheries in SPM (Roussel, 2019). American lobsters have high seasonal mobility, and are distributed from Labrador to North Carolina, USA (DFO, 2018; Goldstein *et al.*, 2025). They are better adapted to temperatures higher than 3°C and shallower depths, and have very few natural predators (DFO, 2018).

Catch

Commercial shrimp fisheries officially began at the beginning of the 1970s in NAFO 3Ps; no catches were recorded between 1960-1969. Total reconstructed landings of shrimps by all fleets fishing in NAFO 3Ps were $0.007 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Landings of large crustaceans were almost nonexistent in the 1960s, with catches only from the Canadian fleets equaling to less than $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, while landings were $0.088 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Landings of lobsters were exclusively from Canadian fleets in 1960-1969 and amounted to $0.004 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, and $0.012 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. There were no recorded landings of shrimps by SPM for either of the two periods. Landings of snow crab amounted to $0.003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ and landings of lobster to $0.0003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009.

Total reconstructed discards of large crustaceans were $0.003 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969, while there were no recorded discards of shrimps or lobsters. Juvenile and egg bearing lobster females are generally released alive when caught (Roussel, 2019), therefore not counted in discards.

Biomass

No biomass estimates specific to NAFO 3Ps were available for shrimps and lobsters. Northwest Atlantic trends of shrimp biomass show a surge in biomass post cod collapse, as well as a TAC augmentation of 20% between 1993-1994 and a biomass almost two times higher from 1995 to 1998 (Lilly *et al.*, 2000). As 3Ps is not included in the NAFO shrimp assessment unit, and as little is known on the biomass of the group prior to 1990, shrimp biomass estimates were taken from Tam and Bundy (2019) for the Newfoundland Shelf. They calculated a biomass of $0.840 \text{ t} \cdot \text{km}^{-2}$ in the 1980s, which was used for the 1960-1969 model, and of $2.440 \text{ t} \cdot \text{km}^{-2}$ in the 2010s, which was used for the 2000-2009 model and is reflective of assumptions on trends stated by Lilly *et al.* (2000).

Snow crab exploitable biomass was available for 3Ps (Mullowney *et al.*, 2016). The oldest trawlable biomass assessments from 1996 to 1999 show a biomass of $0.540 \text{ t} \cdot \text{km}^{-2}$, and the pre-recruit biomass survey estimates a biomass of $0.067 \text{ t} \cdot \text{km}^{-2}$, giving a total biomass of $0.608 \text{ t} \cdot \text{km}^{-2}$. The biomass assessment from 2000 to 2009 shows a trawlable biomass of $0.166 \text{ t} \cdot \text{km}^{-2}$, and a

pre-recruit biomass of $0.082 \text{ t} \cdot \text{km}^{-2}$, giving a total biomass of $0.248 \text{ t} \cdot \text{km}^{-2}$. Since crabs are known to be not accurately sampled (Mullooney *et al.*, 2016), biomasses were conservatively doubled to represent the other crab species making up the large crustacea group, as well as to take into account, for the first model, that 1960s biomass could have been higher with the lesser fishery pressure on snow crabs. The biomass $B = 1.216 \text{ t} \cdot \text{km}^{-2}$ was chosen for the 1960-1969 model, and $B = 0.496 \text{ t} \cdot \text{km}^{-2}$ for the 2000-2009 model.

Lobster legal size biomass was an average of 1500 t in 2004-2009 for the southern region of Newfoundland sampled by DFO's (2023) assessments which could entail an average of $0.034 \text{ t} \cdot \text{km}^{-2}$ for the entire 3Ps zone. However, as the stock is only partially assessed in 3Ps, and as no biomass estimates of high certainty were available for adjacent zones, *EE* was set to 0.95 to get a biomass estimate from the model of $0.042 \text{ t} \cdot \text{km}^{-2}$ in 2000-2009. Due to the absence of direct survey estimates for lobster between 1960-1969, and as fishing pressure was much lower in the 1960s, this biomass estimate was conservatively doubled to get an estimate of $0.080 \text{ t} \cdot \text{km}^{-2}$ in 1960-1969.

Production:Biomass

P/B ratio for shrimp was estimated to be 1.744 year^{-1} by Morissette (2003) for the Gulf of Saint Lawrence, while Hopkins and Nilssen (1990) estimated a total mortality of 1.83 year^{-1} in Norway, and Hopkins (1988) estimated a *P/B* of 1.70 year^{-1} using length converted catch curves. These estimates were used by Bundy *et al.* (2000) to estimate a range of *P/B* values from 1.20 to 1.70 year^{-1} , taking into account the differences in growth between Norway and the Newfoundland Shelf (Bundy *et al.*, 2000). The average value of 1.450 year^{-1} was used for both models.

Several natural mortality estimates were available for snow crab of $M = 0.49 \text{ year}^{-1}$ for males and 0.36 year^{-1} for females in the Bering Sea (Murphy *et al.*, 2018), and a range of 0.10 to 0.30 year^{-1} by Bundy *et al.* (2000). The averaged value of 0.40 year^{-1} was used, alongside the *F* of 0.183 year^{-1} in the 2000-2009 model to get $P/B = 0.583 \text{ year}^{-1}$. As catches were almost nonexistent in the 1960s, *P/B* ratio was averaged from estimates in the 1980s of 0.335 year^{-1} in the Gulf of Saint Lawrence (Morissette *et al.*, 2003), 0.300 year^{-1} on the Scotian Shelf (Bundy, 2004), and 0.460 year^{-1} on the Newfoundland Shelf (Tam and Bundy, 2019). The average value of 0.395 year^{-1} was used for the 1960-1969 model. *P/B* ratio for lobster was calculated using a natural mortality estimate of $M = 0.20 \text{ year}^{-1}$ (Tanaka *et al.* 2019) and the fishing mortalities $F = 0.05 \text{ year}^{-1}$ in 1960-

1969 and 0.277 year^{-1} in 2000-2009. The resulting ratios were $Z = P/B = 0.250 \text{ year}^{-1}$ and $Z = P/B = 0.477 \text{ year}^{-1}$.

Consumption: Biomass

As no consumption estimates were available for northern shrimp, it was assumed gross efficiency was equal to 0.20 to obtain consumption estimates of $22.554 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969 and $43.188 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009, resulting in $Q/B = 7.250 \text{ year}^{-1}$. Snow crab consumption data was available for the Gulf of Saint Lawrence (Brêthes *et al.*, 1984), with a daily ration estimate of 0.4% of body mass, resulting in $Q/B = 1.460 \text{ year}^{-1}$. This value was used for both models. Lobster consumption rates were calculated by Bundy *et al.* (2000) from data from Reddin (1973) on lobster feeding habits, estimating a Q/B ratio of 5.850 year^{-1} which was used for both models.

Diet composition

Northern shrimp diet was available for the Newfoundland Shelf by Bundy *et al.* (2000) through DFO studies on benthic and pelagic diet compositions. This diet was used for both models, and shrimps are mainly detritivore, while other prey items include copepods, euphausiids and bottom plants. Large crustaceans diet was taken from snow crabs stomach content analysis in the Southern Gulf of Saint Lawrence by Brêthes *et al.* (1984) and on the west coast of Newfoundland by Wieczorek and Hooper (1995). This diet composition was used for both models. Snow crab feed mainly on decapods, polychaetes, small molluscs and echinoderms. Lobster diet composition was available through seasonal feeding analysis by Ennis (1973) in Bonavista Bay, Newfoundland, and diet estimates in the Gulf of Maine in the 1980s and 1990s by Zhang and Chen (2007). Main prey items include rock and spider crabs, echinoderms (e.g. sea urchin and sea stars) and molluscs. The diet composition was used for both models (Table 4.26).

Table 4.26. Diet composition of shrimp, large crustaceans and lobster as input in the two models. Values with an asterisk (*) indicate that the group is present in the diet composition in very small amounts.

<i>Prey</i>	Shrimp	Large crustaceans	Lobster
Small demersals	–	0.018	–
Shrimp	–	0.018	–
Large crustaceans	–	0.040	0.298
Sea cucumber	–	0.030	0.050
Echinoderms	–	0.092	0.155
Molluscs	–	0.269	0.109
Polychaetes	0.015	0.160	0.025
Other benthic invertebrates	0.015	0.179	0.348
Large zooplankton	0.120	0.144	–
Small zooplankton	0.240	0.018	–
Phytoplankton	0.085	–	0.016
Detritus	0.525	0.036	–

Balancing the model

As shrimp *EE* was too high, *EE* was set to 0.95: the model estimated a biomass of 3.770 t·km⁻² for 1960-1969 and 7.198 t·km⁻² for 2000-2009. In the 1960-1969 model, large crustaceans' proportion in the diet of large cod, American plaice and small pelagics – its main predators – was lowered, and *EE* was ultimately set to 0.95 to obtain a new estimate of 3.852 t·km⁻² and balance the model, as biomass was fairly uncertain.

In the 2000-2009, lobster *EE* was set to 0.95 to obtain a new biomass estimate of 0.036 t·km⁻² and balance the model. As lobster *GE* was lower than the typical range for crustaceans (i.e., 0.15 to 0.30) in both models, and consumption estimates were uncertain, *P/Q* was conservatively set to 0.15 to obtain new estimates of 1.667 year⁻¹ in 1960-1969 and 3.180 year⁻¹ in 2000-2009.

4.3.1.17 Squid

Background

The squid group is mainly represented by northern shortfin squid (*Illex illecebrosus*) and other less abundant species of squid (*Teuthida* spp.). Northern shortfin squid is widespread from Northern Labrador to Florida, USA, and is mostly managed as one stock unit in the Northwest Atlantic for NAFO subareas 3 and 4 (Hendrickson and Showell, 2016). The species has the

particularity of having a very short life expectancy, of one year only, and undergoes large migrations associated with environmental variations and optimal spawning conditions (Coelho *et al.*, 1994). In 3Ps, shortfin squid has been commercially harvested since the 1960s.

Catch

Total reconstructed catch of squid by all countries fishing in NAFO 3Ps amounted to $0.005 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969 and less than $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 2000-2009. SPM artisanal boats landed an average of $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 1960-1969, while it was less than $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ between 2000-2009. Total reconstructed discards were an average of $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969, and less than $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Discards by SPM boats were lower than $0.0001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in both periods.

Biomass

Squid biomass was sampled in NAFO 3Ps in 1979 and estimated to amount to 70.280 t (Dupouy and Poulard, 1980) and 48.480 t in 1977 (Chevalier, 1978). The average biomass estimate of $0.683 \text{ t} \cdot \text{km}^{-2}$ was divided by two to be representative of the highly migratory nature of the species, and $B = 0.341 \text{ t} \cdot \text{km}^{-2}$ was used for the 1960-1969 model. There is no recent biomass estimate of this species for 3Ps, however both US and Canadian stocks on the East Coast are showing similar behaviors, and two low productivity periods in the 1970s and since 1982 (Hendrickson, 2004). Most other models of adjacent areas included squid in multi-species groups, and no precise biomass estimates were available. In the Scotian Shelf model, Bundy (2004) used a biomass estimate of $0.04 \text{ t} \cdot \text{km}^{-2}$. As this estimate is considerably lower than the previous estimates, and does not seem to be reflective of the study area nor Northwest Atlantic trends, the value $B = 0.341 \text{ t} \cdot \text{km}^{-2}$ was conservatively used for both models.

Production: Biomass

No production estimates were available for shortfin squid. P/B was estimated to be 0.932 year^{-1} in 1960-1969 and 1.980 year^{-1} in 2000-2009 by setting the P/Q ratio to 0.15. This is reasonable knowing short-lived species tend to have P/B ratios higher than 1.00 year^{-1} (Christensen *et al.*, 2005).

Consumption: Biomass

Shortfin squid consumption and Q/B estimates in the Gulf of Maine and Cape Hatteras in 1979 and 1980 (Maurer and Bowman, 1985) gave a range of Q/B from 1.24 year⁻¹ and 6.21 year⁻¹. Vinogradov and Noskov (1979) estimated a daily ratio range of 3.2-3.8% of body mass per day for longfin inshore squid (*Loligo paelei*), and 5.8% of body mass per day for shortfin squid in Nova Scotia and New England, which entails a Q/B range of 12-21 year⁻¹. As squid have a high turnover, the Q/B value 12.00 year⁻¹ was used for both models.

Diet composition

Diet composition data by Dawe (1988) was compared with a study from Dawe *et al.* (1997) of otoliths collected in squid stomachs in Newfoundland between 1980-1993. Results were observed for two locations, Baie d'Espoir and Hermitage which are southern regions closest to SPM and included in NAFO 3Ps. These results shown that shortfin squids feed more on capelin and small cod in the south, than on sand lance in the northern areas. Main prey items include large zooplankton, shrimp and other small crustaceans. This data was used for both models, and slightly adjusted in 2000-2009 to reflect the diminution of cod biomass in the ecosystem (Table 4.27).

Table 4.27. Diet composition of squid as input in the two models. Values with an asterisk (*) indicate that the group is present in the diet composition in very small amounts.

<i>Prey</i>	Squid	
	<i>1960-1969</i>	<i>2000-2009</i>
Small cod	0.003	0.001
Capelin	0.002	0.004
Sand lance	0.001	0.001
Arctic cod	0.002	0.002
Plank. small pelagics	0.012	0.010
Shrimp	0.046	0.048
Squid	0.000*	0.000*
Polychaetes	0.025	0.025
Other benthic invertebrates	0.042	0.042
Large zooplankton	0.867	0.867

Balancing the model

No adjustments to input parameters were necessary to balance the two models.

4.3.1.18 Echinoderms

Background

Echinoderms in 3Ps are mostly represented by the green sea urchin (*Strongylocentrotus droebachiensis*), common sand dollar (*Echinarachnius parma*) and various species of sea stars, brittle stars, Echinoidea and Holothuroidea. Knowledge on echinoderms is very little in 3Ps, despite their important presence in the ecosystem as a key prey of many higher trophic species, and prevalence in fisheries discards.

The orange footed sea cucumber (*Cucumaria frondosa*), of economic interest for commercial fisheries, was put into the separate group ‘sea cucumber’. Sea cucumbers are widely distributed across the North Atlantic and Arctic Oceans, ranging from Greenland to Cape Cod, USA (Hamel and Mercier, 1996). The species is slow growing and goes through a planktonic larvae stage, and a benthic stage where adults inhabits rocky substrates in subtidal zones. Spawning season occurs from February to May in Newfoundland (Gianasi *et al.*, 2020). They are sought commercially for consumption and various traditional medicine uses (Gianasi *et al.*, 2020).

Catch

Fisheries for sea cucumber started in the 1980s in the United States, though later in Canada, and SPM officially began commercially harvesting sea cucumber in 2008; nowadays, it is the most important commercial fishery of SPM. Catches of sea cucumber were therefore nonexistent between 1960-1969. Between 2000-2009, reconstructed landings by Canadian fleets were $0.002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ and $0.0005 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ by SPM fleets. There were no recorded discards for both time periods. Echinoderm discards are mainly associated with bottom gear such as dredges and bottom trawls. Discards amounted to $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ for both periods.

Biomass

Echinoderm biomass was estimated from data from Hutcheson *et al.* (1981) on Grand Banks, where Saint Pierre Bank was included as a sampling station. Total biomass was estimated to be $112.300 \text{ t} \cdot \text{km}^{-2}$, and as this was the only estimate available in 3Ps, was assumed to be the biomass for both models. Sea cucumber biomass was assessed between 2004 and 2008 on Saint Pierre Bank (DFO, 2016) and was an average of $2.415 \text{ t} \cdot \text{km}^{-2}$. As these were the earliest points

available and sea cucumber had not been previously assessed, and as fishing pressure was significantly higher in the 2000s, a biomass estimate of $3.000 \text{ t} \cdot \text{km}^{-2}$ was conservatively chosen for the 1960-1969 model. The estimate of sea cucumber biomass was subtracted from Echinoderms biomass, and the final biomass for echinoderms input in the models was $109.3 \text{ t} \cdot \text{km}^{-2}$ in 1960-1969 and $109.9 \text{ t} \cdot \text{km}^{-2}$ in 2000-2009.

Production:Biomass

Two echinoderms P/B estimate were available on the southern British Columbia Shelf, of 0.60 year^{-1} (Jarre-Teichmann *et al.*, 1996) and 0.65 year^{-1} (Robertson, 1979). Morissette *et al.* (2003) used a production estimate of 0.323 year^{-1} in the Northern Gulf of Saint Lawrence. Other production estimates were available for various areas, and ranged from $0.11 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in England (Buchanan and Warwick, 1974) to $70.11 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ (Warwick *et al.*, 1978), the closest estimate in distance to the study area being on Georges Bank of $64.22 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ (Steimle, 1987). This range of production estimates gives an average P/B estimate of 0.321 year^{-1} in 1960-1969 and 0.319 year^{-1} in 2000-2009. The averaged value from all P/B estimates was 0.473 year^{-1} , and was used for both models. In the absence of species-specific data, sea cucumber P/B was assumed to be the same as Echinoderms.

Consumption:Biomass

Jarre-Teichmann *et al.* (1996) estimated gross efficiency for benthic organisms on the southern British Columbia shelf and that all detritus feeders have a GE of 9%, or 0.09. This value was input in the model, and gave a Q/B estimate of 5.256 year^{-1} for echinoderms. As orange footed sea cucumber is a planktonic feeder, GE was set to 0.15 to obtain a Q/B estimate of 3.153 year^{-1} .

Diet composition

Echinoderms are mostly deposit feeders, feeding on detritus. Diet composition estimates were available for *E. parma*, *S. pallidus* and *Ophiura robusta* in NAFO 2J3KL from Bundy *et al.* (2000), and additional information on echinoderms predation from Gianasi *et al.* (2020) was used to compute a diet composition used for both models. Orange footed sea cucumber is different from other sea cucumber species in the way its diet is mostly planktonic, and feeds mostly on small

zooplankton including fish larvae and eggs, and phytoplankton. Diet composition estimates from Hamel and Mercier (1998) in the Saint Lawrence Estuary were used for both models (Table 4.28).

Table 4.28. Diet composition of sea cucumber and echinoderms as input in both models.

<i>Prey</i>	Sea cucumber	Echinoderms
Sea cucumber	–	0.002
Other benthic invertebrates	–	0.002
Small zooplankton	0.200	–
Phytoplankton	0.700	0.328
Detritus	0.100	0.668

Balancing the model

To balance the *EE* of sea cucumber in the 2000-2009 model, its proportion in the diet of echinoderms was lowered. No adjustments to input parameters were necessary to balance the 1960-1969 model.

4.3.1.19 Other benthic invertebrates

Background

The rest of the benthic invertebrate species occurring in NAFO 3Ps were split into three groups: molluscs – including commercially important species such as the Atlantic deep-sea scallop (*Placopecten magellanicus*), the Iceland scallop (*Chlamys Islandica*) and the blue mussel (*Mytilus edulis*) – polychaetes (i.e., *Exogenes hebes* and other species), and other benthic invertebrates including small crustaceans and nematodes.

Molluscs such as the waved whelk (*Buccinum undatum*) and the soft-shell clam (*Mia arenaria*) have been important for artisanal fisheries in SPM, as they were largely used as bait (Bultel and Zylich, 2015). Other benthic fauna is not well assessed on Saint Pierre Bank, but is comparable to benthic diversity on Grand Banks, of which the distribution is dependent on the oceanographic regimes at play on the banks and the variation of the bottom substrate (Scheider *et al.*, 1987).

Catch

Molluscs was the only group of other benthic invertebrates to be targeted by commercial and subsistence fisheries. Total reconstructed landings of molluscs by all fleets fishing in NAFO 3Ps were $0.008 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969 and $0.034 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Landings by SPM were $0.002 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969 and $0.0006 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. Total reconstructed discards were $0.0005 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 1960-1969 and $0.001 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in 2000-2009. The increase in molluscs landings is due to the rise of deep-sea scallop fisheries post 1990s.

Biomass

Only a fraction of molluscs biomass is transferred through the system: the soft tissues, and biomass estimates need to account for this particularity. Iceland scallop and deep-sea scallop biomasses were estimated on Saint Pierre Banks in the 2000s, with a biomass minimum and maximum of 359 t and 4,371 t for Iceland scallop, and an additional 1,231 t within the SPM EEZ, and a minimum and maximum of 188 t and 776 t for deep-sea scallop, and an additional 977 t in the SPM EEZ, for a sampled area of 4071.76 km^2 (Foucher, 2018). The minimum and maximum estimates from this study were $0.676 \text{ t} \cdot \text{km}^{-2}$ and $1.806 \text{ t} \cdot \text{km}^{-2}$. As these estimates were only encompassing a small portion of NAFO 3Ps, and were considerably lower than estimates in adjacent areas for all molluscs species, these estimates were not input in the models. Instead, biomass estimates for benthic invertebrates were available through Hutcheson *et al.*'s (1981) biomass surveys on Grand Banks (NAFO 2J and 3KLNO), where Saint Pierre Bank was included as a sampling station, and where the ratio between tissue wet weight and whole-body weight was estimated for molluscs species. Molluscs biomass was estimated to be $42.100 \text{ t} \cdot \text{km}^{-2}$, polychaetes $11.900 \text{ t} \cdot \text{km}^{-2}$ and other benthic invertebrates $7.800 \text{ t} \cdot \text{km}^{-2}$. As no other or more recent estimates were available, these estimates were used for both models.

Production: Biomass

Molluscs *P/B* was averaged through several estimates from the literature in other areas. Warwick *et al.* (1978) estimated a mollusc production of $3.820 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in England, and Sanders (1956) estimated $4.670 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ along the coast of New York, while Steimle (1985)

estimated a production of $82.121 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in the same area. Buchanan and Warwick (1974) gave a lower estimate of $0.600 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$. This gives a wide range of P/B values from 0.014 year^{-1} to 1.95 year^{-1} . Several other P/B estimates of 0.57 year^{-1} on southern Grand Banks (Hutcheson *et al.*, 1981), 0.76 year^{-1} (Robertson, 1979) and 0.70 year^{-1} in British Columbia (Jarre-Teichmann and Guenette, 1996). An average estimate of 0.60 year^{-1} was used for both models.

A range of production estimates for polychaetes from 0.206 (Buchanan and Warwick, 1974) and 74.564 in New York (Steimle, 1985) gave a range of P/B from 0.017 and 6.265 year^{-1} . Other P/B estimates of 1.4 year^{-1} in Greenland (Curtis, 1977), 2.0 year^{-1} on the Scotian Shelf (Mills and Fournier, 1979) and 3.0 year^{-1} in British Columbia (Jarre-Teichmann and Guenette, 1996) were available. To be concordant with other models of the Grand Banks (Bundy *et al.*, 2000) and Gulf of Saint Lawrence (Morissette *et al.*, 2003) the value of 2.00 year^{-1} was used for both models. Bundy *et al.* (2000) used a P/B estimate of 2.50 year^{-1} for other benthic invertebrates, which is concordant with estimates of 2.50 year^{-1} from Collie (1985) on Georges Bank, Mills and Fournier (1979) and Jarre-Teichmann and Guenette (1996). This value was used for both models.

Consumption: Biomass

As no consumption study was available for the area, Q/B ratios were estimated by setting P/Q to a fixed value. Jarre-Teichmann and Guenette (1996) estimated a GE of 9%, i.e., 0.09, for molluscs and polychaetes, and a GE of 20%, i.e., 0.20, for other benthic invertebrates. Using these values, Q/B estimates were 6.677 year^{-1} for molluscs, 22.22 year^{-1} for polychaetes, and 12.50 year^{-1} for other benthic invertebrates.

Diet composition

Molluscs diet was adapted from Bundy (2000), using feeding habits data from Hutcheson *et al.* (1981) stating that most of the mollusc species are detritivore or deposit feeders, while some are suspension feeders. Polychaetes diet was taken from studies in the Gulf of Saint Lawrence and the Scotian Shelf by Nesis (1965) and the Laurentian channel by Desrosiers *et al.* (2000). Polychaetes are mostly detritivores, though Desrosiers *et al.* (2000) highlighted the presence of phytoplankton in the diet, as well as the occurrence of cannibalism. Other benthic invertebrates

diet was taken from Bundy (2000) through data from Nesis (1965), where main food items are amphipods and organic detritus (Table 4.29).

Table 4.29. Diet composition of molluscs, polychaetes and other benthic invertebrates as input in both models.

<i>Prey</i>	Molluscs	Polychaetes	Other benthic invertebrates
Polychaetes	–	0.130	–
Small zooplankton	–	–	0.010
Phytoplankton	0.100	0.300	–
Detritus	0.900	0.570	0.990

Balancing the model

To balance the *EE* of polychaetes, which was too high in the 1960-1969 model, its proportion in the diet of capelin, as well as the proportion of cannibalism, were lowered. No adjustments to input parameters were necessary to balance the 2000-2009 model.

4.3.1.20 Zooplankton

Background

Zooplankton was split into three groups: large zooplankton, small zooplankton and phytoplankton. The large zooplankton group includes zooplanktonic organisms larger than 5 mm, such as cnidarians, ctenophore, euphausiids, hyperiid amphipods. The small zooplankton group includes zooplankton organisms smaller than 5 mm, such as copepods (e.g., *Calanus finmarchicus* and *Calanus hyperboreus*). As primary consumers, zooplankton plays a key role in the ecosystem of carbon transfer from phytoplankton, as well as being an important food source for many species of the system. Plankton biomass and production undergo significant seasonal fluctuations on the Bank (Maillet *et al.*, 2005).

Biomass

No biomass estimates were available for zooplankton on Saint Pierre Bank. However, estimates for Grand Banks and the Newfoundland Shelf were available. Large zooplankton biomass was estimated by Bundy *et al.* (2000) from trawl surveys in 1996 and 1997 of jellyfish and “others”, which were described to be essentially made up of euphausiids and amphipods, adjusted with the catchability factor of 0.14 (i.e., 14% of the biomass is caught by the trawl). Total

large zooplankton biomass on Grand Banks was estimated to be $18.343 \text{ t} \cdot \text{km}^{-2}$, and used for both models was no other estimates as inclusive of different zooplankton species were available.

Small zooplankton biomass was estimated by Bundy *et al.* (2000) from bongo net surveys on the Newfoundland Shelf between 1994 and 1997, adjusted for seasonality by using monthly displacement volume data by Strong (1981). The average small zooplankton biomass estimate was $21.700 \text{ t} \cdot \text{km}^{-2}$, and assumed to represent both periods of the models.

Production: Biomass

Euphausiids P/B ratio estimates were given by Mauchline (1985) for the Atlantic Northeast, for 3 species occurring in the Atlantic Northwest: *Thysanopoda acutifrons* ($P/B = 2.3 \text{ year}^{-1}$), *Meganyctiphanes norvegica* ($P/B = 1.6 \text{ year}^{-1}$) and *Thysanoessa longicaudata* ($P/B = 6.4 \text{ year}^{-1}$). Additional estimates of euphausiids P/B were available for different areas: 4.0 year^{-1} in the Gulf of Saint Lawrence (Berkes, 1977), 2.75 year^{-1} in the North Sea (Lindley, 1980), and 3.840 year^{-1} in coastal waters of the US (Lindley, 1982). The average of 3.481 year^{-1} was used for the large zooplankton group in both models.

Copepods P/B ratios were available for several species on the Scotian Shelf by McClaren *et al.* (1989), with a P/B estimate of 8.40 year^{-1} for *Calanus finmarchicus*, one of the representative copepod species of the study area. Another P/B ratio of 4.0 year^{-1} was estimated for the Barents Sea (Sakshaug *et al.*, 1997), while Vezina *et al.* (2000) estimated copepod production to be $346 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ in the Gulf of Saint Lawrence, giving a P/B ratio of 4.86 year^{-1} . The average value from this range of P/B was 6.2 year^{-1} , and was used for both models.

Consumption: Biomass

Sameoto (1976) estimated energy budgets from three euphausiids species occurring in the Gulf of Saint Lawrence: *Thysanopoda acutifrons*, *Meganyctiphanes norvegica* and *Thysanoessa longicaudata*. Bundy *et al.* (2000) estimated the respective Q/B ratios of 5.0 year^{-1} , 16.0 year^{-1} and 37.0 year^{-1} for these species from the aforementioned data. The average Q/B of 19.5 year^{-1} was assumed to represent the large zooplankton group and used for both models.

Bundy *et al.* (2000) estimated a Q/B ratio for small zooplankton of 20.7 year^{-1} , using a GE of 0.32 from Christensen (1995), while Vezina *et al.* (2000) estimated copepod consumption to be

438 t·km⁻²·year⁻¹ in the Gulf of Saint Lawrence, giving a Q/B ratio of 20.2 year⁻¹. The averaged value of 20.43 year⁻¹ was used for both models.

Diet composition

Bundy *et al.* (2000), Morissette *et al.* (2003) and Bundy (2004) estimated large zooplankton diet to be 38% small zooplankton, 37% phytoplankton, 20% detritus and 5% cannibalism, from various sources on euphausiids, chaetognaths and jellyfish consumption habits (Mauchline, 1980; Sullivan, 1980; Smayda 1993). Small zooplankton diet was assumed to be 100% phytoplankton in most models of areas adjacent or similar to NAFO 3Ps (Bundy *et al.*, 2000; Bundy, 2004; Tam and Bundy, 2019). These diet compositions were used for both models.

Balancing the model

To balance the models, and as biomass was uncertain on Saint Pierre Bank, large zooplankton EE was set to 0.95. The model gave new biomass estimates of 33.229 t·km⁻² in 1960-1969 and 28.133 t·km⁻² in 2000-2009.

When adjusting other groups in the system, the small zooplankton group became unbalanced. EE was therefore set to 0.95 as well in both models, to let the models give biomass estimates of 51.654 t·km⁻² in 1960-1969 and 49.549 t·km⁻² in 2000-2009. These new estimates were similar to small zooplankton biomass estimates in the Gulf of Saint Lawrence in the 1980s (Morissette *et al.*, 2003).

4.3.1.21 Phytoplankton

Background

The phytoplankton group is mostly made up of diatom species, and other autotrophic and mixotrophic organisms. Diatom species are mostly abundant on the shelf during spring and winter, with a diatom bloom in the spring on Grand Banks, while autotrophic and mixotrophic organisms, including dinoflagellates and nanoflagellates, are mostly abundant in the summer and fall (Bundy *et al.*, 2000). As phytoplankton are primary producers, no consumption or diet input is necessary for the models. Very little to no data on primary production and chlorophyll a is available for Saint

Pierre Bank: data on adjacent areas, such as Grand Banks and the Scotian Shelf, was used to estimate biomass and production.

Biomass

Phytoplankton biomass, measured as chlorophyll *a* biomass, was similarly taken from Bundy *et al.* (2000) estimates on the Newfoundland Shelf, using the Mobil Oil company study on Grand Banks (Hollibaugh and Booth, 1981), global remote sensing data from Feldman *et al.* (1995) and oceanographic studies on Grand Banks by the Bedford Institute of Oceanography, available between 1980 and 1988. Seasonal data was compared between studies, then converted to phytoplankton data using the Chl:C ratio (Hollibaugh and Booth, 1981), and averaged for the year to obtain an estimate of 24.600 t·km⁻² for Grand Banks (Bundy *et al.*, 2000). This value was used for both models of NAFO 3Ps, as no area-specific data was available, nor surveys done for either of the two periods of the study.

Production:Biomass

Phytoplankton primary productivity was estimated from the same sources used to estimate chlorophyll *a* biomass as seen in Bundy *et al.* (2000). The range of productivity produced from the studies on Grand Banks was 155.6 to 194 gC·m⁻², or 1,556.3 to 1,940.0 t·km⁻², giving a range of *P/B* estimates from 63.300 year⁻¹ to 78.900 year⁻¹. The mid value of this range, 71.100 year⁻¹, was used for both models.

Balancing the model

No adjustments to input parameters were necessary to balance the models.

4.3.1.22 Detritus

Detritus biomass was calculated using the empirical relationship derived from Pauly *et al.* (1993), as follows:

$$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E \quad (14)$$

where D is the detritus standing stock expressed in $\text{gC}\cdot\text{m}^{-2}$, PP is the primary productivity expressed in $\text{gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ and estimated from the phytoplankton group, and E is the euphotic depth expressed in meters.

The primary production value estimated from the P/B ratio of 71.100 year^{-1} was $1,749.060 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$, giving a PP of approximately $174.906 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ using gC/g wet weight ratio of 0.100 (Christensen and Pauly, 1992).

The euphotic depth can be calculated from the Beer-Lambert Law with the following equation (Swinehart, 1962):

$$\ln I_1 - \ln I_2 = k (D_1 - D_2) \quad (15)$$

where I_1 is the 100% irradiance at the surface, I_2 is the 1% irradiance at the euphotic depth, D_1 is the depth at surface (i.e., 0 meters), D_2 is the euphotic depth and k is the light attenuation coefficient.

Hollibaugh and Booth (1981) estimated average values of light attenuation on Grand Banks, which were substituted into the equation to get a mean euphotic depth estimate of 54.7 m . This euphotic depth value and the primary production were substituted into the first equation to get an estimate of detritus biomass of $16.9 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$, or $169.0 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$, using the conversion factor of $10 \text{ g wet weight} = 1 \text{ gC}$ (Christensen and Pauly, 1992).

4.3.2 Results from the balanced models

Following the parameters input in the two models as defined in the previous section of this chapter, and the necessary adjustments to balance both models, the results from the balanced models are shown in the following tables (Tables 4.30 and 4.31).

Table 4.30. Input parameters and selected results of the balanced NAFO 3Ps model for the 1960-1969 period.

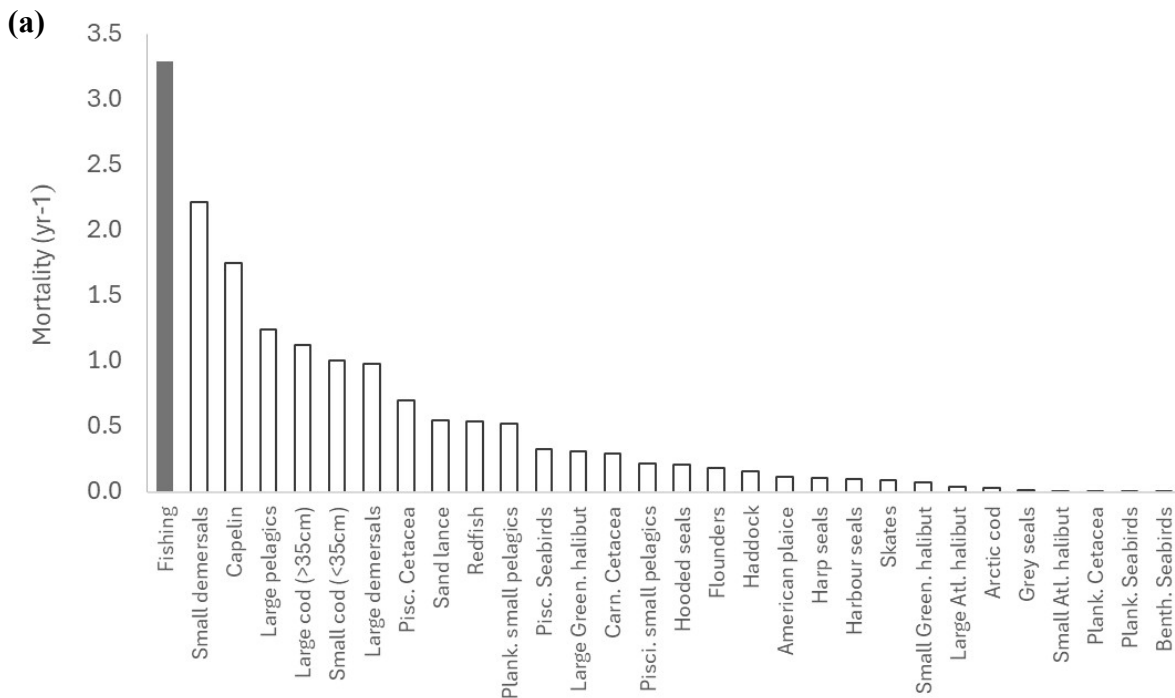
#	Group name	TL	B (t·km ⁻²)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	GE
1	Pisc. Cetacea	4.225	0.221	0.110	5.526	0.172	0.020
2	Plank. Cetacea	3.527	0.028	0.055	3.468	0.857	0.016
3	Carn. Cetacea	5.031	0.001	0.084	8.100	0.000	0.010
4	Harp seals	4.359	0.021	0.149	16.78	0.322	0.009
5	Hooded seals	4.477	0.004	0.115	18.23	0.555	0.006
6	Grey seals	4.436	0.001	0.105	11.80	0.642	0.009
7	Harbour seals	4.302	0.010	0.128	13.00	0.570	0.010
8	Pisc. Seabirds	4.221	0.010	0.250	119.4	0.000	0.002
9	Benth. Seabirds	3.178	0.000	0.130	45.30	0.000	0.003
10	Plank. Seabirds	3.324	0.002	0.150	64.61	0.000	0.002
11	Large cod (>35cm)	3.771	2.260	0.683	2.790	0.574	0.245
12	Small cod (<35cm)	3.486	1.872	0.600	5.221	0.301	0.115
13	Large Green. Halibut	4.030	0.348	0.340	1.300	0.162	0.254
14	Small Green. Halibut	3.756	0.089	0.918	3.764	0.337	0.282
15	Large Atl. Halibut	3.895	0.054	0.188	1.360	0.507	0.138
16	Small Atl. Halibut	3.335	0.011	0.417	3.181	0.473	0.131
17	American plaice	3.096	1.169	0.698	2.538	0.769	0.275
18	Flounders	3.114	0.789	0.461	2.258	0.950	0.204
19	Skates	3.396	0.259	0.231	1.860	0.950	0.124
20	Redfish	3.429	2.017	0.631	2.750	0.950	0.229
21	Large demersals	3.800	1.744	0.654	2.540	0.950	0.257
22	Small demersals	3.186	5.118	0.546	4.260	0.716	0.128
23	Capelin	3.303	13.770	0.700	4.300	0.535	0.163
24	Haddock	3.055	0.432	0.450	4.380	0.950	0.103
25	Sand lance	3.158	3.800	1.150	6.157	0.950	0.187
26	Arctic cod	3.342	0.352	0.395	2.700	0.950	0.146
27	Large pelagics	4.151	0.282	0.425	3.730	0.950	0.114
28	Pisci. Small pelagics	3.246	2.456	0.518	3.450	0.586	0.150
29	Plank. Small pelagics	3.224	2.534	0.689	4.590	0.613	0.150
30	Shrimp	2.445	3.738	1.450	7.250	0.950	0.200
31	Large crustacea	3.114	3.852	0.365	1.460	0.950	0.250
32	Lobster	3.314	0.080	0.250	1.667	0.875	0.150
33	Sea cucumber	2.200	3.000	0.473	3.153	0.935	0.150
34	Echinoderms	2.004	109.3	0.473	5.256	0.123	0.090
35	Molluscs	2.000	42.10	0.600	6.667	0.154	0.090
36	Squid	3.441	0.341	1.800	12.00	0.876	0.150
37	Polychaetes	2.053	10.50	2.000	22.22	0.958	0.090
38	Other ben. Inver.	2.010	7.800	2.500	12.50	0.681	0.200
39	Large zooplankton	2.453	33.23	3.481	19.50	0.950	0.179
40	Small zooplankton	2.000	51.65	6.200	20.43	0.950	0.303
41	Phytoplankton	1.000	24.60	71.10		0.910	
42	Detritus	1.000	169.0			0.737	

Table 4.31. Input parameters and selected results of the balanced NAFO 3Ps model for the 2000-2009 period.

	Group name	TL	B (t·km⁻²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE	GE
1	Pisc. Cetacea	4.161	0.145	0.110	5.394	0.201	0.020
2	Plank. Cetacea	3.526	0.025	0.055	3.468	0.816	0.016
3	Carn. Cetacea	5.135	0.001	0.084	8.100	0.000	0.010
4	Harp seals	4.342	0.057	0.149	17.64	0.312	0.008
5	Hooded seals	4.529	0.012	0.115	18.33	0.712	0.006
6	Grey seals	4.504	0.016	0.105	11.80	0.025	0.009
7	Harbour seals	4.258	0.015	0.128	13.00	0.672	0.010
8	Pisc. Seabirds	4.227	0.007	0.250	119.4	0.000	0.002
9	Benth. Seabirds	3.238	0.002	0.130	45.30	0.000	0.003
10	Plank. Seabirds	3.297	0.006	0.150	64.60	0.000	0.002
11	Large cod (>35cm)	3.823	0.765	0.565	2.790	0.596	0.203
12	Small cod (<35cm)	3.635	0.998	1.100	6.370	0.405	0.173
13	Large Green. Halibut	4.116	0.690	0.330	1.438	0.109	0.254
14	Small Green. Halibut	3.664	0.386	0.918	3.511	0.198	0.261
15	Large Atl. Halibut	3.854	0.022	0.191	1.270	0.707	0.150
16	Small Atl. Halibut	3.250	0.004	0.333	2.854	0.974	0.117
17	American plaice	3.385	0.277	0.328	1.700	0.895	0.193
18	Flounders	3.183	0.668	0.229	2.258	0.957	0.101
19	Skates	3.391	0.395	0.233	1.352	0.691	0.172
20	Redfish	3.473	2.556	0.248	2.450	0.851	0.101
21	Large demersals	3.840	0.312	0.208	2.000	0.950	0.104
22	Small demersals	3.648	4.397	0.404	4.000	0.876	0.101
23	Capelin	3.269	7.648	0.705	4.300	0.950	0.164
24	Haddock	3.057	0.442	0.510	4.380	0.950	0.116
25	Sand lance	3.158	14.84	0.620	4.250	0.672	0.146
26	Arctic cod	3.339	0.178	0.395	2.700	0.950	0.146
27	Large pelagics	4.093	0.114	0.323	3.735	0.949	0.086
28	Pisci. Small pelagics	3.246	1.231	0.517	3.450	0.589	0.150
29	Plank. Small pelagics	3.197	3.596	0.688	4.590	0.511	0.150
30	Shrimp	2.445	7.189	1.450	7.250	0.950	0.200
31	Large crustacea	3.083	0.496	0.583	1.460	0.955	0.399
32	Lobster	3.053	0.036	0.477	3.180	0.950	0.150
33	Sea cucumber	2.200	2.415	0.473	3.153	0.785	0.150
34	Echinoderms	2.004	109.9	0.473	5.256	0.041	0.090
35	Molluscs	2.000	42.10	0.600	6.666	0.058	0.090
36	Squid	3.046	0.341	1.800	12.00	0.555	0.150
37	Polychaetes	2.053	10.50	2.000	22.22	0.797	0.090
38	Other ben. Inver.	2.010	7.80	2.500	12.50	0.385	0.200
39	Large zooplankton	2.453	28.133	3.481	19.50	0.950	0.178
40	Small zooplankton	2.000	49.549	6.200	20.43	0.950	0.303
41	Phytoplankton	1.000	24.60	71.10		0.865	
42	Detritus	1.000	169			0.722	

4.3.2.1 Predation and fishing mortalities

In the 1960-1969 model, fishing mortality for all commercially harvested species in the system is higher than the mortality induced by each vertebrate predators on all preys in the system (i.e., the fishery is the main predator of the system). The other most important predators in the system are small demersals (mainly due to their predation on benthic invertebrates), capelin, large pelagics and large cod (Figure 3.2). In the 2000-2009 model, the most important predators in the system are small demersals, sand lance and capelin, mainly due to their predation on benthic invertebrates, and large cod. The fishery has decreased, and is only fourth in order of importance of relative mortality on preys in the system.



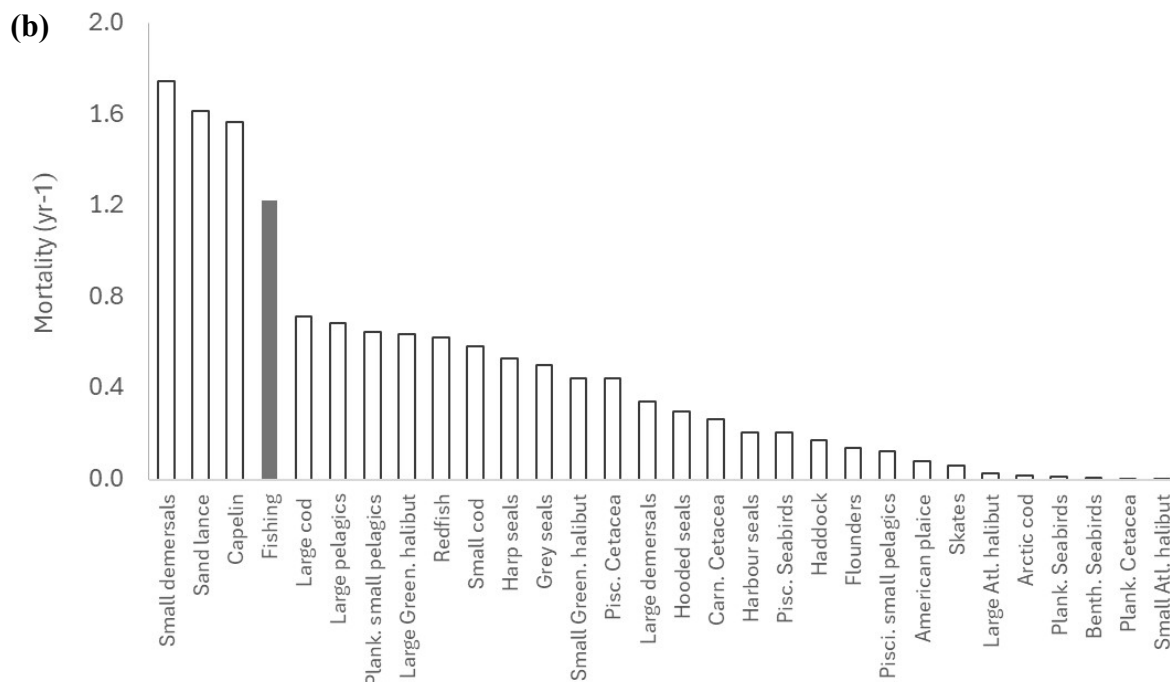


Figure 4.2. Distribution of predation mortality among all vertebrate predators on all preys, including fishing, in the (a) 1960-1969 and (b) 2000-2009 Ecopath models of NAFO 3Ps.

When comparing fishing and predation mortalities for commercially harvested groups in the system in the 1960-1969 model, fishing mortality is significantly higher for large cod, American plaice, redfish, large demersals and large pelagics. In the 2000-2009 model, fishing mortalities have strongly decreased, and predation mortality is the higher mortality for most groups with the exception of large cod, large Greenland halibut, large Atlantic halibut, and lobster (Figure 4.3).

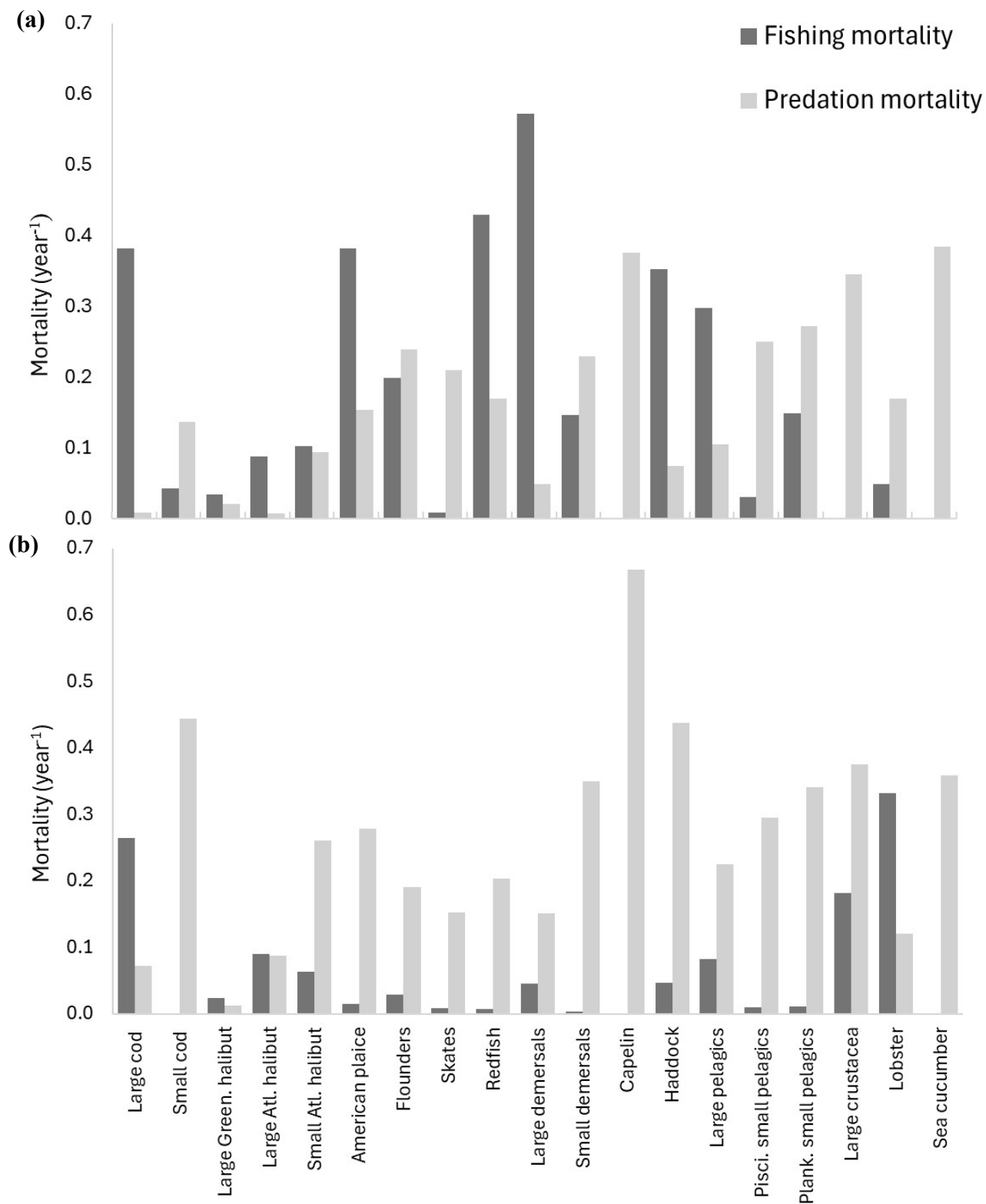


Figure 4.3. Comparison of fishing and predation mortality on selected prey groups, in the (a) 1960-1969 and (b) 2000-2009 Ecopath models of NAFO 3Ps.

4.3.2.2 System statistics comparison between the two models

Several ecosystem indices are given by the balanced models and comparable between the two periods of interest. Total system throughput (TST), as the sum of all flows of energy within the system, does not vary significantly between the two periods of study. Gross Efficiency (*GE*) is significantly higher in the first model ($GE = 0.003$), as a reflection of stronger fishing pressure on the system. The net system production is high in both models ($NSP > 350$), a sign of strong system autotrophy (Table). Total biomass is lower in the 2000-2009 model, a reflection of the decrease in demersal (e.g., Atlantic cod) and pelagic fishes biomass (e.g., capelin) (Table 4.32).

The Connectance index of both system is similar, indicating similar proportions of possible predator-prey links that are realized in the food web between both models, i.e., similar food-web complexity. The system omnivory index is slightly higher in the 2000-2009 model, indicating a higher variance in the trophic levels of prey across all consumers in the system. Similar Shannon Diversity Index of the system between both periods indicates similar biomass diversity among groups (Table 4.32).

Table 4.32. Biomass comparison for major groups between the two Ecopath models of NAFO 3Ps. Absolute change is deemed significant when higher than 20%.

Major group	1960-1969	2000-2009	% change	Significance
Cetaceans and birds	0.262	0.185	-22.3	***
Seals	0.035	0.098	179	***
Demersal fishes	20.31	26.93	32.6	***
Pelagic fishes	19.04	12.59	-33.9	***
Crustaceans	7.670	7.721	0.66	—
Other invertebrates	173.0	173.1	0.01	—
Zooplankton	84.88	77.68	-8.48	—
Phytoplankton	24.60	24.60	0.00	—
Total	330.0	322.9	-2.15	—

Table 4.33. Comparison of system statistics between the 1960-1969 and 2000-2009 Ecopath models of NAFO subdivision 3Ps.

Parameter	1960-1969	2000-2009	Units
Total consumption	3,102	2,977	t·km ⁻² ·year ⁻¹
Sum of all exports	371.9	393.9	t·km ⁻² ·year ⁻¹
Sum of all respiratory flows	1,380	1,355	t·km ⁻² ·year ⁻¹
Sum of all flows into detritus	1,396	1,417	t·km ⁻² ·year ⁻¹
Total system throughput (TST)	6,251	6,143	t·km ⁻² ·year ⁻¹
Total biomass (excluding detritus)	330.0	322.9	t·km ⁻²
Sum of all production	2,339	2,307	t·km ⁻² ·year ⁻¹
Calculated total net primary production	1,749	1,749	t·km ⁻² ·year ⁻¹
Gross efficiency (catch/net primary production)	0.003	0.0003	—
Total primary production /total respiration	1.267	1.291	—
Net system production	368.7	393.9	t·km ⁻² ·year ⁻¹
Total catch	4.908	0.546	t·km ⁻² ·year ⁻¹
Mean trophic level of the catch	3.465	3.385	—
Connectance index	0.224	0.229	—
System omnivory index	0.108	0.112	—
Shannon diversity index	2.222	2.179	—
Finn's Cycling Index (FCI)	7.753	7.659	% of TST
Total transfer efficiency	12.32	11.12	%

4.3.2.3 Trophic levels

Several groups in the system have seen an increase of their trophic level in the 2000-2009 system, like grey seals (+1.53%), large cod (+1.37%), flounders (+2.22%), while some others have seen a decrease, like large Atlantic halibut (-1.04%), capelin (-1.02%) or large pelagics (-1.40%). An overall 0.22% increase in average trophic level between the 1960-1969 and 2000-2009 models can be observed. In terms of trophic levels prevalence, most of the system's biomass is distributed among the trophic levels II (> 240 t·km⁻²) and III (> 44 t·km⁻²) (Figure 4.4). The composition of biomass in terms of trophic levels does not substantially vary between the models, while the

composition of the catch does, with a reduction in the prevalence of trophic level III and IV species and an increase in the prevalence of trophic level II species (Figure 4.5).

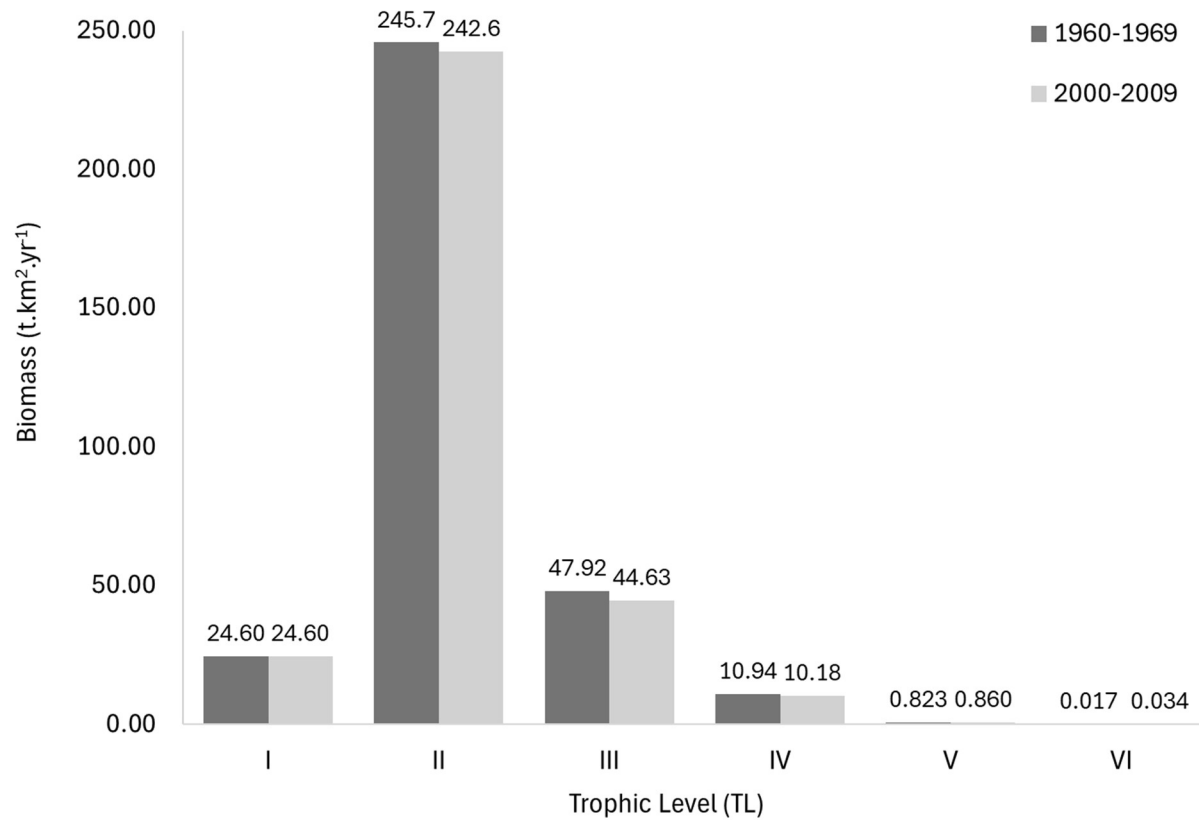


Figure 4.4. Comparison of the distribution of biomass in the system among trophic levels, between the 1960-1969 and 2000-2009 Ecopath models of NAFO 3Ps.

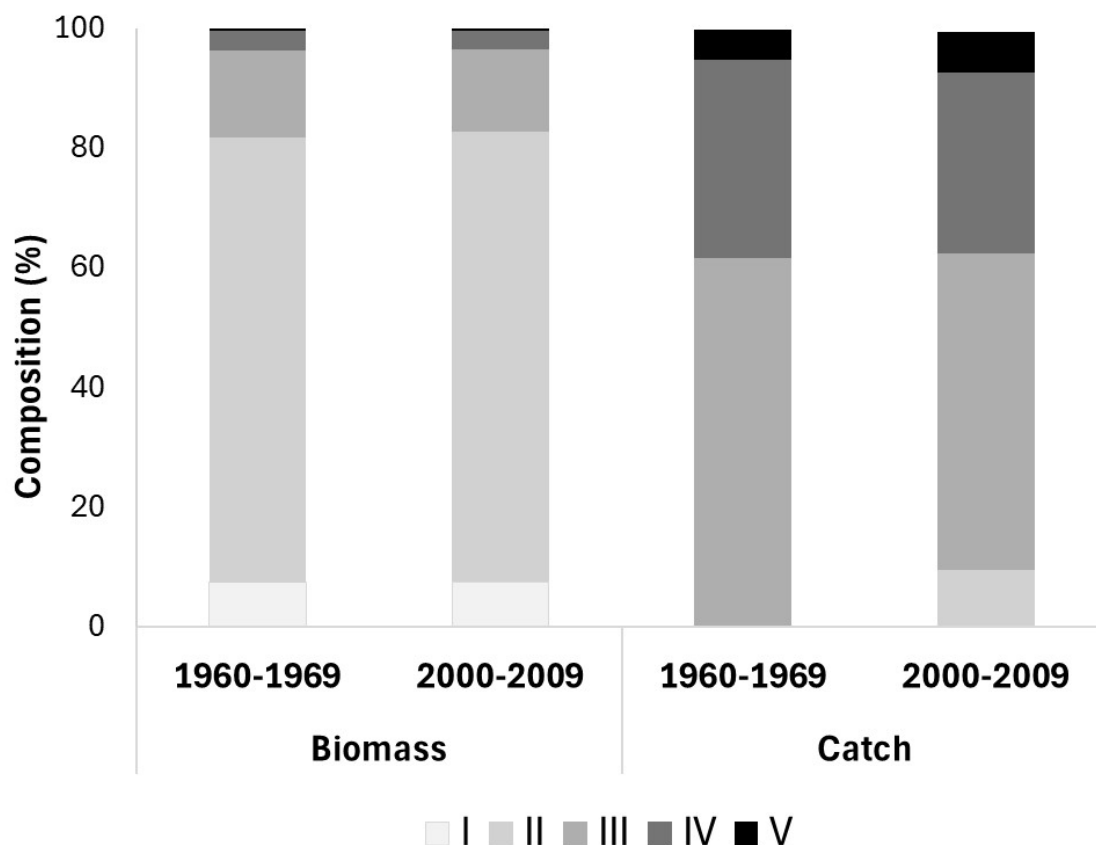


Figure 4.5. Composition of the system biomass and catch in terms of the six main trophic levels, for the 1960-1969 and 2000-2009 models of NAFO 3Ps.

4.3.2.4 Particle size distribution

A PSD was constructed for each of the two balanced Ecopath models. The size spectrum allowed the comparison of the slope between both models: in 1960-1969, slope and standard error of the PSD were -0.656 ± 0.096 , and -0.635 ± 0.066 in 2000-2009 (Figure 4.6). The steeper slope of the 1960s model is associated with the higher fishing pressure then prevailing (Zhai and Pauly, 2020).

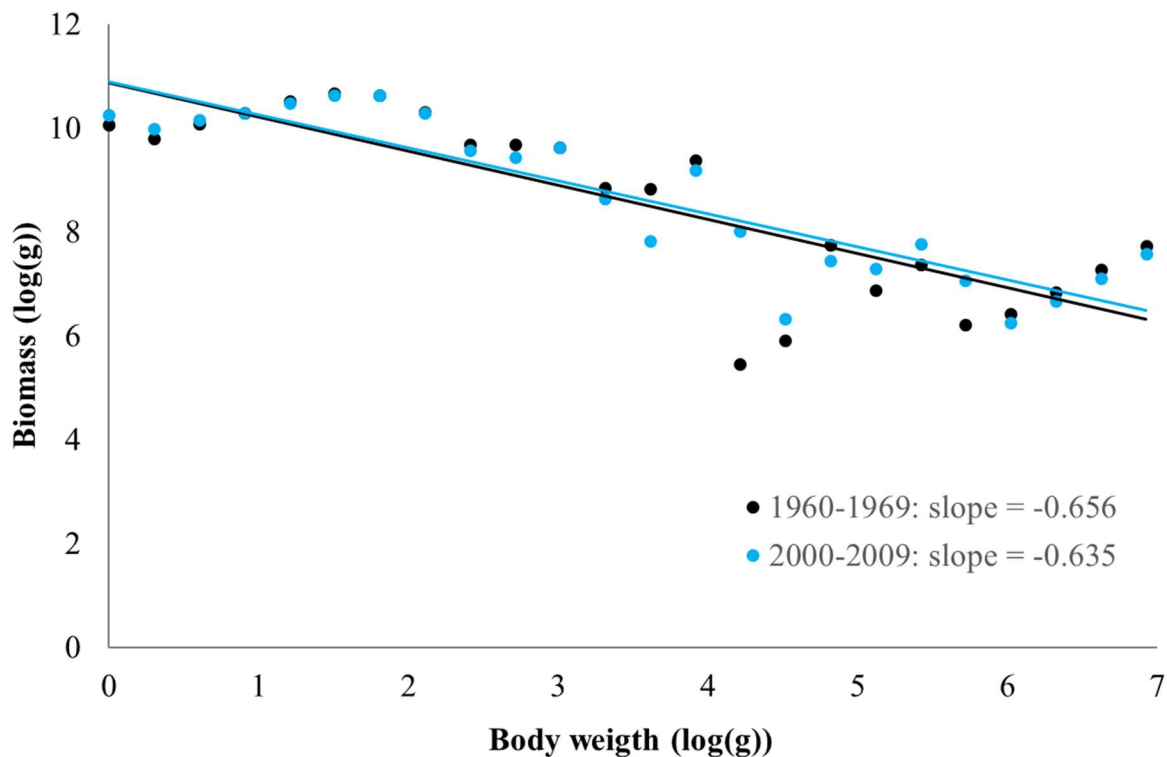


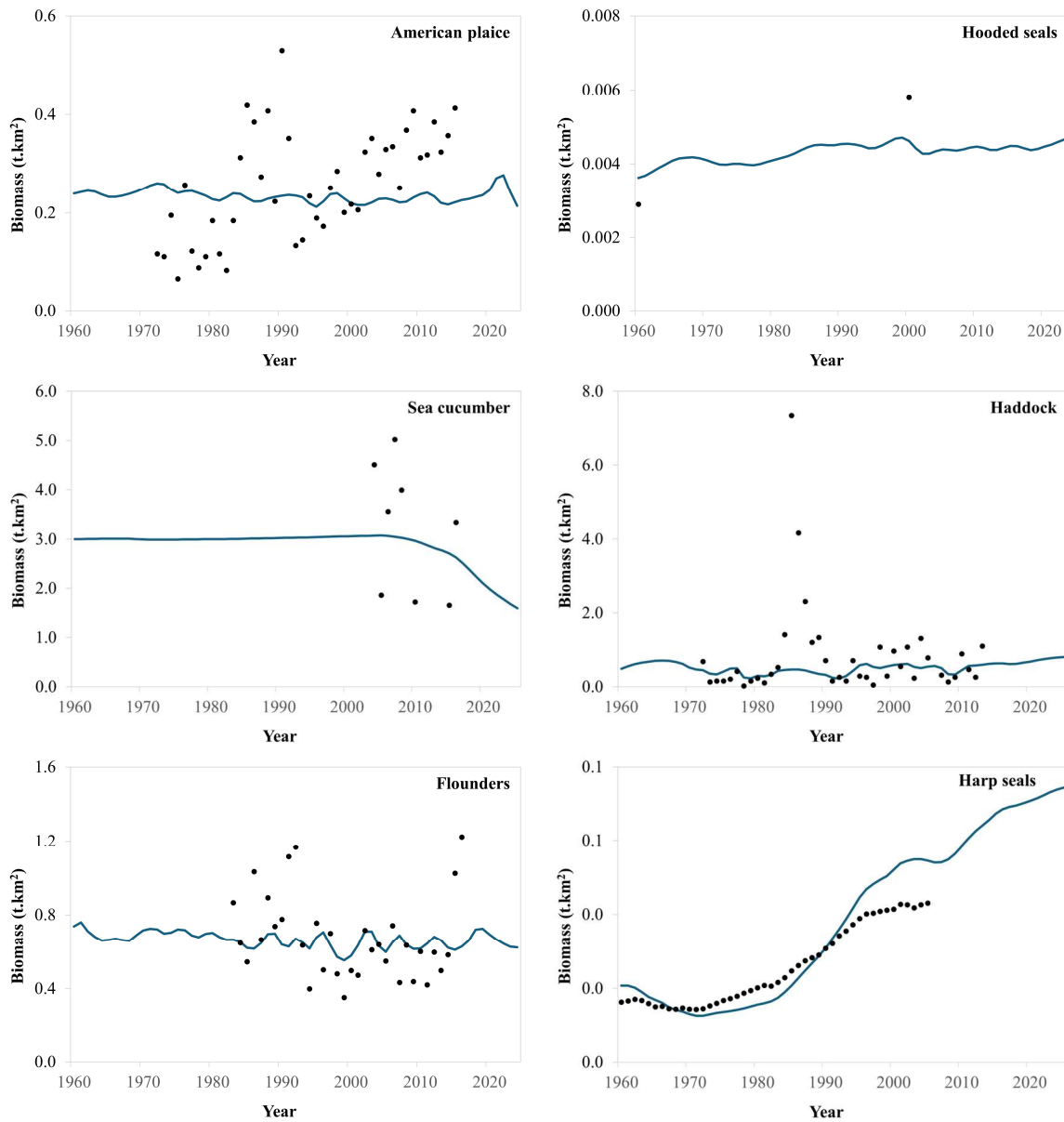
Figure 4.6. Comparison of the slope of the Particle Size Distribution (PSD) spectra for the two Ecopath models. Values in black are for the 1960-1969 model, and in blue for the 2000-2009 model

4.3.3 Ecosim time-dynamic simulations

4.3.3.1 Model calibration

The Ecosim simulation was based on data from the balanced Ecopath model for the 1960-1969 time-period. It was calibrated using time series of catch, biomass (i.e., for species with biomass assessments undertaken in NAFO 3Ps), fishing mortality and fishing effort. Model performance was evaluated based on the agreement between observed and predicted trends: overall, the fit was satisfactory for most functional groups, particularly in terms of fit to catch data for groups such as large cod and sea cucumber (Figures 4.7 and 4.8). Some discrepancies were observed for benthic invertebrates and small pelagic fishes, likely reflecting data limitations and natural variability not captured by the model. Vulnerability settings were adjusted within plausible ecological ranges to achieve realistic predator-prey dynamics. The final model produced an

Akaike Information Criterion (AIC) of 2812 and a total sum of squares (SSD) of 9035 across fitted groups.



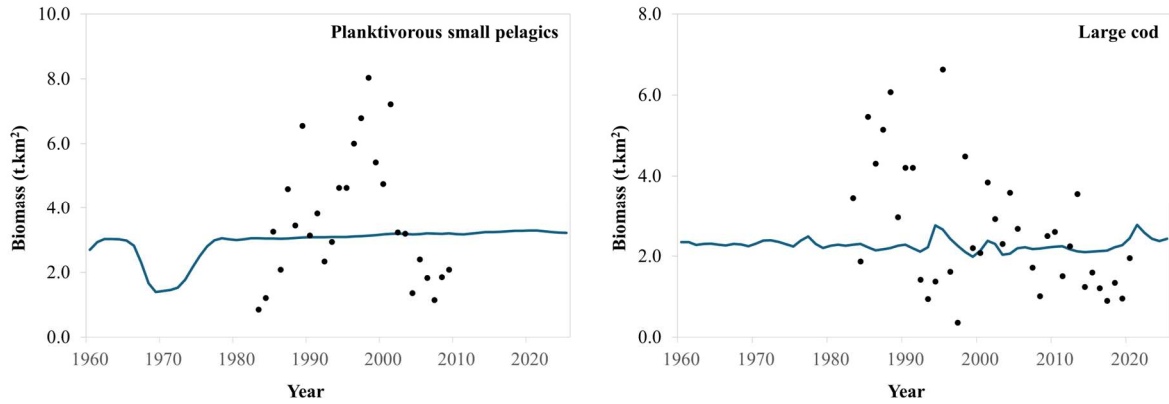


Figure 4.7. Relative biomass fits from the Ecosim model for the groups with biomass data within NAFO 3Ps. The dots are the biomass values as input in the model, and the line represents the model fit.

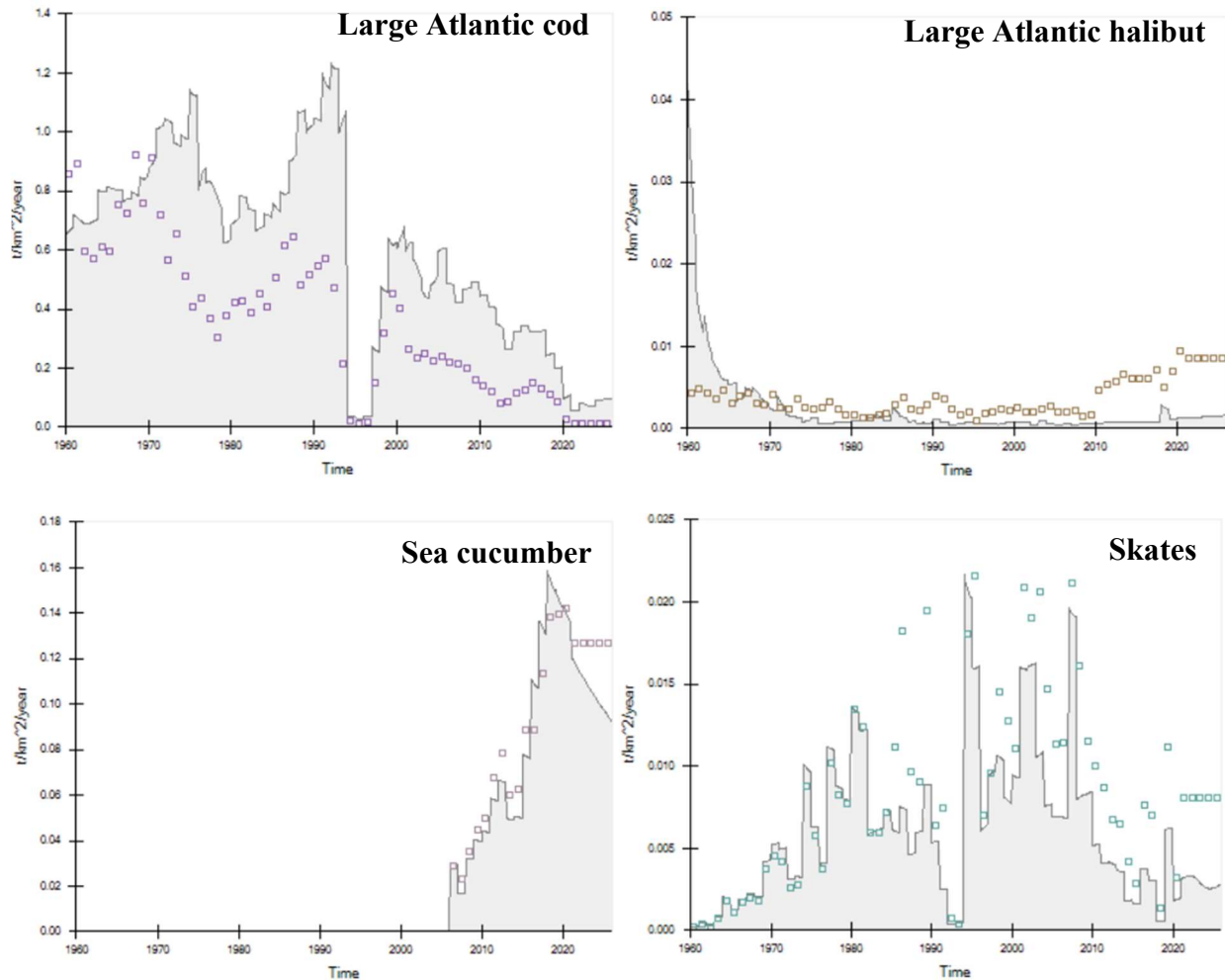


Figure 4.8. Fit to catch time series for four groups from the Ecosim model. Catch is absolute and expressed in tonnes per square kilometer per year, from 1960 to 2025.

4.3.3.2 Fishing effort projection

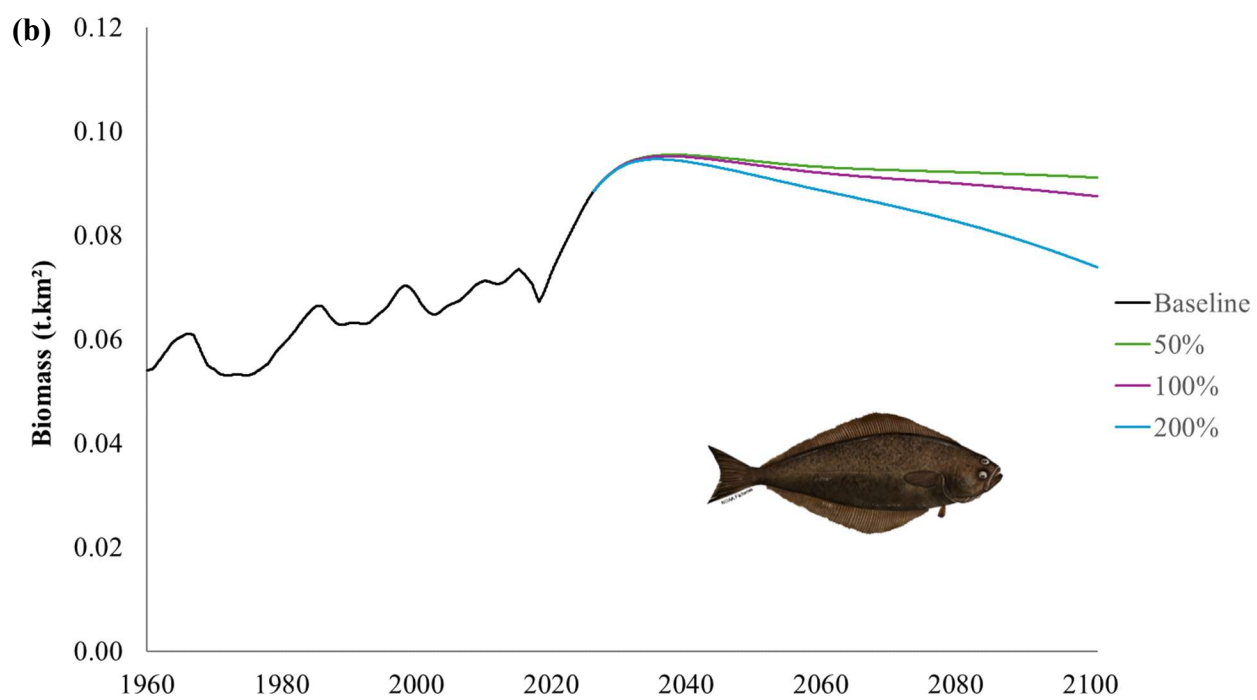
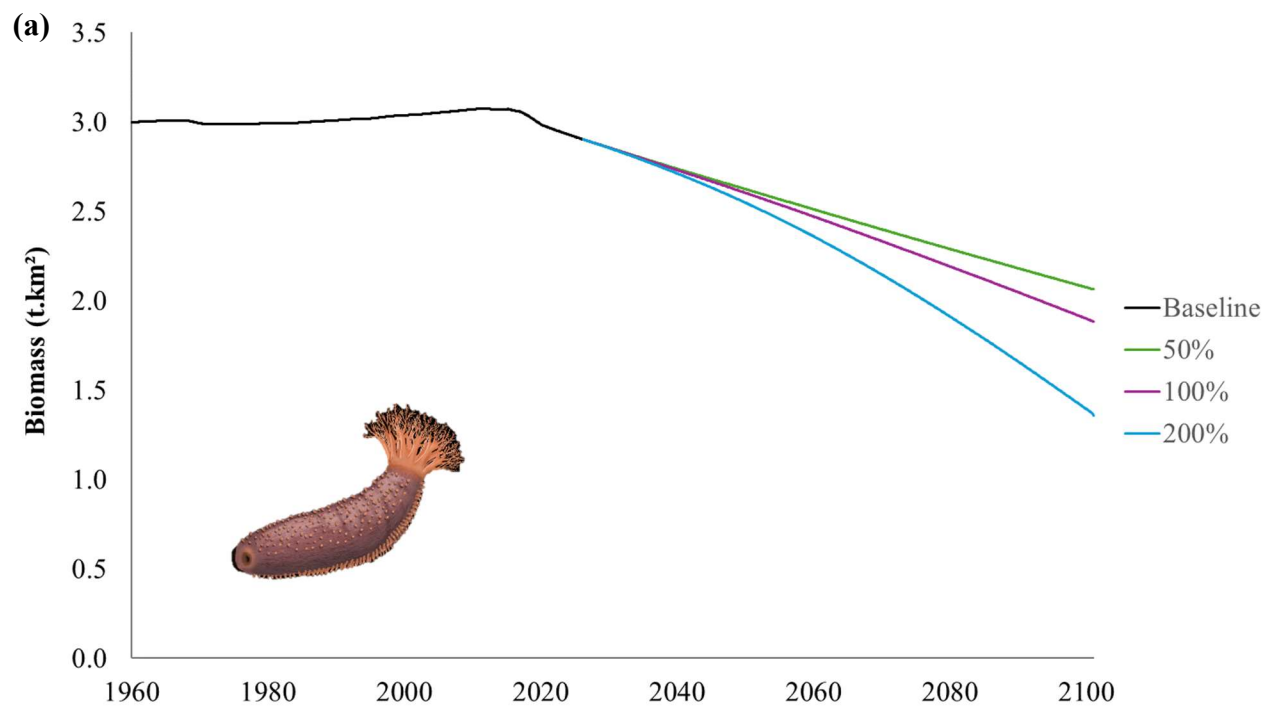
The projections of an increase in fishing effort on SPM's dredges and longlines showed biomass decreases under all three scenarios (i.e., 50%, 100% and 200% effort increase), with a sharper and faster decline under the 200% increase scenario.

Sea cucumber showed respectively a 28.7%, 34.9%, and 53.1% biomass decrease under a 50%, 100% and 200% effort increase scenario. A 200% increase is presently the increase seen in the catches of sea cucumber by SPM dredges from 2008 to 2018 (c.f. *Chapter 2: Reconstructing what SPM has caught from 1950 to 2022*) (Figure 4.9(a)).

Atlantic halibut's biomass is predicted by the model to increase between 1960 and 2025. The three scenarios of effort increase implied a decrease in biomass more moderate than for sea cucumber. Atlantic halibut's biomass seems to show relative stability under a gradual effort increase of less than 100%. Under a 200% effort increase scenario, biomass shows a 16.4% gradual decrease (Figure 4.9(b)).

For the purpose of projections scenarios, and as both sea-scallop biomass on Saint Pierre Bank and historical scallop-dredges effort was available (Foucher, 2018), the molluscs group was split to isolate deep-sea scallops as an independent functional group, and molluscs catches were similarly split. This allowed to observe the effect of the three effort increase scenarios on deep-sea scallop biomass. Deep-sea scallop seemed to be the group most impact by increases in the effort of their associated fleet. A 50% and 100% effort increase respectively results in a 33.8% and 59.6% gradual biomass decrease, while a 200% effort increase results almost in a biomass crash, with a 92.3% gradual biomass decrease (Figure 4.9(c)).

Main predators for sea cucumber and sea-scallop include echinoderms, large crustacea, large cod and lobster. No significant variation in predators biomass was observed in the 50% or 100% increase scenarios. Under the 200% increase scenario, however, a slight and gradual diminution in the biomass of large crustacea (2.0%) and lobster (5.6%) can be observed. These declines are, however, not strong enough to trigger subsequent declines in the predators of the aforementioned groups. No significant variations were observed in the biomass of Atlantic halibut's main predators (i.e., grey seals and hooded seals) or their main preys (i.e., shrimps and small demersals).



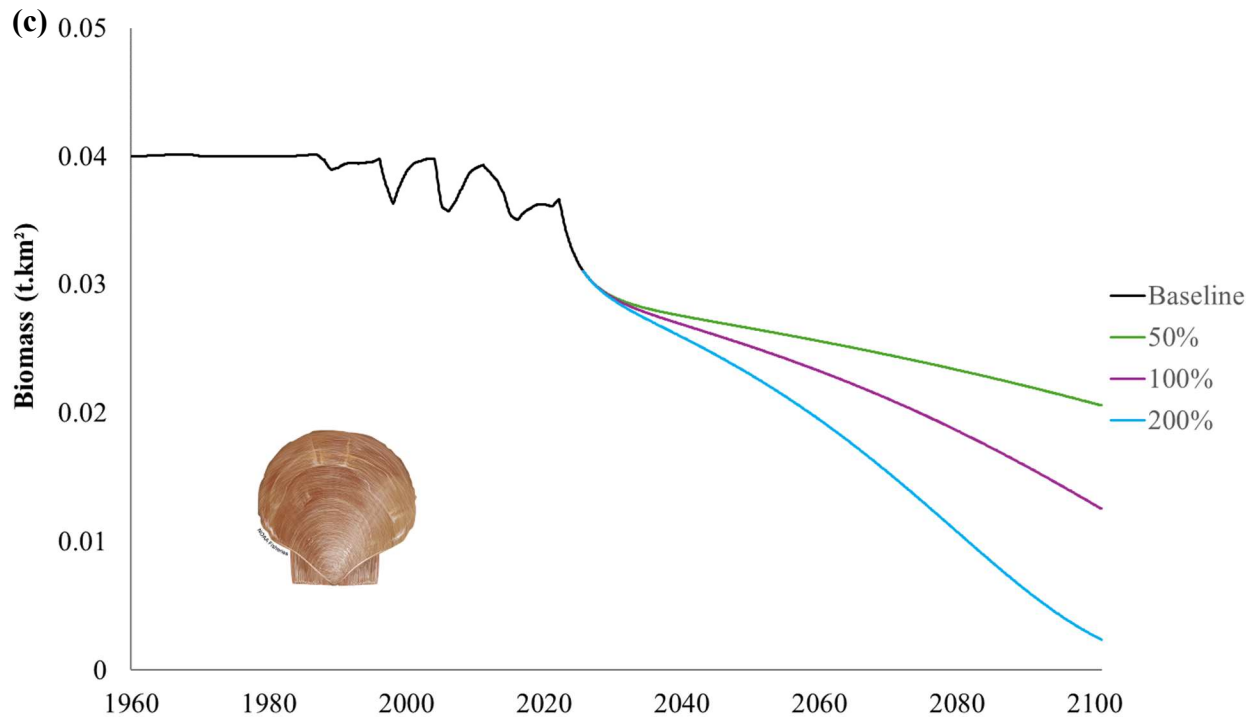


Figure 4.9. Projection of a 50%, 100% and 200% increase in fishing effort in NAFO 3Ps on the biomass of sea cucumber (a), Atlantic halibut (b), and deep-sea scallop (c), from 2025 to 2100. Baseline effort data covers the 1960-2025 period. Biomass is absolute.

4.3.4 Ecospace spatial simulation

The Ecospace spatial module was run based on the balanced 1960-1969 Ecopath model and subsequent Ecosim simulations. The habitat capacity and depth ranges defined for each functional group (see Appendix E), as well as the feeding interactions defined in the balanced model, allowed the creation of relative biomass distribution maps for each of the 42 functional groups in the NAFO 3Ps model. The Saint Pierre Bank is here shown to concentrate the biomass of seals, small pelagics, and some invertebrates such as sea cucumber, lobster, and molluscs (Figure 4.10).

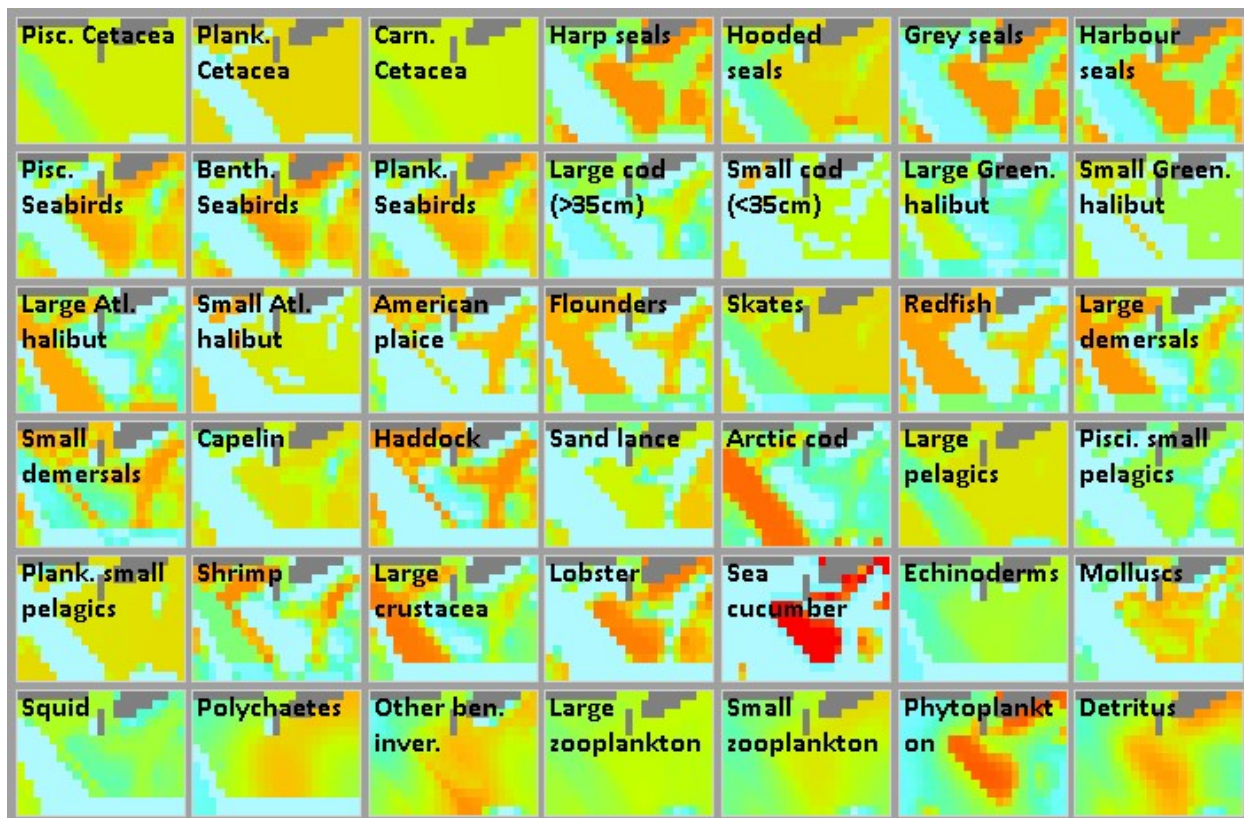


Figure 4.10. Ecospace distribution maps for the 42 groups of the NAFO 3Ps ecosystem model. Distribution maps are based on each group's habitat capacity (suitability ranging from 0 to 1 for each of the defined habitat type: shelf, slope and offshore deep), preferred depth ranges, and feeding interactions. The color gradient shows relative biomass for each group, from high (red) to low (blue).

4.4 Discussion

The construction of two Ecopath models of NAFO subdivision 3Ps allowed the comparison of two different states of the ecosystem, at a period preceding peaks in fishery exploitation and the Northwest Atlantic cod collapse (i.e., 1960-1969 model), and at a period succeeding the cod collapse and marking the initial reliance on invertebrate fisheries (i.e., the 2000-2009 model). Main results highlighted shifts in fishing pressures in the system, shaping shifts in biomass and trophic structure. The subsequent Ecosim analysis highlighted biomass decreases in three economically important species for SPM fisheries, under different effort increase scenarios. An Ecospace simulation allowed to spatialize relative biomass in the system, and highlighted the Saint Pierre

Bank as the zone in 3Ps with a higher concentration of benthic invertebrates and small pelagic fishes.

4.4.1 Biomass fluctuations from 1960-1969 to 2000-2009

Comparing the two Ecopath models built for NAFO 3Ps highlights distinctive changes of biomass in some groups that are known to have fluctuate sharply in the Northwest Atlantic pre and post cod collapse. Thus, Atlantic cod biomass have decreased significantly for both the large and small stanza in the 2000-2009 model, following Northwest Atlantic trends, though less sharp in NAFO 3Ps than on the adjacent Grand Banks (Rideout *et al.*, 2016). The other strongest declines in the more recent model can be seen in the capelin, large crustaceans and large demersals (i.e., all groups of large demersal species included) groups.

Capelin has a key role in the ecosystem, as a forage species responsible for energy transfers between top predators and lower trophic levels, including plankton (Buren *et al.*, 2014). What used to be a species harvested in considerable quantities for subsistence and commercial profit in SPM (Ancellin, 1955; Eynaud, 1986) suffered a decline on the Saint Pierre Bank that is reflected through the significant absence of capelin from recent-years fisheries (see *Chapter 2*), and has likely been driven by similar processes as nearby areas. On the Newfoundland Shelf, capelin decline has been mainly attributed to a regime shift, in which removal of the system's top predators through intensive exploitation coupled with climate change induced shifts in the Arctic current circulation patterns have contributed to drive capelin biomass fluctuations (Buren *et al.*, 2014). As species providing ecosystem services both as preys for important predators in the ecosystem, and as preys with consumption value for humans (e.g., used to produce fish meal and fish oil), forage fish are important components of the marine with needs for renewed conservation efforts (Nissar *et al.*, 2022).

Large crustaceans have suffered a decline that could impact SPM fisheries, as snow crab is a resource harvested on Saint Pierre Bank which has a growing prevalence in the composition of the catch in SPM's EEZ (see *Chapter 2*). Where the snow crab fishery peaked in the mid-2000s in Newfoundland, the SPM fishery has experienced a new peak since 2021 while the resource depletion rate was still high (see *Chapter 2*). Biomass declines around Newfoundland have been

attributed to low productivity and recruitment, tied to a warming oceanographic regime (Mullowney *et al.*, 2014).

A similar decline in large demersals can be observed in NAFO 3Ps as on Grand Banks or NAFO 3M (Pérez-Rodríguez *et al.*, 2013). Large demersals, including halibut, other flounders and redfish, have been the principal target of commercial fisheries on Grand Banks and Saint Pierre Bank since the beginning of historical exploitation in the area. Sharp biomass declines can be observed throughout the Northwest Atlantic, as a direct result of high fishing intensity and catches for high trophic level fishes (Christensen *et al.*, 2003; Koen-Alonso *et al.*, 2010)). Coupled with climate change pressures and warming waters, extensive exploitation have contributed to major biomass depletions and shifts in community structure (Pérez-Rodríguez *et al.*, 2013). Cod and other large demersals declining in the system had top-down effects on the trophic web, while similar declines in key preys such as snow crab had consecutive bottom-up effects on cod populations (Boudreau *et al.*, 2011). This interplay of controls and the numerous shifts in species composition have extensive effects on the ecosystem dynamics and the stability of the trophic web (Hunt and McKinnell, 2006).

Considerable biomass increases in the 2000-2009 picture of the system can be observed for sand lance, seals and shrimp. Sand lance has shown a significant increase in biomass in the mid-2000s (Bundy, 2004), while experts warn of projected declines in abundance linked to shifts in forage fish complexes in the Northwest Atlantic (Suca *et al.*, 2021). Just like capelin, sand lance is considered an essential forage fish for its functional roles in the ecosystem, on which multiple species depend for their diet (Staudinger *et al.*, 2020). Although most seal species don't have breeding or whelping sites inside NAFO 3Ps, and are only transient in the area, large increases in seal populations across the Northwest Atlantic had notable impacts on the 3Ps ecosystem structure, as seals are key predators on numerous groups, including cod, capelin and small pelagic fish (Tam and Bundy, 2019). Shrimp biomass increase in the system post 1990s has been linked to predation release as a consequence of the cod biomass decline (Lilly *et al.*, 2000).

4.4.2 Ecosystem indices in NAFO subdivision 3Ps

Most ecosystem indices (i.e., connectance, system omnivory index, and Shannon diversity index) are within their expected range in both pictures of the NAFO 3Ps ecosystem (Malek *et al.*,

2014; Plagányi and Essington, 2014; Sánchez-Hernández and Amundsen, 2018). Gross efficiency is in its normal range in the 1960-1969 model, but very low in the second model (Christensen and Walters, 2024): this reflects both the 1960s being the period preceding the strongest exploitation rates on Saint Pierre Bank (i.e., the 1980-1990s), and the 2000s having much lower fishing intensity as demersal species of interest became less available, and invertebrates fisheries (e.g., bivalves, sea cucumber) were yet to become more prevalent in SPM. The net system production (NSP) is considerably high in both models, which can indicate excess production in the system (i.e., primary producers are generating more organic matter than the system is respiring or consuming), but is also consistent with the banks being a highly productive system. High NSP can also be representative of immature or expending systems, according to the Ecopath theory taking after Odum's system ecology (Odum, 1983; Christensen *et al.*, 2005), like systems recovering after perturbations and biomass declines (e.g., recovery in the 2000s after the 1992 cod collapse) (Pedersen *et al.*, 2017).

Additionally, looking at the total flows from detritus and Finn's Cycling Index (FCI) being low in both models, i.e., indicating low proportion of energy recycled through detrital loops, indicate that the system is not detritus driven, but instead relies more on primary production from phytoplankton (Finn, 1967; Christensen and Walters, 2024). The additionally low transfer efficiency between trophic levels supports the idea of a food chain influenced by historical fishing and reduced top predator biomass (Eddy *et al.*, 2021).

Mean trophic level (MTL) of the system has shown a slight increase between the two time-periods, in contrast to what was hypothesized. This increase can be linked to rises in abundance of higher trophic level predators such as seals (Hammill and Stenson, 2005). It can also relate to an increase in piscivory, i.e., increased consumption of preys on a higher trophic level (Bundy, 2004). The MTL of the catch, on the contrary, has decreased between the two models, with the catch having shifted towards lower trophic level species. This echoes the MTL of the catch decrease highlighted for SPM in *Chapter 2* in relation to a fishing down the marine food web phenomenon (Pauly *et al.*, 1998), and extends the shift from the SPM EEZ to the NAFO 3Ps subdivision.

Fishing mortality has decreased significantly between both models, with fishing pressure release on demersal and pelagic fish species. However, it has significantly increased for most invertebrate groups: lobster, large crustacea, sea cucumber and molluscs. Where it was

hypothesized to replace predation mortality as the dominant source of mortality for most commercial invertebrate groups, this was only the case for lobsters. Additionally, the steeper slope observed in the 1960-1969 PSD is linked with higher fishing pressure: the PSD allows for a supplementary observation of the impact of fishing on the system, and high fishing pressure towards larger size classes, i.e., higher trophic levels, in the past (Zhai and Pauly, 2020). Though the slope differences reflect that the ecosystem's trophic structure has not dramatically changed between the two periods, it still suggests a potential (if partial) recovery of larger-bodied groups. However, the fact that small organisms still dominate biomass highlights continued fishing pressure on large-bodied fish, consistent with known patterns in exploited shelf ecosystems.

4.4.3 Comparison to Ecopath models of nearby areas

Comparing the NAFO 3Ps subdivision model to models constructed for nearby divisions in the Northwest Atlantic reveals numerous similitudes. Tam and Bundy's (2019) models of the Newfoundland Shelf highlighted the same decrease in fishing pressures and release of pressure on large demersal species, between the 1980s and the 2010s, as well as the key role of forage fish such as capelin for energy transfers to higher trophic levels. The aforementioned models and the 3Ps models constructed highlight capelin as a species that would benefit from low fishing rates, given its important contribution in the system. Bundy's (2004) model of the Scotian Shelf similarly shown an increase in MTL of the system, linked with an increase in piscivory in the system, and a decrease in MTL of the catch, between the early 1980s and late 1990s.

Bundy *et al.*'s (2000) model of the Newfoundland-and-Labrador Shelf showed a weak benthic-pelagic coupling, and a higher domination of the pelagic side of the food web. Bundy's (2004) models of the Scotian Shelf highlighted moderate benthic-pelagic coupling, which is also observed in the NAFO 3Ps model through diet compositions revealing that several demersal and pelagic species rely substantially on benthic invertebrates. Flows between benthic and pelagic groups are moderately high in both 3Ps models.

4.4.4 Potential effects of an increase in SPM's fleets fishing efforts

Ecosim simulations can shed light on exploitation patterns in highly pressured systems. In an Ecosim model of an area encompassing multiple fishing actors operating with different influence, projections vary in their sensitivity. In the case of NAFO 3Ps, fishing influence varies substantially between Canada and SPM: Canada can be seen as the 'big player,' a dominant fishing actor with broader spatial coverage, while SPM is the 'small player,' with smaller fishing effort and smaller catches. This imbalance can affect the interpretation of the model outputs, as the overall ecosystem response may be primarily driven by the activities of the larger player, potentially masking or diluting the ecological or management signals associated with the smaller one. Consequently, looking at the overall Ecosim results may be of a lesser interest when focusing on SPM and its fishing dynamics. Projections involving changes in fishing effort are therefore more significant when applied to highly specific local fleets. In such cases, isolating these fleets allows for a more accurate assessment of how changes in SPM's fishing activities could influence the biomass of their target species and related trophic interactions, without the confounding effects of the much larger Canadian fisheries.

SPM's sea cucumber dredges, scallop-dredges and Atlantic halibut longlines showed different strengths in biomass decrease of their target species, when exponential fishing effort increases were projected. While a 200% effort increase might seem unrealistic, it mirrors in NAFO 3Ps what was observed for the SPM dredges in the past over a 10 years period. A consequent decrease in deep-sea scallops and sea cucumber, two invertebrate species occupying low trophic levels in the food web, raises concerns similar to those previously explored through the fishing down the marine food web effect highlighted in *Chapter 2: Reconstructing what SPM has caught from 1950 to 2022*, where SPM shows increase fishing pressure towards marine invertebrates. While subsequent trophic effects of such decreases were not obvious in the models, numerous studies have highlighted the potential cascade effects the ecosystem could be subject to under invertebrate depletion scenarios (Eddy *et al.*, 2017). Marine invertebrates are essential preys upon which many commercially exploited fishes rely, e.g., scallops are important preys for Atlantic cod and various species of flounders (Jamieson, 1981). They occupy key roles in the structuration of the ecosystem, by being responsible for multiple ecosystem services, such as water filtration and seafloor structuration (Anderson *et al.*, 2011). Bivalves such as sea scallops are the ecosystem's

‘water purifiers,’ by the important water filtration and nutrient removal roles they perform (Catherine, 2024). Echinoderms, and particularly sea cucumbers, possess similar filtration roles, and participate in the bioturbation of the system, i.e., the reworking of sediments on the seafloor (Purcell *et al.*, 2016). Invertebrates’ importance in the trophic chain lies as well in the wider variety of ecological roles they play, in comparison to fishes (Anderson *et al.*, 2011; Eddy *et al.*, 2017).

Ecosim results highlighted that the two invertebrates species in focus were more sensitive to increased exploitation, while Atlantic halibut seemed to show a relative resilience to increased effort from SPM fleets. The species, however, possesses a much lower biomass in the system, as a higher trophic level predator: while biomass fluctuations might be minimal under increased effort, the fisheries might present an inherent vulnerability, with a stock potentially reaching the threshold of sustainable exploitation quicker in 3Ps. Additionally, Atlantic halibut has already experienced a collapse in the past, under extended exploitation (Shackell *et al.*, 2022). Nonetheless, biomasses have been rapidly increasing since the 2000s, and along with it the economic value of halibut, (Shackell *et al.*, 2022). The species shows high productivity with low natural mortality, rapid growth and a long lifespan (Trzcinski and Bowen, 2016). These characteristics contribute to the population’s resilience and rebound capacities (Trzcinski and Bowen, 2016). It is also relevant to mention that longlines, the fishing gear used by SPM’s fleets, present higher selectivity and lower discard-mortality for undersized halibut caught, which can make them a sustainable fishing method for halibut when managed properly (Trzcinski and Bowen, 2016).

The biomass decreases resulting from effort increase did not present significant effects at other trophic levels in the system, except under the highest effort increase scenario (200%) where crustaceans biomass presented a slight decrease over time. This outcome likely reflects several structural and ecological factors within the model. First, sea cucumber and sea-scallop have relatively few predators that depend on them exclusively, and the predators present can switch to alternative prey, dampening potential trophic cascades (Andersen and Pedersen, 2009). Additionally, the overall contribution of sea cucumbers and scallops to total energy flow in the system is relatively small, meaning their depletion represents only a minor perturbation to the broader food web. Finally, the time scale of the simulation may be too short to capture slow (i.e., long term cascading effects) or delayed effects. Changes in predator populations resulting from reduced prey availability often occur gradually through growth, reproduction, or recruitment

processes, and may not fully manifest within the simulated period (Wang *et al.*, 2009; Eklöf *et al.*, 2020).

4.4.5 Implications for management initiatives

By explicitly linking fishing pressure to ecosystem structure and function, EwE provides a platform to evaluate trade-offs among species and sectors, and potentially inform management initiatives. The varying strength of biomass decreases between species for the same effort increase projections can be informative for the management of SPM fisheries in NAFO 3Ps. The simulations suggest that maintaining moderate effort on a demersal species like Atlantic halibut while constraining exploitation of lower-trophic-level invertebrates can better sustain biomass across these functional groups. This has direct relevance for SPM, where fisheries have experienced several shifts in main species of interest (Teletchea, 2022) and management must balance ecological integrity with local livelihoods. Concerns have been raised on the redevelopment of a productive fishing industry (Teletchea, 2022): EwE simulations could provide a framework for better envisaging where to direct effort.

The simulation of relative biomass distributions through the Ecospace spatial module of EwE can additionally inform fishery management on areas of interest to concentrate fishing effort, and optimize yield, but also on areas of higher sensibility where fishing pressure should be minimized or restricted to support conservation objectives. Ecospace can be used to identify critical habitats (e.g., such as spawning or nursery areas) by analyzing spatial biomass hotspots and species overlap (Mutsert *et al.*, 2024). By incorporating spatial heterogeneity in habitat types and species interactions, Ecospace is a powerful tool allowing the visualization of ecosystem interactions across a geographic grid, and the exploration of spatial management alternatives when used as a predictive tool (Walters *et al.*, 1999). These outputs are essential for developing ecosystem-based management (EBM) and marine spatial planning (MSP) strategies that aim to balance exploitation with biodiversity protection (Shabtay *et al.*, 2018).

4.4.6 Strengths and weaknesses of the ecosystem modelling approach

Modelling a system with low data availability is a challenge when trying to project the impact of fishing on the system's biomass: while the 3Ps subdivision is an important fishing area

for both Canada and SPM, limited biomass surveys are conducted within its boundaries. While part of this is explained by stocks being assessed for larger areas that often don't encompass 3Ps, numerous species are assessed in subdivisions on the higher-exploited Grand Bank, and Saint Pierre Bank is forgotten. Additionally, a lot of biomass assessments are underestimates, as most stock structure assumptions are based on management-based stock units and not biological units (Kerr *et al.*, 2017). Adjustment for catchability, which would hope to account for size-classes excluded from assessments, is not always available. Estimations of diet compositions are also scarce in the NAFO 3Ps area, necessitating reliance on assessments in other Northwest Atlantic Areas (or further, if non-available or lacking details). Some of the functional groups' biomasses were broad estimates when assessments were non-available, such as carnivorous cetaceans, harp seals, and polychaetes. These factors contribute to a lack of precision in the parameters to input in Ecopath models. Lack of precision in biomass lessens the prediction strength of the models (Susini and Todd., 2021). Subsequent Ecosim simulations remain informative, but they can lack ecological realism, which is why an approach expressed in terms of relative biomass is preferred over absolute biomass.

An additional issue may lie in the aggregation of species into functional groups, which can obscure finer ecological differences. But disaggregating species by adding more groups increase's model complexity, by adding input parameters and interaction terms among groups. This does not necessarily enhance model reliability and can instead introduce greater uncertainty. A model with higher complexity can present lower interpretability, where complex structures make the identification of clear cause-effect relationships harder, and management implications subsequently less insightful (Fulton *et al.*, 2003).

Overall, the fact that Ecopath assumes steady state, i.e., gives a static snapshot of energy balance, can oversimplify the temporal variability of parameters dynamics (Christensen and Walters, 2004). The balancing procedure assumes that, over the modeled time period, inputs and outputs for each functional group are in equilibrium. Yet, the 3Ps ecosystem, like other Northwest Atlantic ecosystems, is in reality subject to significant interannual fluctuations, be it only in fishing pressure. While Ecosim introduces temporal dynamics, small changes in vulnerabilities can alter model behavior and outcome, which emphasizes the need for careful calibration and clear communication of uncertainty (Ren *et al.*, 2025; Christensen and Walters, 2004). The sensitivity

in the estimation of vulnerability multipliers, combined with possibly incomplete drivers of change, are reflected through the moderately good fit obtained in the Ecosim simulation created for NAFO 3Ps. The available time series input in the models may not fully capture the true variability or magnitude of historical pressures acting on the system, leading to weaker fit.

EwE nonetheless provides a structured and standardized workflow that allows comparability across systems. By allowing the incorporation of diverse data types (e.g., biomass, consumption, catches), it provides a way to synthesize fragmented ecological data into a coherent model. Routines have been developed to address data uncertainty through defining a ‘pedigree’ for the input parameters, and through the Monte Carlo and Ecosampler routines providing probability distributions (Christensen and Walters, 2004). Even with fragmented trophic data, EwE models have proven to provide critical insights on where research and management attention are needed (Christensen and Walters, 2004). Such modelling approach is especially relevant for areas that have experienced strong exploitation pressures and undergone major changes through the years, like the Northwest Atlantic.

4.5 Conclusion

EwE modeling for NAFO subdivision 3Ps allowed the comparison of several ecosystem indices between the 1960-1969 and 2000-2009 periods, where the ecosystem had experienced different drivers of change. The system was characterized by moderate connectance, low transfer efficiency, and a mean trophic level of the catch, total fishing mortality and gross system efficiency that significantly decreased between the two periods. These observations reflect an ecosystem impacted by significant shifts in fishing pressures through the years, and remaining potentially vulnerable to environmental and anthropogenic disturbances. Further dynamic spatio-temporal analyses through Ecosim and Ecospace allowed to explore potential impacts of fishing effort increase. Simulations highlighted the sensitivity of sea cucumber and sea-scallop to increased exploitation rates, and the higher resilience of Atlantic halibut. General projections involving evolution of fishing mortality and changes in fishing effort may be more reflective of large-scale dynamics than of the specific contributions or vulnerabilities of smaller actors. Recognizing the asymmetry in the role SPM has in NAFO 3Ps when compared to Canada is crucial for contextualizing results, and ensuring that management recommendations account for differences

in fishing capacity. Dynamic modelling is a powerful tool to inform ecosystem-based management on effort recommendations and potential critical habitats.

Despite providing valuable insights, the models are limited by data gaps. More research on predator diet variability specifically in NAFO 3Ps would be beneficial to bring more precision on trophic relationships and their sensibility to biomass depletions, when looking at making more informative predictions incorporating fishing effort. SPM or NAFO 3Ps would benefit from up-to-date and comprehensive biomass and diet assessments to target the remaining scarcity of available data for modeling. Further explorations of the Ecospace module, and further modeling analysis incorporating environment variables (such as temperature and productivity) as forcing functions in NAFO 3Ps would shed light on parameters additionally impacting the ecosystem's productivity and resilience to perturbations – this is especially relevant in the context of climate change.

Overall, the modeling of the 3Ps ecosystem offers a comprehensive understanding of trophic interactions and fishing effects in the region. By quantifying ecosystem structure and testing alternative fishing scenarios, this work contributes to a broader effort to implement ecosystem-based fisheries management in Northwest Atlantic waters and provides a foundation for future modeling and monitoring initiatives around Saint Pierre and Miquelon.

Chapter 5: Conclusion

5.1 Summary of findings

As a small French archipelago highly reliant on fisheries for local livelihoods, in an area of the world that has undergone strong ecosystem shifts through the last hundred years, Saint Pierre and Miquelon occupies a sensitive position that puts it at high socio-ecological risk under environmental and anthropological disturbances (Palomares and Pauly, 2022; Teletchea, 2022). The Northwest Atlantic and the Grand Banks and Saint Pierre Banks have witnessed large population depletions driven by disproportionate fishing effort over time (Forest, 2022). With an Exclusive Economic Zone enclaved in the Eastern Canadian EEZ and shaped as a narrow ‘tunnel’, SPM faces the challenge of accessing exploitable stock resources (Teletchea, 2022). These spatial and jurisdictional constraints complicate efforts to rebuild its fisheries sector while ensuring ecologically responsible management. Such concerns cannot be answered without asking the appropriate questions: what do we know about the local ecosystem? What has been historically caught from this ecosystem? What will happen of said ecosystem under the fishing dynamics initiated? Building on these considerations, this thesis aimed to address three main questions:

1. What is the relative position of SPM on a global insular gradient of marine biodiversity, and can these gradients in islands and archipelagos around the world be used to test the application of Island Biogeography Theory to marine ecosystems?
2. How much has SPM really caught from 1950 to 2022, and how have fishing pressures shifted over time?
3. How have historical changes in fishing activity shaped the structure of the ecosystem in the waters around SPM (i.e., NAFO subdivision 3Ps), and how could projected fishing scenarios affect its future dynamics?

While *Chapter 2* built a marine biodiversity foundation for SPM, and positioned the archipelago on a global insular biodiversity gradient for key marine groups, *Chapter 3* provided an up-to-date reconstruction of the total amount of fish and invertebrates caught by SPM since 1950. *Chapter 4* used both the biodiversity data from *Chapter 2* and the catch data from *Chapter 3* to build Ecopath with Ecosim models of the wider sea around SPM.

The first step of this work relied on supplementing biodiversity databases with a new assessment of 727 marine non-fish vertebrates and invertebrates present around the archipelago. As understanding how SPM compares to global islands and archipelagos is an essential component of grasping local specificities, *Chapter 2* took a wider approach and highlighted that SPM presents high similitude to other archipelagos of similar latitudes, and similar surface area of their continental shelf, in terms of fish, marine mammal, molluscs, crustaceans and cnidarians species richness, and possesses the highest ratio of threatened marine fishes in the sample of study (n=40). This comparison sparked the investigation of a possible application of Island Biogeography Theory (IBT; McArthur and Wilson, 1967) to marine species, to look at which independent variables explain global marine species distribution. The analyses revealed that both latitude and shelf-area are significant predictors of marine species richness across islands of the world.

The reconstruction of marine catch carried out in *Chapter 3* highlighted three key findings. The tonnage caught by SPM between 1950-2022 is over 1.2 times higher than officially reported, with bait and industrial discards accounting for a considerable part of the catch surrounded by uncertainty and high unreported rates. Fisheries that were once mostly reliant on Atlantic cod have now shifted to lower trophic level species such as sea cucumber, following a fishing down the food web phenomenon (Pauly, 1998) and resulting in a decrease of the mean trophic level of the catch by a factor of 0.63 (i.e., 37%) over 72 years. The Mean Temperature of the Catch differs from established global trends (Cheung *et al.*, 2013), and showed a gradual decrease over time, which could be explained by fisheries having shifted to deeper grounds of exploitation.

Because understanding the deeper interconnections in an ecosystem relies strongly on modeling approaches, *Chapter 4* proposed two Ecopath mass-balance models of the greater area around SPM, using SPM's assessed biodiversity and catches to inform the models. These models served to build subsequent dynamic spatio-temporal Ecosim and Ecospace simulations. The Ecopath models illustrated high productivity and high sensitivity to fishing pressures, and highlighted reduced fishing mortality and a shift to the exploitation of lower trophic level species between 1960-1969 and 2000-2009, as well as moderate shifts in predator-prey relationships and the structure of the ecosystem. Time-dynamic simulations projected that three different magnitudes of increase in the effort of SPM fishing fleets would all have negative impacts on the biomass of sea cucumber and deep-sea scallops, while Atlantic halibut showed relative resilience

under a moderate increase in effort. Spatial simulations provided distributions maps of the functional groups' relative biomass in NAFO subdivision 3Ps, and emphasized a higher occurrence of benthic invertebrates and small pelagic fishes on the Saint Pierre Bank than in other zones of the subdivision.

5.2 Strengths and limitations of the study

This research, using a transdisciplinary approach, provides a strong foundation to better understanding biodiversity, fisheries and ecosystem dynamics around Saint Pierre and Miquelon. Each part of this research presented strengths and limitations, summarized here.

Chapter 2 relied on the large and global availability of marine species data from FishBase and SeaLifeBase for biodiversity analyses. While such databases are highly informative sources, an important constraint can occur with data assessed and input: restricted taxonomic and spatial sampling coverage linked to the economic or ecological interest disparities between regions. This limitation can potentially skew analyses results by giving disproportioned attention to regions which benefit from higher sampling effort, while underrepresenting areas that remain insufficiently surveyed. In this research, this issue was mitigated through careful evaluation of known sampling biases and by excluding islands and archipelagos identified as being clearly under sampled.

Additionally, despite its widespread use, the multiple regression approach has inherent limitations when applied to complex ecological systems. It assumes linearity and independence among predictors, which may not hold true in marine environments characterized by dynamic processes and trophic interactions. As a result, its predictive capacity and the proportion of variance explained can be relatively weak (Graham, 2003). To address these limitations, this research carefully selected ecologically meaningful predictors and verified statistical assumptions to ensure model reliability. One of the limitations also explored in this chapter lies in using functional groups for biodiversity analyses that are too aggregated, i.e., comprising of multiple ecological strategies, which has the potential to obstruct finer-scale patterns associated with different life-histories (Kolasa and Pickett, 1991). Moreover, assuming steady-state equilibrium, a core concept of IBT, might fail to account for disturbances' role in shaping species richness at the island level (Villa *et al.*, 1992).

In *Chapter 3*, the existence of heterogeneity in the language used to characterize fisheries in different systems of the world, and the numerous differences in the way fisheries are managed and assessed, can make the application of general reconstruction methods challenging. This challenge was approached by developing additional sets of methods that fitted the specificities of historical fisheries in SPM. While some sources of data can present high uncertainty with scarce estimates making them hard to reconstruct, such as discards, the reconstruction approach remains powerful to produce catch assessments with increased accuracy.

Lastly, modelling the waters around SPM in *Chapter 4* presented important challenges related to data availability and model uncertainty. Biomass estimates for several key species being limited or inconsistent, combined with uncertainties in stock structure assumptions, limited diet data, and reliance on broad biomass approximations for some functional groups, reduced parameter precision. This relatively low ecosystem data availability in the waters surrounding SPM lessens the predictive abilities of subsequent dynamic simulations. However, the standardized interface provided by EwE models renders comparison between models and systems possible (Christensen *et al.*, 2005). EwE remains a powerful tool for contextualizing SPM fisheries within the broader ecological dynamics of NAFO 3Ps. By ensuring transparency on uncertainty and enabling scenario testing, the modelling method provided valuable insights into the functioning of the 3Ps ecosystem and its response to exploitation.

5.3 Implication of findings for fisheries and ecosystem management

Because highly exploited areas present an interplay of actors, as well as multiple scales and regimes of exploitation and management, creating a comprehensive marine biodiversity overview for SPM is the essential foundation for understanding dynamics and potential conflicts, and evaluating ecosystem services. Biodiversity richness underpins productivity and resilience in an ecosystem (Isbell *et al.*, 2015). Highlighting the occurrence of threatened species is informative for conservation strategies and can foster renewed conservation efforts in the area (Johnson and Ray, 2025). While concerns can be raised on the use of theory for predictions (Doak and Mills, 1994), the integration of theory in management strategies, such as IBT, links patterns to underlying ecological processes and help understand *why* changes occur. Proposing an application of IBT to marine species can potentially help management to prioritize large and topographically complex

shelf areas, as areas harboring higher biodiversity, envision the possible higher vulnerability or small or fragmented shelves, and guide marine spatial planning (Tittensor *et al.*, 2010; Costello *et al.*, 2017). Additionally, it can support, though advised cautiously, generalization and transferability (Moon *et al.*, 2017; Yates *et al.*, 2018). In SPM, a small and remote region where empirical data is limited, this theoretical framework enables management strategies to extrapolate knowledge from well-studied systems to similar ones. The predictions of IBT, through the positive relationship observed between shelf surface area and marine species richness, emphasize that SPM limited shelf area may inherently be more vulnerable to biodiversity loss (McArthur and Wilson, 1967; Costello *et al.*, 2017).

Secondly, reconstructing the tonnage caught by SPM by integrating multi-sector unreported data, and a new detailed disaggregation of this data by fishing sector, gear, area, catch type and status, provides up-to-date and comprehensive fishery information to management actors (Tesfamichael and Pauly, 2011). Stock assessments and management rely on the higher degree of realism that reconstructions supply, by highlighting fishery dynamics that often go under the radar of official reporting bodies, for accuracy in evaluations (Zeller and Pauly, 2016). Reconstructed data also allows the contextualization of SPM within a global fishery context, by evaluating shifts in mean trophic level and mean temperature of the catch, and comparing these shifts to known generalities and adjacent areas.

Incorporating these biodiversity and fishery data into trophic mass-balance ecosystem models creates an additional informative layer, through the representation of energy flows, species interactions and ecosystem structure (Christensen and Walters, 2024). EwE models are mechanistic and deterministic: they integrate ecological processes and produce practical outcomes (Christensen and Walters, 2004). This enables the evaluation of how fishing changes affect ecosystem dynamics, thereby informing ecosystem-based management decisions (Pikitch *et al.*, 2004). Ecosim simulations shed light on the vulnerability of some invertebrate species to extensive fishing effort, highlighting the need for caution and integration of ecological preoccupations in local fishery management. Spatial distribution maps inform on key areas for fisheries and conservation. This component of the research can inform local strategies, aimed at rebuilding a sustainable fishery sector, on trade-offs between species and fleets, and translate complex ecosystem processes into policy-relevant metrics (Craig and Link, 2023). Furthermore, it provides

a tool that can be used for subsequent fishing scenario simulations, and extended spatial exploration of the NAFO 3Ps ecosystem dynamics, like the potential effects of a Marine Protected Area in the region (Beattie *et al.*, 2002).

5.4 Final remarks and future directions

This study presented the first global contextualization of Saint Pierre and Miquelon's biodiversity and fisheries, and the first attempt at building Ecopath with Ecosim models for the NAFO subdivision 3Ps that surrounds the archipelago, integrating multiple sources of data from SPM. This global contextualization of SPM is essential in the present context of multi-faceted climate change dynamics. Adaptation strategies to climate change in small islands and archipelagos rely on establishing a robust framework of integrated ecosystem knowledge (Graham *et al.*, 2011; Bernhardt and Leslie, 2013). SPM can serve as an example for other small archipelagos with high reliance on fisheries.

Several additional questions were raised throughout this research, highlighting further directions that could be taken to strengthen the ecological relevance of this work, or conduct supplementary studies. Multiple regression analyses integrating more diversity of marine functional groups, or parsing groups into more ecologically similar subgroups, as well as testing for additional environmental independent variables, would provide finer understanding on the extent to which IBT principles versus oceanographic processes govern the distribution of marine species around islands of the world. Refining the concept of isolation for each island by including oceanic barriers (e.g., currents) (Hourigan and Reese, 1987) would be relevant to potentially include it as an independent variable in marine analyses of IBT.

Secondly, catch reconstructions are an iterative process, subject to evolve when new sources of information get uncovered or become accessible, making disaggregation and allocations more precise (Zeller and Pauly, 2016). Additional expertise (and improvement in reporting) on local discards and contemporary bait fisheries would provide an improved layer of accuracy to SPM's reconstruction, for the upcoming years to reconstruct.

Last, though not the primary focus of this thesis, the EwE models built for NAFO 3Ps integrate catches from Canadian fleets, and can be used for further simulations on Canada's fishing effort and its impact on the dynamics of the ecosystem. Suggestions for further research also

include the incorporation of environmental data to the ecosystem models constructed, to account for other dynamics influencing ecosystem structure. The Ecosim and Ecospace models serve as a baseline for additional scenario testing on other adaptive management strategies in NAFO 3Ps (e.g., effort redistribution, MPAs or seasonal closures) (Wang *et al.*, 2015; Adebola and de Mutsert, 2019).

These further directions would help enhance our understanding of ecosystem dynamics around the archipelago of Saint Pierre and Miquelon, an essential component for the sustainable management of local fisheries. Overall, this work lays the groundwork for assessing the long-term capacity of SPM's marine ecosystem to maintain ecological integrity and productivity, through a macroecological lens (Diniz-Filho, 2023), linking biogeographic theory, historical catches, and trophic modeling to anticipate future biodiversity and ecosystem trajectories.

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Appendices

Appendix A

Additional tables for Chapter 2.

Table A.1. Latitude, shelf surface area and number of species for each of the 40 islands and archipelagos selected for the multiple regression analyses (MRAs). Archipelagos in italics were only included in the MRA of fish species, but not in the MRAs of other species groups. Values marked with an Asterix (*) have a high level of uncertainty and are considered to be an incomplete representation of the actual value. Archipelagos and islands in italic have been excluded from the MRAs for all groups other than fish, due to uncertainty.

	Latitude (°)	Shelf area (km ²)	Fish species	Marine mammals	Crustacean species	Molluscs species	Cnidarians species
Azores	38	2,166	360	15	151	196	84
Bermuda	32	1,140	476	7	150	590	155
British Virgin Islands	18	3,093	478	7	37	84	30
Canaries Islands	28	6,366	558	13	178	150	64
Cayman Island	19	506	468	7	38	163	44
Cook Islands	21	1,213	570	24	40	194	113
<i>Corsica-Sardinia</i>	<i>41</i>	<i>19,269</i>	<i>423</i>	<i>0*</i>	<i>34*</i>	<i>45*</i>	<i>3*</i>
Crozet Islands	46	7,449	77	12	82	51	6
Faeroe Islands	62	27,410	132	14	48	57	44
Falkland Islands	51	165,343	95	22	77	263	57
Fiji Islands	18	43,264	1266	24	267	405	310
Galapagos island	1	8,500	674	12	244	403	142
Guadeloupe	16	2,150	422	29	71	238	66
Hawaii	20	20,511	1238	29	496	720	269
Indonesia	5	1,975,418	3745	33	1215	1724	890
Kerguelen island	49	63,888	115	18	421	182	68
Madagascar	20	121,865	1087	26	666	410	313
Maldives	4	31,488	1123	27	200	112	237
Marshall Islands	7	20,891	960	23	128	509	304
Mauritius	20	39,992	1087	9	280	235	221
New Zealand	42	272,271	1072	45	458	1096	284

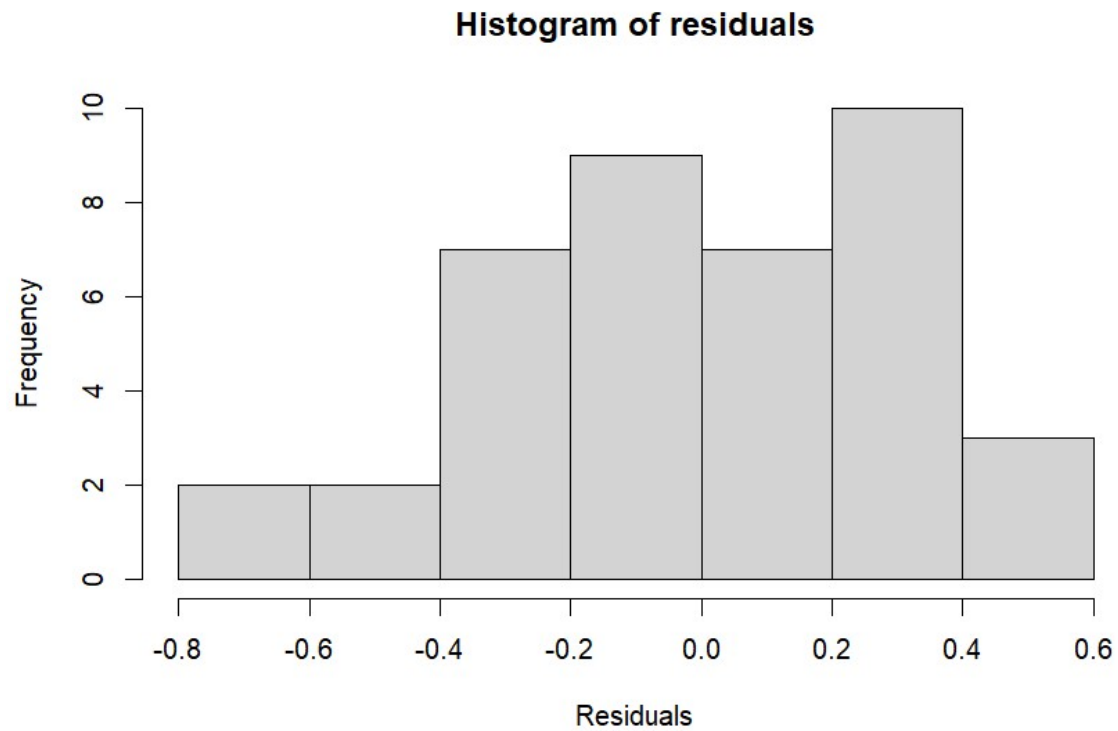
	Latitude (°)	Shelf area (km ²)	Fish species	Marine mammals	Crustacean species	Molluscs species	Cnidarians species
Northern Marianas Islands	16	1,004	785	22	82	197	250
Palau	7	3,467	1531	23	294	671	496
Philippines	13	271,428	3241	29	1566	4590	867
Pitcairn Islands	25	155	392	21	51	375	107
Rapa Nui (Easter Island)	27	291	187	15	227	223	63
Reunion	21	595	943	15	284	158	156
Saint Paul and Amsterdam	37	164	39	22	35	12	23
<i>Saint Paul and Saint Peter</i>	<i>1</i>	<i>11</i>	<i>62</i>	<i>7*</i>	<i>2*</i>	<i>5*</i>	<i>0*</i>
Saint Pierre and Miquelon	46	7,844	121	14	108	319	67
Saint Vincent and the Grenadines	13	2,340	484	28	63	305	103
Seychelles	4	54,833	1168	26	411	194	289
<i>Socotra archipelago</i>	<i>12</i>	<i>11,054</i>	<i>449</i>	<i>1*</i>	<i>4*</i>	<i>4*</i>	<i>5*</i>
South Georgia Island	54	21,579	65	14	445	263	164
Svalbard	78	255,222	59	17	219	159	69
<i>Trinidad & Martim Vaz Island</i>	<i>20</i>	<i>203</i>	<i>88</i>	<i>7*</i>	<i>3*</i>	<i>8*</i>	<i>2*</i>
Tristan da Cunha	37	1,645	32	12	23	11	7
Turks and Caicos	21	5,560	380	7	36	56	32
Tuvalu	8	4,449	194	22	39	217	178
Vanuatu	17	8,681	800	24	150	380	368

Appendix B

Results from the statistical tests to verify regression assumptions in *Chapter 2*.

Table A.2. Variance Inflation Factors (VIF) for the two independent variables of the multiple regression analysis. VIF values lower than 3 imply no multicollinearity in the variables.

Variable	VIF value	1/VIF
Latitude	1.05	0.95
Shelf area	1.05	0.95



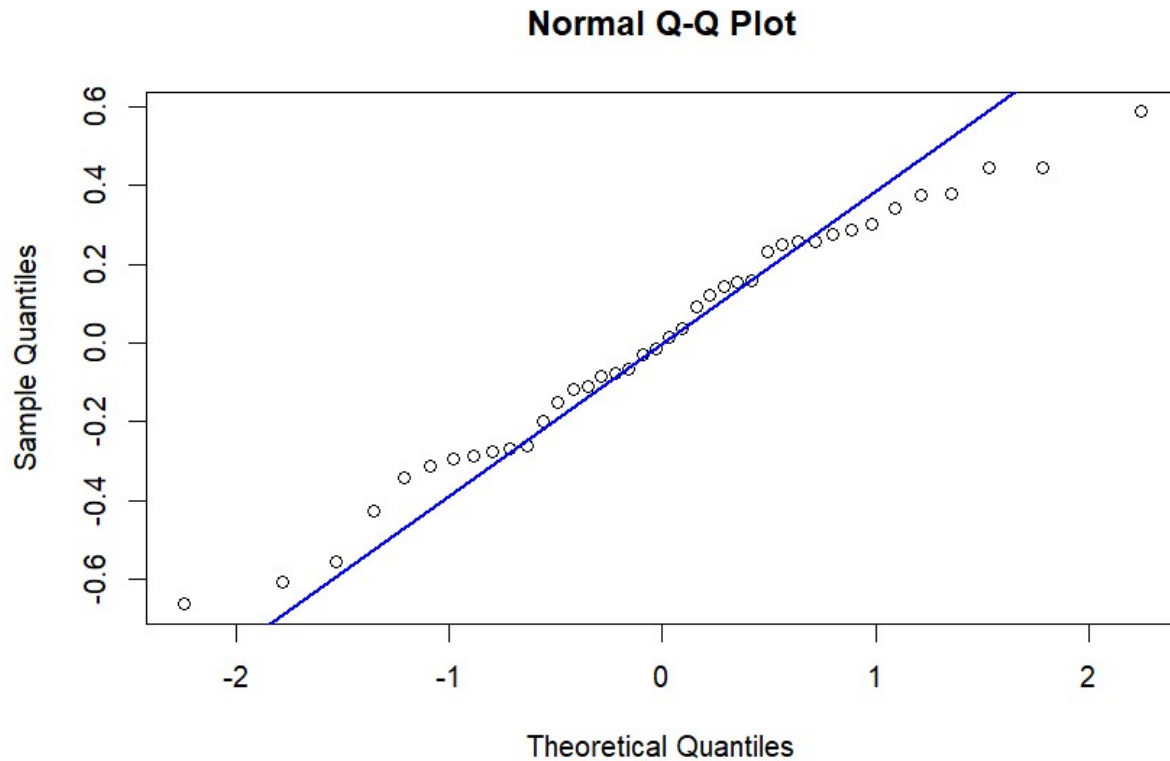


Figure A.1. Histogram of residuals and Normal Q-Q plot from the Shapiro-Wilk test of normality ($p\text{-value} > 0.05$), for the multiple regression analysis of fish species richness (dependent variable) by latitude and shelf surface area (independent variables). A $p\text{-value} > 0.05$ fails to reject the null hypothesis of normality, implying data are likely to be normally distributed.

Table A.4. Additional results from statistical tests to test the multiple regression assumptions. A $p\text{-value} > 0.05$ in the Shapiro-Wilk (normality of residuals) and Durbin-Watson (autocorrelation of residuals) tests fails to reject the null hypothesis of normality, implying data are likely to be normally distributed. A $p\text{-value} < 0.05$ in the F-test implies the model is statistically significant. A DW value close to 2 in the Durbin-Watson test indicated no autocorrelation.

Statistical test	Statistic value	p-value
Shapiro-Wilk	w = 0.98	0.053
Durbin-Watson	dw = 1.34	0.013
F-test	f-statistic = 34.33, 2 and 37 df	3.712^{-09}

Appendix C

Additional results from the multiple regression analyses in *Chapter 2*.

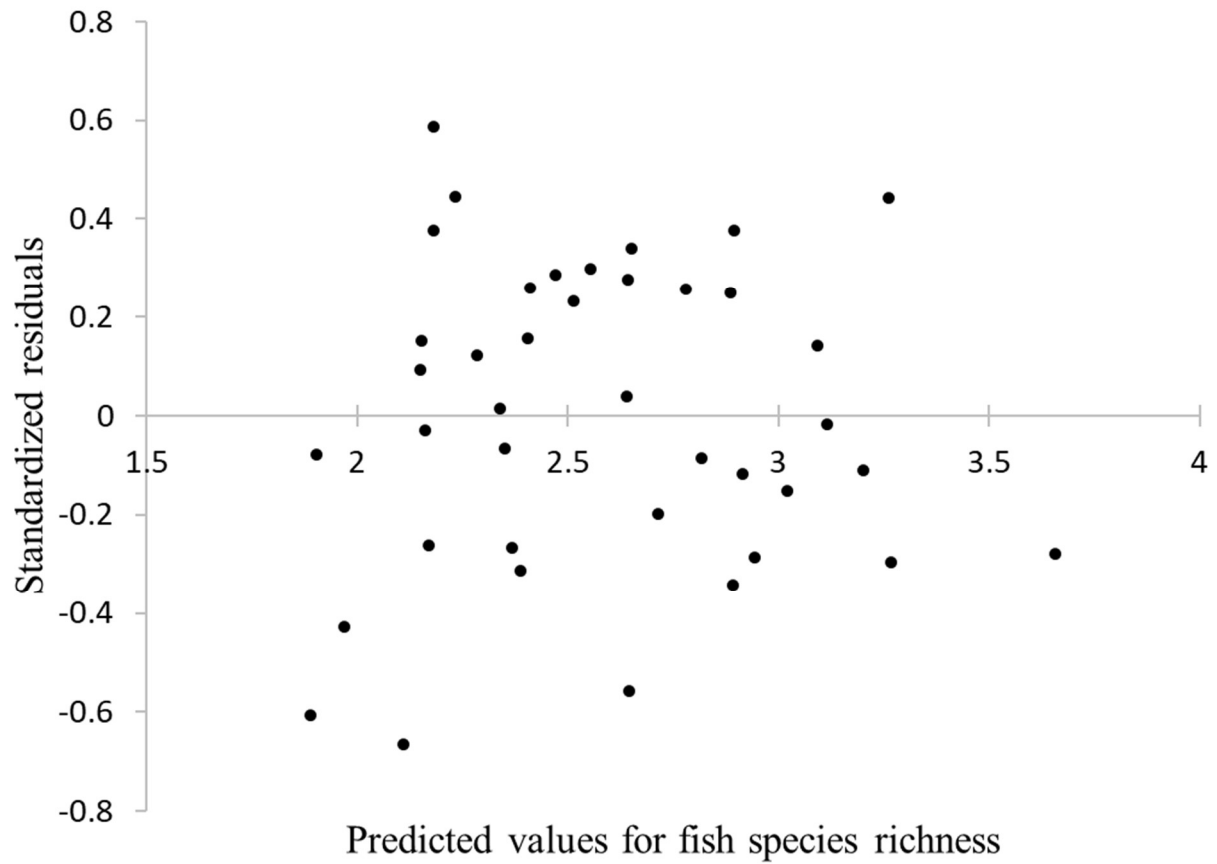


Figure C.1. Plots of residuals from the multiple regression analysis of fish species richness (dependent variable) by latitude and shelf surface area (independent variables).

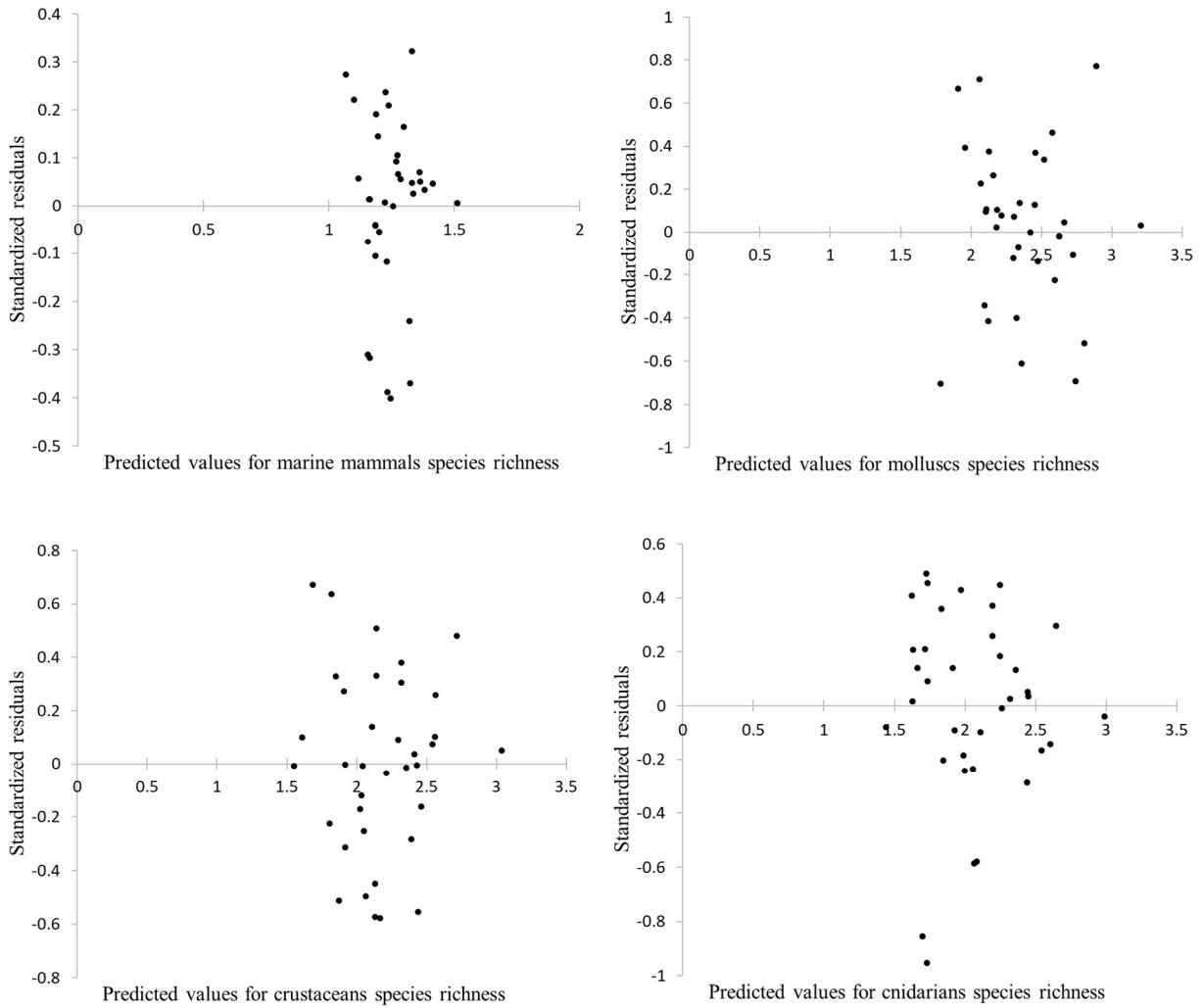


Figure C.2. Plots of residuals from the multiple regression analysis of species richness (dependent variable) by latitude and shelf surface area (independent variables), for four groups of marine species.

Appendix D

Supplementary results from the catch reconstruction in *Chapter 3*.

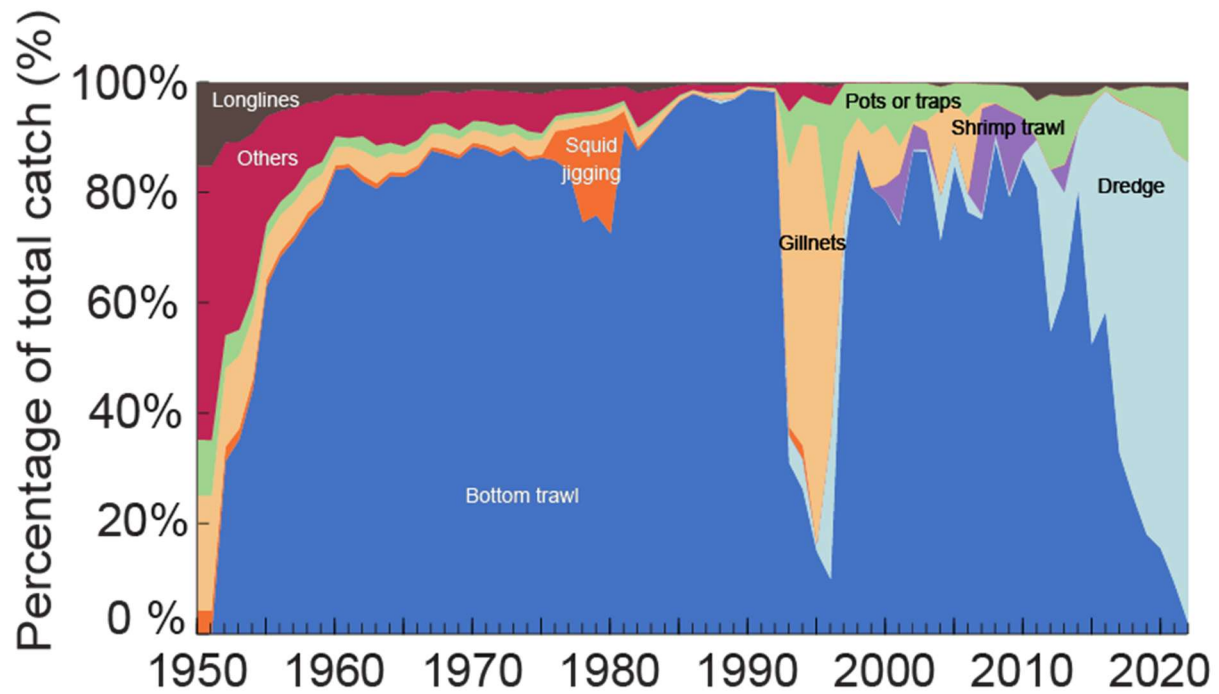


Figure D.1. Percentage of the total catch by fishing gear for SPM inside and outside the EEZ, from 1950 to 2022. ‘Others’ include other small-scale gear (i.e., handlines and other nets), recreational fishing gear and unknown class.

Appendix E

Additional tables for *Chapter 4*.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13
1 Pisc. Cetacea			0.47										
2 Plank. Cetacea			0.148										
3 Carn. Cetacea													
4 Harp seals			0.1										
5 Hooded seals			0.02										
6 Grey seals			0.007										
7 Harbour seals			0.07										
8 Pisc. Seabirds													
9 Benth. Seabirds													
10 Plank. Seabirds													
11 Large cod (>35cm)				0.016	0.111	0.205	0.019						
12 Small cod (<35cm)	0.002			0.048	0.107	0.31	0.057	0.01			0.004	0.001	0.031
13 Large Green. halibut			0.055		0.022								
14 Small Green. halibut			0.03		0.23	0.001		0.004					0.005
15 Large Atl. halibut			0.005		0.005	0.001							
16 Small Atl. halibut						0.004	0.001						
17 American plaice	0.01					0.022		0.004			0.009	0.001	0.135
18 Flounders	0.05			0.001	0.146	0.074	0.019	0.004			0.003		0.031
19 Skates	0.007					0.013	0.001	0.004					0.028
20 Redfish				0.401	0.131	0.003	0.004				0.004	0.001	
21 Large demersals				0.005	0.012	0.045	0.027				0.005		
22 Small demersals	0.001			0.004	0.057	0.12	0.031	0.026			0.019	0.004	0.177
23 Capelin	0.575	0.048	0.05	0.433	0.005	0.085	0.06	0.253			0.27	0.039	0.106
24 Haddock						0.01					0.001		0.054
25 Sand lance	0.083	0.048		0.057		0.037		0.454			0.077	0.122	0.155
26 Arctic cod				0.001	0.02	0.005		0.008					
27 Large pelagics							0.089	0.002					
28 Pesci. small pelagics			0.044		0.064	0.005	0.198	0.078				0.002	0.014
29 Plank. small pelagics	0.061		0.001	0.031	0.09	0.054	0.425	0.005	0.05		0.029	0.002	0.044
30 Shrimp				0.001		0	0.062				0.078	0.105	0.094
31 Large crustacea						0.001	0.004				0.1		
32 Lobster													
33 Sea cucumber											0.001		
34 Echinoderms											0.025		0.003
35 Molluscs							0.002		0.2		0.059	0.047	
36 Squid	0.13			0.001		0.005					0.011	0.001	0.031
37 Polychaetes									0.03		0.03	0.057	
38 Other ben. inver.							0.001		0.32	0.011	0.115	0.09	0.06
39 Large zooplankton	0.081	0.904		0.002					0.15	0.537	0.159	0.509	0.025
40 Small zooplankton										0.202	0.001	0.021	
41 Phytoplankton													
42 Detritus													
Import	0	0	0	0	0	0	0	0.15	0.25	0.25	0	0	0

Table E.1. Final diet matrix of the 1960-1969 balanced Ecopath model of NAFO subdivision 3Ps.

Prey \ predator	14	15	16	17	18	19	20	21	22	23	24	25	26
1 Pisc. Cetacea													
2 Plank. Cetacea													
3 Carn. Cetacea													
4 Harp seals													
5 Hooded seals													
6 Grey seals													
7 Harbour seals													
8 Pisc. Seabirds													
9 Benth. Seabirds													
10 Plank. Seabirds													
11 Large cod (>35cm)													
12 Small cod (<35cm)		0.039	0.1	0.002				0.02	0.001		0.009		
13 Large Green. halibut													
14 Small Green. halibut													
15 Large Atl. halibut													
16 Small Atl. halibut													
17 American plaice	0.016	0.136						0.005			0.001		
18 Flounders	0.007	0.136				0.01		0.003			0.001		
19 Skates						0.01		0.005					
20 Redfish		0.039				0.01		0.025			0.004		
21 Large demersals						0.005							
22 Small demersals	0.039	0.195	0.05	0.006	0.007	0.015		0.09	0.01				
23 Capelin	0.29			0	0.025			0.108	0.02	0.013	0.001		0.038
24 Haddock	0.005												
25 Sand lance	0.05				0.025	0.01		0.134	0.01	0.013	0.004		
26 Arctic cod								0.003	0.005				0.002
27 Large pelagics													
28 Pisci. small pelagics								0.07	0.002		0.002		
29 Plank. small pelagics						0.01		0.028	0.003		0.002		
30 Shrimp	0.35	0.323	0.16	0.03	0.007	0.148	0.279	0.054	0.02				
31 Large crustacea		0.094	0.025	0.041	0.001	0.099		0.024	0.007				
32 Lobster								0.001	0				
33 Sea cucumber													
34 Echinoderms	0.007	0.008		0.751	0.053			0.054	0.105		0.359		
35 Molluscs	0.007	0.017	0.065	0.047	0.035	0.064		0.022	0.05		0.033		
36 Squid	0.019							0.004					
37 Polychaetes	0.018	0.013		0.028	0.47	0.206	0.001	0.027	0.215		0.229	0.001	
38 Other ben. inver.	0.062		0.55	0.047	0.351	0.102	0.008	0.05	0.301		0.339		
39 Large zooplankton	0.13		0.05	0.049	0.027	0.259	0.673	0.259	0.201	0.599	0.014	0.35	0.64
40 Small zooplankton						0.051	0.04	0.015	0.05	0.375	0.003	0.649	0.32
41 Phytoplankton												0.001	
42 Detritus													
Import	0	0	0	0	0	0	0	0	0	0	0	0	0

Table E.1. (cont.) Final diet matrix of the 1960-1969 balanced Ecopath model of NAFO subdivision 3Ps.

Prey \ predator	27	28	29	30	31	32	33	34	35	36	37	38	39
1 Pisc. Cetacea													
2 Plank. Cetacea													
3 Carn. Cetacea													
4 Harp seals	0												
5 Hooded seals	0												
6 Grey seals													
7 Harbour seals	0												
8 Pisc. Seabirds													
9 Benth. Seabirds													
10 Plank. Seabirds													
11 Large cod (>35cm)	0.003												
12 Small cod (<35cm)	0.011									0.003			
13 Large Green. halibut	0.005												
14 Small Green. halibut	0.005												
15 Large Atl. halibut													
16 Small Atl. halibut	0.001												
17 American plaice	0.001												
18 Flounders	0.042												
19 Skates	0.004												
20 Redfish	0.031												
21 Large demersals	0.043												
22 Small demersals	0.107				0.018								
23 Capelin	0.005									0.002			
24 Haddock													
25 Sand lance	0.111	0.002								0.001			
26 Arctic cod										0.002			
27 Large pelagics	0.015												
28 Pisci. small pelagics	0.107												
29 Plank. small pelagics	0.072	0.004								0.012			
30 Shrimp	0.009	0.002	0.063		0.018					0.046			
31 Large crustacea	0.003				0.04	0.29							
32 Lobster													
33 Sea cucumber					0.03	0.05		0.002					
34 Echinoderms	0				0.09	0.155							
35 Molluscs	0.016	0.002			0.267	0.108							
36 Squid	0.241									0.001			
37 Polychaetes	0.004			0.015	0.16	0.025				0.025	0.05		
38 Other ben. inver.	0.015		0.046	0.015	0.179	0.356		0.002		0.042			
39 Large zooplankton	0.143	0.540	0.431	0.12	0.144					0.867			0.05
40 Small zooplankton	0.007	0.450	0.46	0.24	0.018		0.2					0.01	0.38
41 Phytoplankton				0.085		0.016	0.8	0.328	0.1		0.3		0.37
42 Detritus				0.525	0.036			0.668	0.9		0.65	0.99	0.2
Import	0	0	0	0	0	0	0	0	0	0	0	0	0

Table E.1. (cont.) Final diet matrix of the 1960-1969 balanced Ecopath model of NAFO subdivision 3Ps.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13
1 Pisc. Cetacea			0.360										
2 Plank. Cetacea			0.126										
3 Carn. Cetacea													
4 Harp seals			0.250										
5 Hooded seals			0.080										
6 Grey seals													
7 Harbour seals			0.140										
8 Pisc. Seabirds													
9 Benth. Seabirds													
10 Plank. Seabirds													
11 Large cod (>35cm)				0.008	0.075	0.145	0.009						
12 Small cod (<35cm)	0.001			0.045	0.079	0.233	0.003	0.01			0.074	0.002	0.011
13 Large Green. halibut			0.003		0.030								
14 Small Green. halibut			0.004	0.028	0.270	0.001		0.004					
15 Large Atl. halibut			0.003		0.005	0.005							
16 Small Atl. halibut						0.004							
17 American plaice	0.010					0.020		0.004			0.004		0.033
18 Flounders	0.010			0.001	0.100	0.093	0.019	0.004			0.010		0.032
19 Skates	0.010					0.018	0.001	0.004					0.029
20 Redfish				0.356	0.111	0.032	0.004				0.004	0.005	
21 Large demersals				0.005	0.012	0.045	0.027				0.010		
22 Small demersals	0.010			0.037	0.107	0.138	0.045	0.026			0.018	0.016	0.169
23 Capelin	0.572	0.048		0.330	0.005	0.085	0.059	0.253			0.270	0.054	0.245
24 Haddock						0.005					0.000		0.074
25 Sand lance	0.105	0.048		0.058		0.023		0.454			0.085	0.194	0.077
26 Arctic cod				0.025	0.020	0.050		0.008					
27 Large pelagics							0.067	0.002					
28 Pisci. small pelagics			0.034		0.086	0.005	0.222	0.078					0.014
29 Plank. small pelagics	0.070		0.001	0.065	0.100	0.054	0.467	0.005	0.05		0.061	0.040	0.094
30 Shrimp				0.001		0.001	0.066				0.057	0.100	0.087
31 Large crustacea				0.009			0.004				0.040	0.004	
32 Lobster													
33 Sea cucumber											0.001		
34 Echinoderms											0.031		0.003
35 Molluscs							0.005		0.2		0.025	0.002	
36 Squid	0.130			0.002		0.044					0.006		0.032
37 Polychaetes									0.03			0.034	
38 Other ben. inver.				0.028			0.003		0.32	0.011	0.217	0.090	0.065
39 Large zooplankton	0.083	0.904		0.002					0.15	0.537	0.089	0.453	0.038
40 Small zooplankton										0.202		0.006	
41 Phytoplankton													
42 Detritus													
Import	0	0	0	0	0	0	0	0.15	0.25	0.25	0	0	0

Table E.2. Final diet matrix of the 2000-2009 balanced Ecopath model of NAFO subdivision 3Ps.

Prey \ predator	14	15	16	17	18	19	20	21	22	23	24	25	26
1 Pisc. Cetacea													
2 Plank. Cetacea													
3 Carn. Cetacea													
4 Harp seals													
5 Hooded seals													
6 Grey seals													
7 Harbour seals													
8 Pisc. Seabirds													
9 Benth. Seabirds													
10 Plank. Seabirds													
11 Large cod (>35cm)													
12 Small cod (<35cm)	0.040				0.001	0.019	0.006		0.009			0.040	
13 Large Green. halibut													
14 Small Green. halibut									0.001				
15 Large Atl. halibut													
16 Small Atl. halibut													
17 American plaice						0.004			0.001				
18 Flounders		0.001				0.003							0.001
19 Skates						0.020							
20 Redfish		0.000	0.004	0.002	0.007	0.024			0.004				0.000
21 Large demersals													
22 Small demersals	0.040	0.002	0.002	0.001	0.007	0.106	0.045					0.040	0.002
23 Capelin		0.090	0.011	0.020	0.052	0.061	0.073	0.023	0.001		0.038		0.090
24 Haddock							0.002						
25 Sand lance		0.058	0.036	0.100	0.004	0.127	0.195	0.005	0.004				0.058
26 Arctic cod						0.017					0.001		
27 Large pelagics													
28 Pesci. small pelagics				0.001	0.002	0.081	0.007		0.002				
29 Plank. small pelagics		0.003		0.003	0.023	0.048	0.012		0.002				0.003
30 Shrimp	0.140	0.166	0.020	0.066	0.340	0.054	0.140	0.100				0.140	0.166
31 Large crustacea	0.025	0.050	0.000	0.004		0.014						0.025	0.050
32 Lobster				0.001		0.002							
33 Sea cucumber													
34 Echinoderms		0.347	0.051	0.000		0.070	0.050		0.359				0.347
35 Molluscs	0.045	0.013	0.035			0.027	0.050		0.033			0.045	0.013
36 Squid		0.001		0.001	0.002	0.004	0.002						0.001
37 Polychaetes		0.049	0.215	0.181		0.027	0.001	0.087	0.229	0.001			0.049
38 Other ben. inver.	0.660	0.085	0.418	0.194	0.083	0.037	0.006		0.339			0.660	0.085
39 Large zooplankton	0.050	0.134	0.209	0.426	0.435	0.240	0.348	0.411	0.014	0.350	0.640	0.050	0.134
40 Small zooplankton					0.046	0.015	0.064	0.375	0.003	0.649	0.321		
41 Phytoplankton										0.001			
42 Detritus													
Import	0	0	0	0	0	0	0	0	0	0	0	0	0

Table E.2. (cont.) Final diet matrix of the 2000-2009 balanced Ecopath model of NAFO subdivision 3Ps.

Prey \ predator	27	28	29	30	31	32	33	34	35	36	37	38	39
1 Pisc. Cetacea													
2 Plank. Cetacea													
3 Carn. Cetacea													
4 Harp seals	0.001												
5 Hooded seals	0.000												
6 Grey seals	0.000												
7 Harbour seals	0.000												
8 Pisc. Seabirds													
9 Benth. Seabirds													
10 Plank. Seabirds													
11 Large cod (>35cm)	0.009												
12 Small cod (<35cm)	0.011									0.001			
13 Large Green. halibut	0.007												
14 Small Green. halibut	0.003												
15 Large Atl. halibut													
16 Small Atl. halibut	0.001												
17 American plaice	0.016												
18 Flounders	0.018												
19 Skates	0.004												
20 Redfish	0.041												
21 Large demersals	0.011												
22 Small demersals	0.164				0.018								
23 Capelin	0.025									0.004			
24 Haddock	0.008												
25 Sand lance	0.026	0.005								0.001			
26 Arctic cod										0.002			
27 Large pelagics	0.026												
28 Pesci. small pelagics	0.075												
29 Plank. small pelagics	0.098	0.001								0.010			
30 Shrimp	0.046	0.002			0.018					0.048			
31 Large crustacea	0.002		0.001		0.005	0.040							
32 Lobster	0.005					0.001							
33 Sea cucumber					0.030	0.050		0.002					
34 Echinoderms	0.000				0.102	0.245							
35 Molluscs		0.002			0.300	0.198							
36 Squid	0.238									0.001			
37 Polychaetes				0.015	0.160	0.025				0.025	0.050		
38 Other ben. inver.	0.112		0.096	0.015	0.169	0.385		0.003		0.042			
39 Large zooplankton	0.055	0.540	0.431	0.120	0.144	0.040							0.050
40 Small zooplankton		0.450	0.472	0.240	0.018		0.200			0.867		0.010	0.380
41 Phytoplankton				0.085		0.016	0.800	0.328	0.100		0.300		0.370
42 Detritus				0.525	0.036			0.668	0.900		0.650	0.990	0.200
Import	0	0	0	0	0	0	0	0	0	0	0	0	0

Table E.2. (cont.) Final diet matrix of the 2000-2009 balanced Ecopath model of NAFO subdivision 3Ps.

Group	a in LW	b in LW	Length at infinity (cm)	Weight at infinity (g)	K in VBGF (/year)	to in VBGF (year)	Tmax Output (year)
1 Pisc. Cetacea	0.006	3.000	2700	110000000	0.274	-0.471	40.714
2 Plank. Cetacea	0.006	3.000	1800	37300000	0.200	-0.570	82.352
3 Carn. Cetacea	0.006	3.200	980	22400000	0.200	-0.613	53.551
4 Harp seals	0.065	2.810	240	314500	0.310	-0.595	29.910
5 Hooded seals	0.005	3.000	311	141500	0.160	-0.777	38.916
6 Grey seals	0.052	2.860	328	821000	0.140	-0.820	42.685
7 Harbour seals	0.040	2.890	249	339700	0.400	-0.528	34.903
8 Pisc. Seabirds	0.010	3.000	53.0	2600	5.200	-0.200	17.677
9 Benth. Seabirds	0.010	3.000	54.0	950	11.23	-0.141	34.357
10 Plank. Seabirds	0.010	3.000	25.0	163	13.23	-0.144	29.707
11 Large cod (>35cm)	0.007	3.080	101	11200	0.170	-0.865	19.833
12 Small cod (<35cm)	0.001	3.819	35.0	622	0.170	-0.982	3.917
Large Green. 13 halibut	0.004	3.190	116	10600	0.090	-1.134	33.333
Small Green. 14 halibut	0.010	3.000	35.0	365	0.090	-1.308	3.917
15 Large Atl. halibut	0.013	2.920	220	91986	0.100	-1.001	33.333
16 Small Atl. halibut	0.010	3.000	45.0	244	0.100	-1.210	5.917
17 American plaice	0.006	3.060	65.6	2900	0.080	-1.279	6.226
18 Flounders	0.005	3.080	60.5	1800	0.100	-1.168	9.491
19 Skates	0.003	3.250	102	9700	0.060	-1.382	19.155
20 Redfish	0.009	3.040	52.5	1400	0.058	-1.519	6.899
21 Large demersals	0.007	3.060	137	22579	0.120	-0.976	6.652
22 Small demersals	0.005	3.110	62.2	2300	0.280	-0.732	7.992
23 Capelin	0.004	3.210	20.0	60.0	0.480	-0.657	6.208
24 Haddock	0.007	3.080	84.6	5700	0.240	-0.756	9.727
25 Sand lance	0.002	3.160	18.8	21.3	0.240	-0.905	3.749
26 Arctic cod	0.005	3.160	29.0	214	0.230	-0.876	11.105
27 Large pelagics	0.003	3.080	120	7000	0.042	-1.591	10.309
28 Pisci. small pelagics	0.006	3.070	44.5	803	0.269	-0.776	8.439
Plank. small 29 pelagics	0.006	3.090	35.7	352.8	0.409	-0.659	6.314
30 Shrimp	0.431	2.900	3.3	13.0	0.320	-0.979	2.962
31 Large crustacea	0.803	2.674	13.7	879	0.170	-1.098	12.033
32 Lobster	0.991	2.901	114	20000	0.100	-1.083	17.677
33 Sea cucumber	0.010	3.000	50.0	1250	0.300	-0.728	9.247
34 Echinoderms	0.356	3.004	10.0	359.8	0.118	-1.344	9.247
35 Molluscs	0.137	2.840	12.4	173	0.200	-1.033	7.261
36 Squid	0.004	3.550	29.4	600	0.650	-0.548	2.378
37 Polychaetes	0.010	3.000	1.0	0.010	0.837	-0.732	2.136
38 Other ben. inver.	0.010	3.000	5.5	1.664	0.536	-0.730	1.703
39 Large zooplankton	0.006	3.330	3.2	0.270	6.360	-0.255	1.216
40 Small zooplankton	0.010	3.000	0.5	0.001	2.247	-0.510	0.677
41 Phytoplankton	0.010	3.000	0.0	0	0.121	-2.794	0.057

Table E.3. Growth parameters used for the Particle Size Distribution Analysis in the 1960-1969 Ecopath model of NAFO subdivision 3Ps.

Group	a in LW	b in LW	Length at infinity (cm)	Weight at infinity (g)	K in VBGF (/year)	to in VBGF (year)	Tmax Output (year)
1 Pisc. Cetacea	0.006	3.000	2700	110000000	0.274	-0.471	40.714
2 Plank. Cetacea	0.006	3.000	1800	37300000	0.200	-0.570	82.352
3 Carn. Cetacea	0.006	3.200	980	22400000	0.200	-0.613	53.551
4 Harp seals	0.065	2.810	240	314500	0.310	-0.595	29.910
5 Hooded seals	0.005	3.000	311	141500	0.160	-0.777	38.916
6 Grey seals	0.052	2.860	328	821000	0.140	-0.820	42.685
7 Harbour seals	0.040	2.890	249	339700	0.400	-0.528	34.903
8 Pisc. Seabirds	0.010	3.000	53.0	2600	5.200	-0.200	17.677
9 Benth. Seabirds	0.010	3.000	54.0	950	11.230	-0.141	34.357
10 Plank. Seabirds	0.010	3.000	25.0	163	13.230	-0.144	29.707
11 Large cod (>35cm)	0.007	3.080	101	11200	0.170	-0.865	19.833
12 Small cod (<35cm)	0.001	3.819	35.0	622	0.170	-0.982	3.917
13 Large Green. halibut	0.004	3.190	116	10600	0.100	-1.081	33.333
14 Small Green. halibut	0.010	3.000	35.0	365	0.100	-1.247	4.917
15 Large Atl. halibut	0.013	2.920	220	91986	0.100	-1.001	33.333
16 Small Atl. halibut	0.010	3.000	45.0	244	0.100	-1.210	5.917
17 American plaice	0.006	3.060	65.6	2900	0.080	-1.279	13.405
18 Flounders	0.005	3.080	60.5	1800	0.100	-1.168	19.325
19 Skates	0.003	3.250	102	9700	0.060	-1.382	18.988
20 Redfish	0.009	3.040	52.5	1400	0.058	-1.519	17.822
21 Large demersals	0.007	3.060	137	22579	0.120	-0.976	21.310
22 Small demersals	0.005	3.110	62.2	2300	0.280	-0.732	10.854
23 Capelin	0.004	3.210	20.0	60.0	0.480	-0.657	6.165
24 Haddock	0.007	3.080	84.6	5700	0.240	-0.756	8.565
25 Sand lance	0.002	3.160	18.8	21.3	0.240	-0.905	7.023
26 Arctic cod	0.005	3.160	29.0	214	0.230	-0.876	11.105
27 Large pelagics	0.003	3.080	120	7000	0.042	-1.591	13.625
28 Pesci. small pelagics	0.006	3.070	44.5	803	0.269	-0.776	8.439
29 Plank. small pelagics	0.006	3.090	35.7	352.8	0.409	-0.659	6.314
30 Shrimp	0.431	2.900	3.3	13.0	0.320	-0.979	2.962
31 Large crustacea	0.803	2.674	13.7	879	0.170	-1.098	7.476
32 Lobster	0.991	2.901	114	20000	0.100	-1.083	9.168
33 Sea cucumber	0.010	3.000	50.0	1250	0.473	-0.593	9.247
34 Echinoderms	0.356	3.004	10.0	359.8	0.118	-1.344	9.247
35 Molluscs	0.137	2.840	12.4	173	0.200	-1.033	7.261
36 Squid	0.004	3.550	29.4	600	0.650	-0.548	2.378
37 Polychaetes	0.010	3.000	1.0	0.010	0.837	-0.732	2.136
38 Other ben. inver.	0.010	3.000	5.5	1.664	0.536	-0.730	1.703
39 Large zooplankton	0.006	3.330	3.2	0.270	6.360	-0.255	1.216
40 Small zooplankton	0.010	3.000	0.5	0.001	2.247	-0.510	0.677
41 Phytoplankton	0.010	3.000	0.0	0	0.121	-2.794	0.057

Table E.4. Growth parameters used for the Particle Size Distribution Analysis in the 2000-2009 Ecopath model of NAFO subdivision 3Ps.

Species	Depth range (m)	Source
American plaice	100-300	Iglesias-Martínez <i>et al.</i> , 1996; Behan <i>et al.</i> , 2022
Arctic cod	20-1000	Majewski <i>et al.</i> , 2016
Atlantic halibut	50-1000	Murphy <i>et al.</i> , 2014; Luo <i>et al.</i> , 2022
Capelin	0-200	Rose, 2005
Carnivorous cetaceans	0-1000	Lawson and Stevens, 2014
Echinoderms	20-800	Verril, 1895
Flounders	50-1000	Parsons <i>et al.</i> , 2024
Greenland halibut	0-1200	Bassi <i>et al.</i> , 2023; Lindegren <i>et al.</i> , 2025
Grey seals	0-300	Thompson <i>et al.</i> , 1991
Haddock	40-300	Rogers <i>et al.</i> , 2016
Harbour seals	0-400	Ramasco <i>et al.</i> , 2015
Harp seals	0-350	Lavigne, 2009
Hooded seals	0-600	Folkow and Blix, 1995
Large cod	50-400	Ruiz-Diaz <i>et al.</i> , 2024
Large demersals	50-800	Chang <i>et al.</i> , 1999; Neilson <i>et al.</i> , 2003
Large pelagics	0-500	Sulikowski <i>et al.</i> , 2010; Golet <i>et al.</i> , 2013
Lobster	5-150	Chang <i>et al.</i> , 2010
Molluscs	20-200	Coughlan <i>et al.</i> , 2022
Pisc. Small pelagics	0-150	Mbaye <i>et al.</i> , 2019
Piscivorous cetaceans	0-600	Gomez <i>et al.</i> , 2017
Plank. Small pelagics	0-200	Coad and Reist, 2004
Planktivorous cetaceans	0-300	Lesage <i>et al.</i> , 2017
Polychaetes	0-500	Carr, 2012
Redfish	100-950	Cadrine <i>et al.</i> , 2010; Planque <i>et al.</i> , 2013
Sand lance	0-150	Winters, 1989
Sea cucumber	20-100	Charmley <i>et al.</i> , 2025
Shrimp	50-400	Baker <i>et al.</i> , 2025
Skates	50-500	Packer <i>et al.</i> , 2003
Small demersals	30-500	Lock and Packer, 2003
Snow crab	50-900	Mulhoney <i>et al.</i> , 2011; Ruiz-Diaz <i>et al.</i> , 2024
Squid	0-400	Hendrickson and Holmes, 2004

Table E.5. Depth ranges for the Ecopath functional groups, used to create depth functions in the Ecospace spatial simulations.

	Group \ habitat	All	Shallow shelf	Slope	Offshore deep
1	Pisc. Cetacea	1	-	-	-
2	Plank. Cetacea	1	-	-	-
3	Carn. Cetacea	1	-	-	-
4	Harp seals	-	0.5	0.5	-
5	Hooded seals	-	0.5	0.5	-
6	Grey seals	-	0.5	0.5	-
7	Harbour seals	-	0.5	0.5	-
8	Pisc. Seabirds	1	-	-	-
9	Benth. Seabirds	1	-	-	-
10	Plank. Seabirds	1	-	-	-
11	Large cod (>35cm)	-	1	-	-
12	Small cod (<35cm)	-	1	-	-
13	Large Green. halibut	-	0.8	0.2	-
14	Small Green. halibut	-	1	-	-
15	Large Atl. halibut	-	0.5	0.5	-
16	Small Atl. halibut	-	1	-	-
17	American plaice	-	1	-	-
18	Flounders	-	0.8	0.2	-
19	Skates	-	0.8	0.2	-
20	Redfish	-	0.8	0.2	-
21	Large demersals	-	0.8	0.2	-
22	Small demersals	-	0.9	0.1	-
23	Capelin	-	1	-	-
24	Haddock	-	1	-	-
25	Sand lance	-	1	-	-
26	Arctic cod	1	-	-	-
27	Large pelagics	1	-	-	-
28	Pisci. small pelagics	1	-	-	-
29	Plank. small pelagics	1	-	-	-
30	Shrimp	-	0.8	0.2	-
31	Large crustacea	-	1	-	-
32	Lobster	-	1	-	-
33	Sea cucumber	-	1	-	-
34	Echinoderms	-	1	-	-
35	Molluscs	-	1	-	-
36	Squid	-	1	-	-
37	Polychaetes	-	1	-	-
38	Other ben. inver.	1	-	-	-
39	Large zooplankton	1	-	-	-
40	Small zooplankton	1	-	-	-
41	Phytoplankton	1	-	-	-
42	Detritus	1	-	-	-

Table E.6. Habitat foraging usage defined for the functional groups of the Ecospace model

Appendix F

Additional results from the Ecopath mass-balance models in *Chapter 4*.

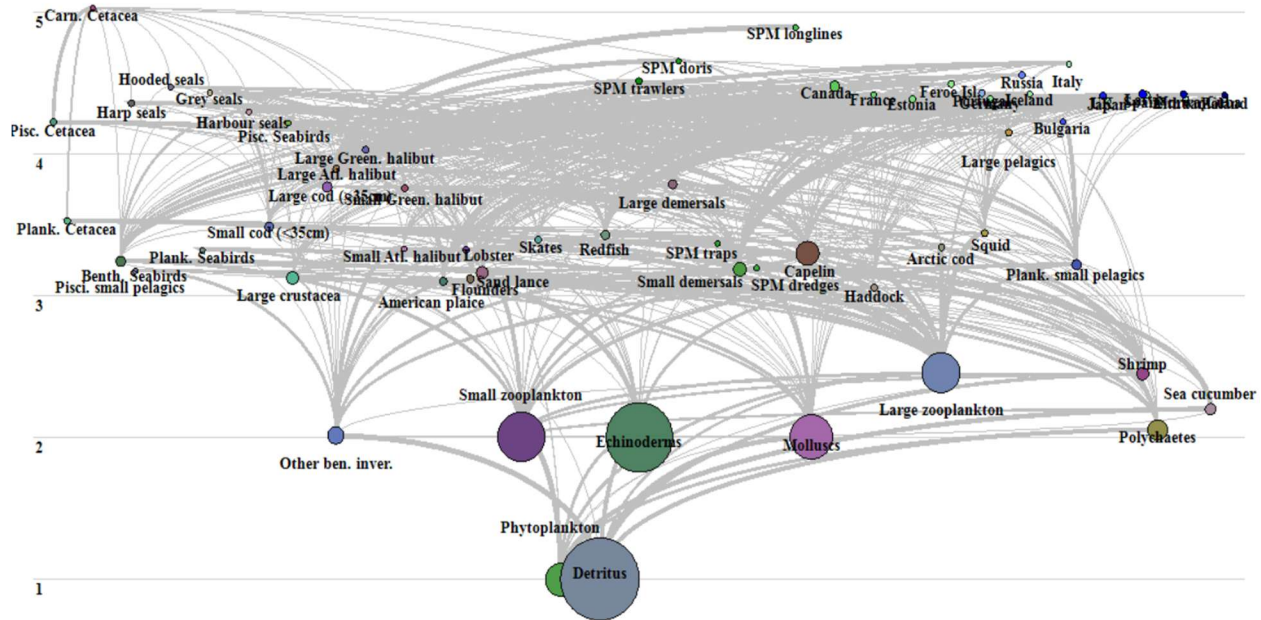


Figure F.1. Ecopath flow diagram for the 1960-1969 balanced model. The size of each ‘box’ reflects the proportion of biomass for each functional group.

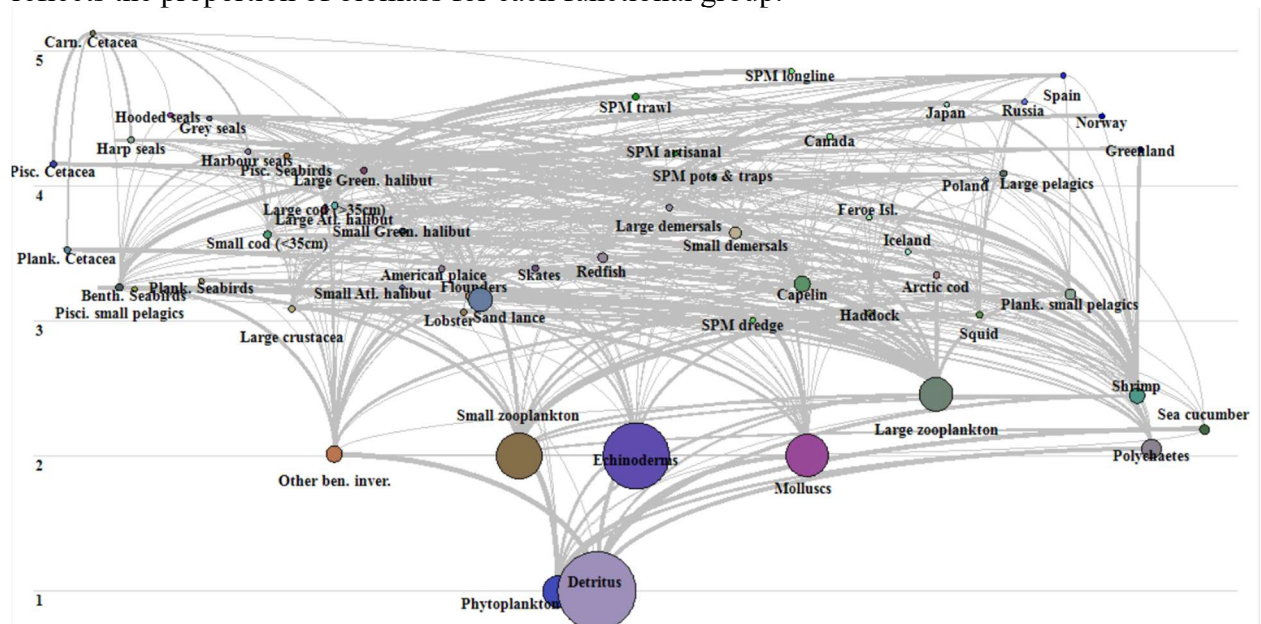


Figure F.2. Ecopath flow diagram for the 2000-2009 balanced model. The size of each ‘box’ reflects the proportion of biomass for each functional group.

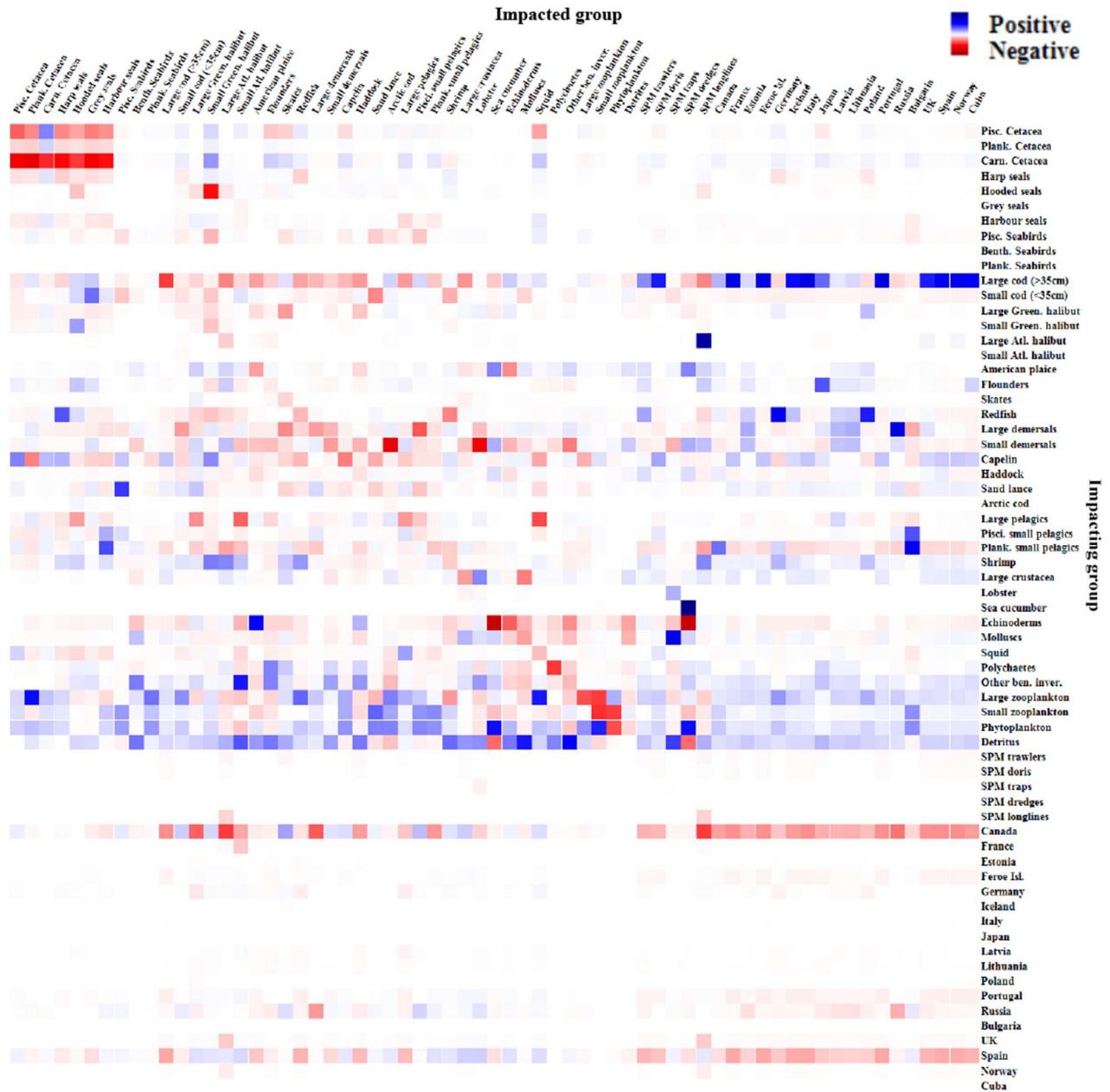


Figure F.3. Mixed Trophic Impact (MIT) analysis in the NAFO 3Ps ecosystem in 1960-1969. Diagram shows the positive (blue) and negative (red) impact of an increase in the biomass or harvest of the impacting group on the impacted group. Impact values are typically expressed in +1 to -1, but here range from 0.99 to -0.73. MIT analysis reveals that the SPM fishery has a much lower impact on the ecosystem than the Canadian fishery.