Trophic Reorganization and Energy Deficit: A Multispecies Size-Spectrum Model of the Grand Banks

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Abstract:

Marine ecosystems face unprecedented pressures from fishing and climate change, with both bottom-up energy transfer and top-down predation influencing ecosystem control, though their relative importance varies across space and time. The Grand Banks of Newfoundland provides a compelling case study, where capelin (*Mallotus villosus*) biomass collapsed by 99% in 1990–1991, followed by the collapse of Atlantic cod (*Gadus morhua*) and most groundfish species. Despite these dramatic shifts, the relative contributions of bottom-up versus top-down control mechanisms to ecosystem structure remain poorly understood. Here, we address this knowledge gap by developing a multispecies size-spectrum model of the Grand Banks fish community to simulate populations and community responses to scenarios of varying capelin, sand lance (*Ammodytes dubius*), and cod biomass recovery and depletion. Our results revealed contrasting patterns of ecosystem control depending on the scale of analysis. At the population level, cod removal generated biomass responses three times greater than equivalent forage fish reductions, indicating strong top-down control. However, these effects were largely buffered at the community scale through compensatory dynamics among non-target species. Conversely, capelin and sand lance depletion produced more modest population-level biomass changes but drove substantial biomass decline at community level. Among forage fish, capelin showed a more important role as energy source for the community. These findings suggest that Atlantic cod and capelin influence the Grand Banks through different mechanisms: trophic reorganization and energy deficit. Cod primarily structures the distribution of biomass among trophic levels, while foragefish govern total system biomass and energy. This work supports an ecosystem-based approach to management by providing a mechanistic understanding of how population changes in keystone predators and forage species lead to fundamentally different consequences for overall ecosystem structure and productivity.

Introduction

A central question in marine ecology concerns the relative importance of top-down (consumer-limited) versus bottom-up (resource-limited) control in structuring food webs. Forage fish serve as critical energy conduits in marine food webs, transferring energy from plankton to commercially important fish, marine mammals, and seabirds (Pikitch et al., 2012; Eddy et al., 2021). Typically short-lived, these species often exhibit boom-and-bust population cycles that can cascade through entire ecosystems, potentially triggering resource-limited control when their populations drop (Lewis et al., 2019; Cury et al., 2011; Gjøsæter et al., 2009). Conversely, biomass-dominant predators may regulate prey populations and maintain community structure through predation pressure, and their removal can result in potentially strong trophic cascades (Frank et al., 2005; Ellingsen et al., 2015). Understanding these mechanisms is critical because the impacts of climate change and overfishing depend fundamentally on which type of trophic control dominates. Early research often framed this as a binary question, with studies providing evidence for either top-down control (Worm & Myers 2003**;** Frank et al. 2005**)** or bottom-up control (Ware and Thompson 2005; Frederiksen *et al.* 2006; Greene and Pershing 2007). However, this dichotomous view has given way to a more nuanced understanding recognizing that both mechanisms can operate simultaneously or vary in dominance across spatial and temporal scales (Frank *et al.* 2006, 2007; Litzow and Ciannelli, 2007; Boyce et al., 2015, Lyam et al., 2017).

The Grand Banks of Newfoundland were subject to an abrupt ecological reorganization in the early 90's: capelin (*Mallotus villosus*) biomass plummeted by 99% between 1990-1991, followed by the collapse of several groundfish populations, which fundamentally altered food web structure and triggered fisheries closures lasting over three decades (Lewis et al., 2019; DFO, 2022a). The Grand Banks is a dynamic system, shaped by the nutrient-rich Labrador Current and the warmer North Atlantic Current, supports distinct seasonal production cycles and experiences decadal climate variability linked to the North Atlantic Oscillation (Cyr and Galbraith, 2021; Cyr et al., 2025). The system's primary forage species are capelin and northern sand lance (*Ammodytes dubius*). Capelin supports an inshore roe fishery in coastal Newfoundland (DFO 2022; Tretyakov, 2015), whereas sand lance is not exploited (Boldt et al., 2022). Atlantic cod serves as the dominant predator in this ecosystem, historically supporting offshore fisheries before its population collapse in the early 1990s (Frank 2005; Link et al., 2009). The northern stock (2J3KL North Atlantic Fisheries Organization -NAFO- divisions) is fished in recreational and inshore fisheries and is bycatch in the otter trawl fisheries of yellowtail flounder, skate and redfish. The offshore fishery reopened in 2024 after a 32 year moratorium, with a total allowable quota of 18,000 tonnes in 2024 (DFO, 2024b). The southern stock (3NO divisions), on the other hand, remains under moratorium (Rideout, 2021).

Species population declines on the Grand Banks have been attributed to overfishing and environmental changes (Dempsey et al., 2017; Lewis et al., 2019). Despite three decades having passed, neither capelin nor cod populations have recovered to pre-collapse levels, suggesting the ecosystem may have shifted to an alternative stable state characterized by lower productivity, and increased invertebrate biomass (Koen-Alonso and Cuff, 2018; Wudrick et al. 2024). However, recent evidence indicates a modest return toward a groundfish-dominated community in the northern NAFO divisions (2J3K) (Solberg et al., 2025). Previous quantitative food web models of the Grand Banks suggest that both resource-driven (bottom-up) and predation-driven (top-down) regulation are important (Bundy et al., 2001; Frank et al., 2005; Wudrick et al., 2024; Vaja et al., 2025). However, these approaches do not resolve the full size structure of populations, which is critical for understanding mechanistic trophic interactions. To address this gap, we use a multispecies size-spectrum model to directly contrast the relative strengths of forage-driven versus predator-driven regulation, allowing us to investigate unresolved questions about the mechanisms underlying ecosystem control on the Grand Banks.

Multispecies size spectrum food web models offer a powerful approach for testing competing hypotheses by mechanistically representing energy flow through ecosystems based on physiological principles (Scott et al., 2014; Blanchard et al., 2014, 2017). Under the modeling framework, the size structure of populations are fully resolved and individual growth, mortality, and reproduction rates are functions of size-dependent predation and resource availability, enabling simulation of how changes in key species propagate through size-structured food webs (Andersen and Pedersen, 2010; Andersen et al., 2016). Here, we develop a multispecies size spectrum model of the Grand Banks fish community to assess population and community responses to perturbations in the biomass of key forage species, capelin and sand lance (*Ammodytes dubius*), and the dominant predator, Atlantic cod, under varying levels of fishing intensity to better understand the relative importance of bottom-up food-limitation and top-down predation effects on community structure. We tested (1) whether changes in cod biomass drive larger population-level responses relative to equivalent changes in forage fish biomass, and (2) if capelin and sand lance have similar effects on community structure. Our approach distinguishes between population-level compensatory responses and community-level structural changes, providing insight into the mechanisms governing ecosystem function in the post-collapse Grand Banks.

Materials and Methods

General approach

To evaluate the relative roles of forage species and Atlantic cod on the Grand Banks community, we developed a multispecies size spectrum model using the mizer modeling framework (Scott et al., 2014). Mizer is a dynamic, size-based ecosystem model that represents predation interactions and growth processes at the individual level while fully resolving the size structure of both species and the community (Scott et al., 2014). The model includes nine species: Atlantic cod, turbot, American plaice, thorny skate, redfish, witch and yellowtail flounder, capelin and sand lance (Table S3). We developed and calibrated the model using 11-year average biomass estimates (2000-2010) from multispecies bottom trawl surveys, so the model represents average ecosystem conditions during this period. This approach enables the model to capture general long-term trends but makes it less suitable for reproducing year-to-year fluctuations in biomass. We calibrated the model by forcing with time series of fishing mortality and evaluating its ability to reproduce biomass and yield trends over the entire study period (1996-2019) as well as size-at-age growth patterns. It is important to note that this calibration period is well after the major ecosystem reorganization of the early 1990s. Therefore, the model is configured to represent the dynamics of the post-collapse state.

We classified mid trophic level species in the food web as mesopredators: American plaice, thorny skate, redfish, witch flounder, and yellowtail flounder.

Multispecies size spectrum model description

The model framework relies on three key assumptions: (i) individual organism energy budgets drive community-level energy flows; (ii) predator-prey size ratios primarily determine trophic interactions; and (iii) vital rates scale allometrically with individual body size, following established scaling relationships for biological rates (Andersen et al., 2016). These processes enable dynamic growth, reproduction, and mortality rates to emerge from trophic interactions (Andersen et al., 2006; Hartvig et al., 2011). Encountered prey are assimilated, and energy is allocated to respiration, growth, and reproduction according to individual size. The model formulates the size spectrum using mortality (μ) and growth rate (g) through the McKendrick–von Foerster equation (McKendrick, 1925; von Foerster, 1959):

$$\frac{\partial N_i(w)}{\partial t} + \frac{\partial g_i(w) N_i(w)}{\partial w} = -\mu_i(w) N_i(w) \qquad (1)$$

with the boundary condition:

$$g_i(w_0) N_i(w_0) = R_i \qquad (2)$$

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

Recruitment introduces individuals into the size spectrum at the smallest body size (typically egg size). The feeding kernel determines the distribution of prey sizes consumed by predators by predator-prey size ratios and described by a log-normal function (Scott et al., 2014). The model includes a background resource spectrum that feeds smaller individuals and planktivorous species. Resource spectrum dynamics are governed by predation rates and growth rates based on a semi-chemostat formulation (de Roos et al., 2008; Scott et al., 2014; see Table S1 for complete model equations, and Table S2 for input parameters).

For fish, recruitment depends on egg production and follows a Beverton-Holt stock-recruitment function, with maximum recruitment scaling species abundance (Table S1). Body growth rates depend on prey availability, while mortality rates are influenced by predation, fishing, and background mortality. Additional documentation is available in the R package *mizer* (Scott et al., 2014).

Model parameterization

Study domain and data sources

The model domain encompasses NAFO divisions 3L, 3N, and 3O (Figure 1). We obtained regional biomass estimates for groundfish from Fisheries and Oceans Canada (DFO) spring trawl surveys conducted annually on the Grand Banks between 1996 and 2019. These surveys have operated since 1971 but underwent modifications in survey design, sampling gear, and spatial coverage over time (Brodie and Stansbury, 2007). Notably, the survey transitioned from Engels (145 high lift otter trawl) to Campelen trawl (1800 shrimp trawl) gear in 1995-1996, improving catches of small fish and enabling abundance estimates for commercial shellfish species (Brodie and Stansbury, 2007).

We calculated groundfish biomass estimates using design-based methods implemented in the Rstrap package (Regular et al., 2020). For forage fish, which have low trawl catchability, we used capelin biomass estimates from acoustic data covering the 3L region where most capelin occur (DFO, 2022b), and bottom trawl survey biomass indices for northern sand lance since they are not surveyed using acoustics.

Species parameters

Fixed and species-specific parameters, including maximum size, size at maturation, and length-weight relationships, are detailed in Tables S3 and S4. For groundfish, we set maximum length (L_{inf}) to the maximum observed length from trawl surveys between 2000-2010, following established recommendations (Delius et al., 2023). Age- and length-at-maturity were obtained primarily from stock assessments when available, otherwise they were collected from the literature (see Table S5). Size-at-maturation corresponds to females, as they limit reproductive output and mature at larger sizes than males. Length-weight relationship parameters were estimated from DFO trawl survey data, except for thorny skate which were sourced from Fishbase (www.fishbase.org) for a Flemish Cap population (Froese and Pauly, 2024).

(Insert Figure 1)

Predation interactions

Predation interactions in *mizer* are based on predator size selectivity and prey preference, represented by a log-normal feeding kernel. We adjusted the mean preferred predator-to-prey mass ratio and kernel width during initial calibration, starting with default values of 100 and 1, respectively, for cod-like predators (Hartvig et al., 2011). We modified these values as needed: lower ratios for piscivores and higher ratios for omnivores and planktivores (Szuwalski et al., 2017; Jacobsen et al., 2016; Table S4). The predator-prey interaction matrix was parameterized using values ranging from 0 to 1, representing the relative strength of feeding interactions between species pairs, informed by stomach content data from González et al. (2006) (see supplement material and Table S6 for further detail).

Fishing mortality

We calculated time series of species biomasses using bottom trawl data and the Rstrap package (Figure 2A). Catch data were obtained from stock assessments (Table S3). We calculated fishing mortality as the ratio between catches and biomass (Figure 2B) because several species lacked assessments (e.g., sand lance) or were assessed at different management units (e.g., Atlantic cod, redfish, turbot and capelin). For Atlantic cod, we used catches from the southern stock (3NO). For redfish, we used catches from the 3O stock (the most exploited). For capelin we used catched from the NAFO STATLANT database. For sand lance we assumed no catches, as it is not targeted in any directed fishery. In the case of turbot, we used catches from the broader NAFO 3KLMNO divisions, as this is the scale of the stock assessment (Regular et al., 2022b). We assumed that one-third of these total catches were harvested from our Grand Banks model domain, a proportion based on the relative biomass distribution of the species across the larger stock area. However, initial calculations of fishing mortality (F), derived by dividing these apportioned catches by the biomass within our study domain, resulted in exceptionally high and unrealistic mortality rates relative to the stock's low biomass on the Grand Banks. Therefore, we set the initial fishing mortality of turbot to 0.1 for the calibration period, a value more consistent with mortality rates observed for other groundfish species in the model.

Fishing mortality (F) is imposed through size-selective fishing gear, calculated as the product of size-dependent gear selectivity, fishing effort, and catchability (Scott et al., 2014). We used a knife-edge fishery selectivity function, with selectivity set to 1 above maturation size. For calibration, we calculated average fishing mortality over the initial calibration period (2000-2010), and set catchability to 1 to use fishing effort as a direct measure of fishing mortality under constant selectivity (Benoit et al., 2022).

(Insert Figure 2)

Model calibration

Model calibration proceeded iteratively following established protocols (Delius et al. 2023, Audzijonyte et al., 2023) :

1. Equilibrium establishment: We brought the model to steady state by adjusting initial reproduction efficiency values using the steady() function in mizer, exploring alternative parameters when unrealistic values (>1) were returned (Blanchard et al., 2014).
2. Biomass calibration: We scaled initial species biomasses to match observed relative biomasses without altering size structure.
3. Growth calibration: We adjusted maximum intake (*h*) and volumetric search (*gamma*) parameters when feeding levels were high but growth was low (Audzijonyte et al., 2023).
4. Reproductive parameter optimization: We calibrated reproductive parameters by adjusting maximum recruitment (R_{max}) while fixing reproductive efficiency (*erepro* = 1), using the quasi-Newton method with box constraints (L-BFGS-B) to minimize sum of squared errors between modeled and empirical relative biomass, with extinction prevention penalties (Blanchard et al., 2014).
5. Background mortality tuning (Z_0): Initial calibration runs yielded unrealistically low maximum recruitment (Rmax) values for Atlantic cod, suggesting the model was attributing the species' low observed biomass solely to poor reproductive output. This approach, however, overlooks strong external mortality factors not explicitly modeled, such as predation from marine mammals, that could maintain cod populations at low levels despite adequate reproductive potential. Harp seals, in particular, are known to be significant predators of cod in this system (Vajas et al., 2025). To account for these unmeasured mortality sources, we systematically evaluated a range of multipliers for cod's background mortality (Z_0) and selected the value of 1.5 based on a likelihood profile, which minimized the root mean square error (RMSE) between modeled and observed biomass.
6. Multi-parameter optimization: We simultaneously optimized R_{max}, *erepro*, and *background mortality* (Z_0) allowing the model to achieve improve correspondence beetween observed and modeled time-averaged biomass levels through higher natural mortality rather than solely through reproduction.
7. Long-term stability: We ensured species coexistence and equilibrium by running 300-year simulations.
8. Fishing sensitivity: We tested different reproduction levels to assess species sensitivity to fishing, comparing results to expected ranges based on life-history characteristics (Audzijonyte et al., 2023).

We evaluated emergent diets, feeding levels, and predation mortality as intended model features during calibration. Full details of the model evaluation procedure is provided in the supplemental materials. The calibrated model produced biomass levels that closely matched average observed values, with no systematic bias observed (Figure S1). The model also produced plausible ontogenetic shifts in the diets of the species groups, with all species initially feeding on background resources and shifts towards piscivory with size (Figure S2). The model also demonstrated plausible resilience to fishing, as indicated by the fishing mortality rate at maximum yield under equilibrium conditions (Figure S3).

We conducted likelihood profiles on key parameters (R_{max}, *erepro,* and Z_0) to assess parameter uncertainty and identify potential estimation issues using root mean square error (RMSE). The analysis revealed that biomass estimates from the model were most vulnerable to underestimation of reproductive efficiency (*erepro*), with

RMSE values exceeding 0.8 log biomass units when *erepro* was reduced below 50% of baseline values and stabilizing near zero when *erepro* was adequate. Maximum recruitment (R_{max}) showed moderate sensitivity with U-shaped response curves, indicating optimal model performance at calibrated values and deteriorating accuracy when R_{max} deviated substantially from baseline, particularly for Atlantic cod. Background mortality (Z_0) generally had minimal impact on biomass estimation accuracy across most species, though turbot and Atlantic cod exhibited increased sensitivity at higher mortality rates (Figure S5).

Model Validation

We validated the model using multiple approaches to improve biological realism and predictive accuracy. First, we compared observed and modeled size-at-age relationships for fish species where data were available, using age-length keys from Rstrap corresponding to 2005 (mid-calibration period; Blanchard et al., 2014). Species growth rates predicted by the model were consistent with observed growth rates (Figure S4).

Finally, we forced the model with time-varying fishing mortality rates and evaluated agreement between predicted and observed biomass and catch time series over the full study period (1996-2019). This approach tested model ability to reproduce historical dynamics beyond the calibration period, providing confidence in model capacity to capture species responses to fishing intensity changes. The model reproduced catch trends more accurately than biomass trends (Figure S6), which is expected given that the model was calibrated to 10-year average conditions rather than annual variability, making year-to-year fluctuations in biomass more difficult to capture than general trends.

Simulation scenarios

We used fishing mortality as a lever to simulate varying levels of biomass depletion and recovery scenarios of target species. In particular, we implemented seven multipliers of baseline fishing mortality: 0.3, 0.5, 0.7, 1.0 (baseline), 1.5, 2.0, and 3.0. We evaluated population-level and community-level responses to biomass changes in: (1) capelin, (2) northern sand lance, and (3) Atlantic cod biomass. Since sand lance had zero fishing mortality during the calibration period (baseline), we applied the same fishing mortality as used for capelin, enabling us to simulate equivalent biomass levels and enable direct comparison of outputs.

Using time-averaged fishing mortality as the starting point, we applied the multipliers according to each scenario and projected the model for 300 years to ensure equilibrium. To account for minor biomass oscillations, we averaged biomass values from the final 11 years of the simulation period (years 290-300). We then calculated relative changes in species level metrics (biomass and predation) and community-level biomass between the calibrated model and equilibrium values under each scenario (Eq. 3) (Reum et al., 2024).

$$Relative\ change_{i,j}\ (\%) = \frac{X_{i,j}^{sim} - X_i^{base}}{X_i^{base}} \times 100 \qquad \text{Eq. (3)}$$

Where $X_{i,j}^{sim}$ is the values of variable X (i.e. biomass, predation), for species i in simulation j, and X_i^{base} is the value of X for species i in the unmanipulated (baseline) simulation.

Results

Applying fishing mortality multipliers produced the biomass changes in target species shown in Table 1.

(Insert table 1)

Simulations revealed that while non-target species biomass responded linearly to changes in all scenarios, the magnitude of these responses was approximately three times greater under Atlantic cod scenarios compared to equivalent forage fish scenarios, indicating a stronger top-down influence at the population level (Figure 3).

(Insert Figure 3)

The removal of Atlantic cod drove pronounced, cascading effects throughout the community (Figure 4). Under the high cod depletion scenario (a -16.8% change in cod biomass), mesopredators like redfish and American plaice showed the strongest responses, with biomass increases of over 10%. Turbot, witch flounder, and yellowtail flounder also increased, though more modestly (5-10%), reflecting the removal of cod's regulatory pressure. In turn, this release of mesopredators intensified predation pressure on lower trophic levels. Forage fish experienced substantial declines, with sand lance biomass dropping by approximately 20% and capelin by 17%. These biomass shifts were mirrored by changes in predation mortality, which increased by ~6% for forage species under cod depletion. Conversely, in the high recovery scenario (+7% cod biomass), these patterns reversed: mesopredator biomass decreased by 2-5%, while forage fish populations increased by 7.5-9.3%

In contrast to the strong trophic cascade driven by cod, reductions in forage fish biomass had a more uniform and pervasive bottom-up effect on the community. Under the high capelin depletion scenario (-14.8% change), nearly all non-target species declined, though by a smaller magnitude than seen in the cod scenarios. Redfish, American plaice, turbot, and witch flounder experienced biomass declines of around 2%. The two forage species demonstrated different roles. Capelin depletion produced generalized declines across most species, establishing its central position as an energy source. In contrast, sand lance depletion produced smaller negative changes overall. Some interspecific compensation was also evident; under capelin depletion, sand lance biomass increased by nearly 2%, whereas capelin showed minimal response to sand lance depletion.

(Insert Figure 4)

These contrasting population-level responses translated into fundamentally different impacts at the community level (Figure 5). Despite causing large biomass shifts among species, the high cod depletion scenario resulted in only a 1.3% increase in total community biomass. Conversely, the high capelin depletion scenario drove a 3% decline in total community biomass, a much larger system-wide impact. Sand lance depletion produced similar, but smaller, community-level effects.

(Insert Figure 5)

Discussion:

Our study used a multispecies size-spectrum model calibrated to the Grand Banks ecosystem of the 2000s to explore the distinct roles of a dominant predator and key forage species. A key consideration when interpreting our findings is that the model represents the post-collapse state of the ecosystem, which may be an alternative stable state characterized by different energy flow pathways than the pre-collapse, cod-dominated system. Consequently, our simulations of "recovery" should be interpreted as potential responses and shifts from the current ecosystem configuration, rather than a straightforward return to a historical state.

Our multispecies size spectrum model identified two distinct pathways through which abundant, large predators and key forage species influence the Grand Banks ecosystem, namely, (1) trophic reorganization through predator removal and (2) energy deficit through forage fish depletion. In the case of the former, we showed that removal of Atlantic cod can spur community reorganization characterized by both vertical and horizontal effects. Vertically, predator release led to turbot and intermediate predators increasing 5-15%, while forage fish declined 16-20% under intensified predation pressure. Horizontally, competitive release occurred as remaining predators benefited from reduced competition for shared forage resources. This pattern is consistent with established predator removal theory (Daskalov 2002; Baum and Worm 2009; Estes et al. 2011), where trophic cascades reorganize energy distribution among levels. Competitive release often occurs in ecosystems where multiple species depend on the same, moderately constrained prey resources, as is the case on the Grand banks (i.e., forage fish) (Smith et al., 2011; Tolimieri et al., 2013; Cyr et al., 2015). Despite these dramatic species-level changes, total community biomass remained relatively stable, fluctuating by only 1%, and demonstrating how compensatory processes can help stabilize biomass at the community level (Gonzalez and Loreau, 2009).

The effects of energy deficits resulting from forage fish reductions highlight possible system-wide effects, with population biomass declines of 2-4% and substantial biomass loss of ~3% at the community level. Ecological communities can be conceptualized as self-organized flows of matter and energy, with higher energy availability supporting greater species biomass (Mendoza and Araujo 2025). Forage fish serves as a critical energy conduit transferring energy from zooplankton to higher predators (Pikitch, 2012), and our finding suggests their depletion creates non-compensable resource limitations that propagate throughout the entire Grand Banks food web. These findings support other ecosystem modeling studies that show forage fish play a fundamental role as an energy conduit across multiple trophic levels in this and other systems (Koen-Alonso et al. 2021; Vajas et al. 2025).

The regime shift theory predicts that ecosystems can transition between alternative stable states characterized by different community compositions and energy flow pathways (Beisner et al., 2003). Once established, these alternative configurations may persist through positive feedbacks that prevent return to the original state, even when the initial perturbation is removed (Suding et al., 2004; Pershing et al., 2015). Our simulations show how both trophic restructuring and energy deficit mechanisms may contribute to maintaining this alternative state. Varying levels of cod depletion modified predation dynamics, with reduced cod biomass decreasing predation pressure on turbot and redfish while increasing predation on other species. These results suggest that expanded turbot and mesopredator populations may limit cod recovery through increased predation pressure and competition, which could be particularly important in early life stages (Hutchings and Rangeley, 2011). Furthermore, while our model accounts for some non-fishery mortality on cod through an increased background mortality parameter, it does not dynamically include predation by marine mammals. The large and growing harp seal population exerts significant predation pressure on cod and other groundfish, which many researchers suggest is a major factor limiting stock recovery (Stenson, 2013; Chassot et al., 2009; Vajas et al., 2025). This sustained, high predation pressure could function as another feedback mechanism that "traps" the ecosystem in its current state, a dynamic our model only partially captures.

The lack of cod recovery has also been attributed to poor feeding and body condition, particularly in relation to low capelin biomass (Mullowney and Rose, 2014; Koen-Alonso et al., 2021; Regular et al., 2022). The persistent failure of capelin stocks to recover creates a critical bottleneck that may perpetuate the alternative ecosystem state through energy limitation. Both 2J3KL and 3NO capelin stocks have shown minimal recovery (Murphy et al., 2021; Murphy et al., 2024; Tretyakov, 2015), with poor recruitment driven by deteriorating life history traits including reduced body condition, earlier maturation at smaller sizes, and delayed spawning linked to weak year classes (Murphy et al., 2021; Buren et al., 2019). Climate variability further compounds these constraints by disrupting fundamental ecological timing. Earlier sea ice retreat has shifted spring bloom phenology, creating a critical mismatch between capelin spawning periods and peak *Calanus finmarchicus* production (Buren et al., 2014; Lewis et al., 2019; Staudinger et al., 2020). This temporal decoupling reduces energy transfer efficiency from primary consumers to capelin, intensifying the energy deficit throughout the food web. The broader decline in Grand Banks ecosystem biomass and productivity (Wudrick et al., 2024) may impose fundamental energetic constraints that limit recovery potential across all trophic levels, effectively reinforcing the alternative stable state through system-wide resource limitation. While our models demonstrate positive species population responses to capelin biomass recovery, the reliance on post-collapse data (2000-2010) constrains our ability to predict ecosystem behavior under different ecosystem stable states (i.e. pre-collapse) or to fully resolve the mechanisms governing transitions between alternative states.

Finally, the contrasting population-level impacts of capelin and sand lance on non-target species reveal important insights into functional roles among forage fish species. Capelin emerges as the dominant forage species, generating biomass responses up to 4% across multiple predator species compared to 2% for sand lance, highlighting its central position in Grand Banks food web. This pattern reinforces previous research establishing capelin's critical role in the ecosystem (Buren et al., 2014, 2019; Regular et al., 2022; Vajas et al., 2025) while revealing the more limited influence of sand lance despite their shared status as small pelagic fish. The contrasting impacts reflect fundamentally different life-history strategies that create complementary rather than substitutable ecological functions. Capelin's dynamic lifestyle enables broad ecosystem connectivity through its occupation of offshore northern Grand Banks waters and extensive inshore migrations during summer spawning (Crook et al., 2017). The species utilizes pelagic waters across depths up to 250 m in temperatures ranging from -1.5 to 6 °C (Rose, 2005). In contrast, sand lance provides more localized ecosystem functions through its specialized shallow-water niche (typically < 100 m) in sandy Grand Banks substrates (Staudinger et al., 2020). Sand lance winter spawning period (November-March), unique burrowing behavior, and preference for warmer waters (1-11 °C) create temporal and spatial ecosystem functions that differ from capelin (Dalley and Winters, 1987; Morrison and Davoren, 2024; Government of Newfoundland and Labrador, 2020). These divergent strategies result in complementary ecosystem functions where each species fills distinct spatio-temporal niches.

Our results provide strong support for ecosystem-based fisheries management (EBFM) that recognizes how keystone species can determine community structure and overall energy availability on marine ecosystems. The transition towards EBFM requires integrating ecosystem considerations into fisheries management decisions, recognizing that keystone species like capelin and sand lance function as critical energy conduits whose ecosystem-wide influence extends far beyond what traditional stock assessments can capture. Although Fisheries and Oceans Canada is formally committed to ecosystem approaches, implementation remains limited with most decision-making frameworks still following traditional single-species approaches (Pepin et al., 2023). Enhanced monitoring of forage fish populations is essential, particularly given their high spatiotemporal variability and the limitations of conventional survey methods (i.e., bottom trawls) for assessing these dynamic stocks (Pikitch et al., 2012; Lewis et al., 2019). Moreover, the contrasting responses observed at population versus community levels underscore the need for indicators that capture broader changes than just species biomass. Such multifaceted indicators must be incorporated into management frameworks to detect broader community and ecosystem changes and provide early warning signals for adaptive responses (Coll et al., 2016; Briton et al., 2019; Link and Watson, 2019). As marine systems worldwide face increasing anthropogenic pressures, our mechanistic demonstration of how keystone species structure the entire community reinforces that ecosystem-based management is not just preferable but may be essential for maintaining ecosystem services and supporting sustainable fisheries in the long term.

Research priorities and future directions

Several research priorities emerge that could strengthen these findings and improve ecosystem-based management. First, enhanced biomass monitoring for highly variable forage fish, given the limitations of current surveys, and higher-resolution diet data would improve model precision and better resolve predator-prey interaction strengths (Engelhard et al., 2014; Robertson et al., 2022). Further sensitivity analyses examining diet composition and growth parameters could provide additional insights for model parameterization and identify other critical uncertainties (Spence et al., 2016). Finally, the logical next steps are to dynamically incorporate other major ecosystem drivers, particularly predation from marine mammals and the effects of climate change. The strong environmental sensitivity of forage fish (Boyce et al., 2015; Cyr et al., 2025) suggests that climate change may amplify the bottom-up control mechanisms identified in this study, making this integration essential for future ecosystem-based approaches

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Tables:

Table 1. Simulated biomass levels of target species (Atlantic cod, capelin, and sand lance) under different fishing mortality scenarios. Note: sand lance scenarios were run with the same fishing mortality levels as capelin.

Fishing mortality multiplier	Atlantic cod biomass	Capelin biomass	Sand lance biomass	Biomass scenario
0.3 x baseline	7%	6.4%	—	Recovey-high
0.5 x baseline	5%	4.5%	—	Recovery-medium
0.7 x baseline	3%	2.7%	—	Recovery-low
baseline	0	0	0	Baseline
1.5x baseline	-4.6%	-4.1%	-10.7%	Depletion - low
2.0x baseline	-9%	-8%	-13.7	Depletion-medium
3.0x baseline	-16.8%	-14.8%	-19.2	Depletion-high

Figures

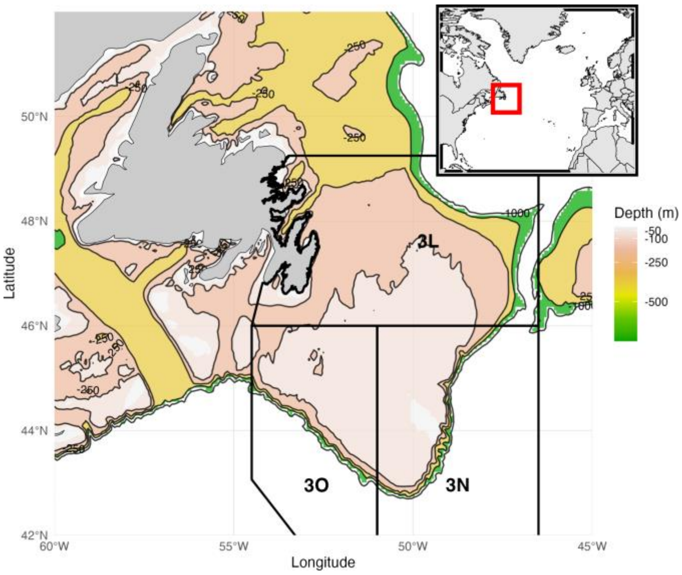

Figure 1. Map of Newfoundland showing the Grand Banks study area. Black rectangles represent NAFO divisions 3L, 3N, and 3O corresponding to the Grand Banks region. Color scale indicates bathymetry (water depth), with black contour lines showing isobaths at 100, 250, 500 and 1000 m depth.

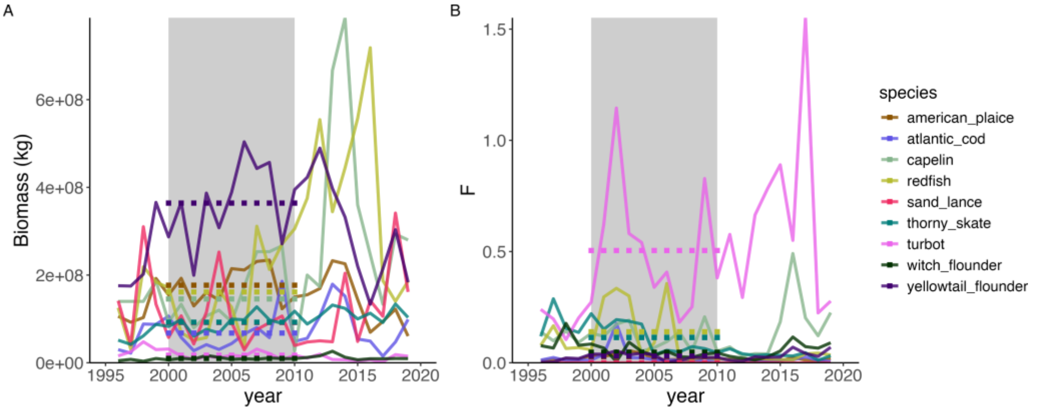

Figure 2. Historical data used for model calibration. A) Biomass time series (kg) for the study domain calculated from RV trawl survey data, and B) fishing mortality rates calculated as the ratio of catches to biomass. The model calibration period (2000-2010) is highlighted in grey, with average values for this period indicated by colored squares. Note that turbot data represent the broader 3KLNO stock area that extends beyond the Grand Banks study domain, resulting in higher biomass values.

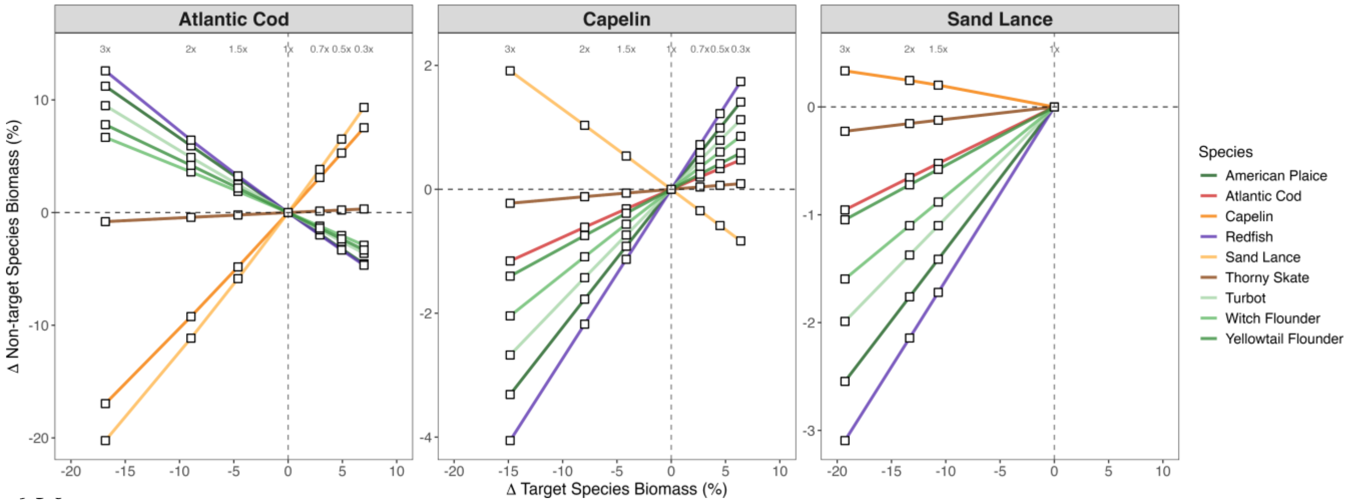

Figure 3. Population-level responses of non-target species to simulated changes in the biomass of target species (Atlantic Cod, Capelin, and Sand Lance). The x-axis indicates the percentage change in biomass of the target species, while the y-axis shows the corresponding percentage change in biomass of non-target species. Colored lines denote different non-target groups: forage fish (orange), flatfish (green), skates (brown), redfish (purple), and cod (red). Squares along the lines mark the fishing mortality multipliers used to achieve the biomass changes, with values annotated above. Note that the y-axis scale for the Atlantic Cod panel (±20%) is approximately three times larger than that for the Capelin and Sand Lance panels.

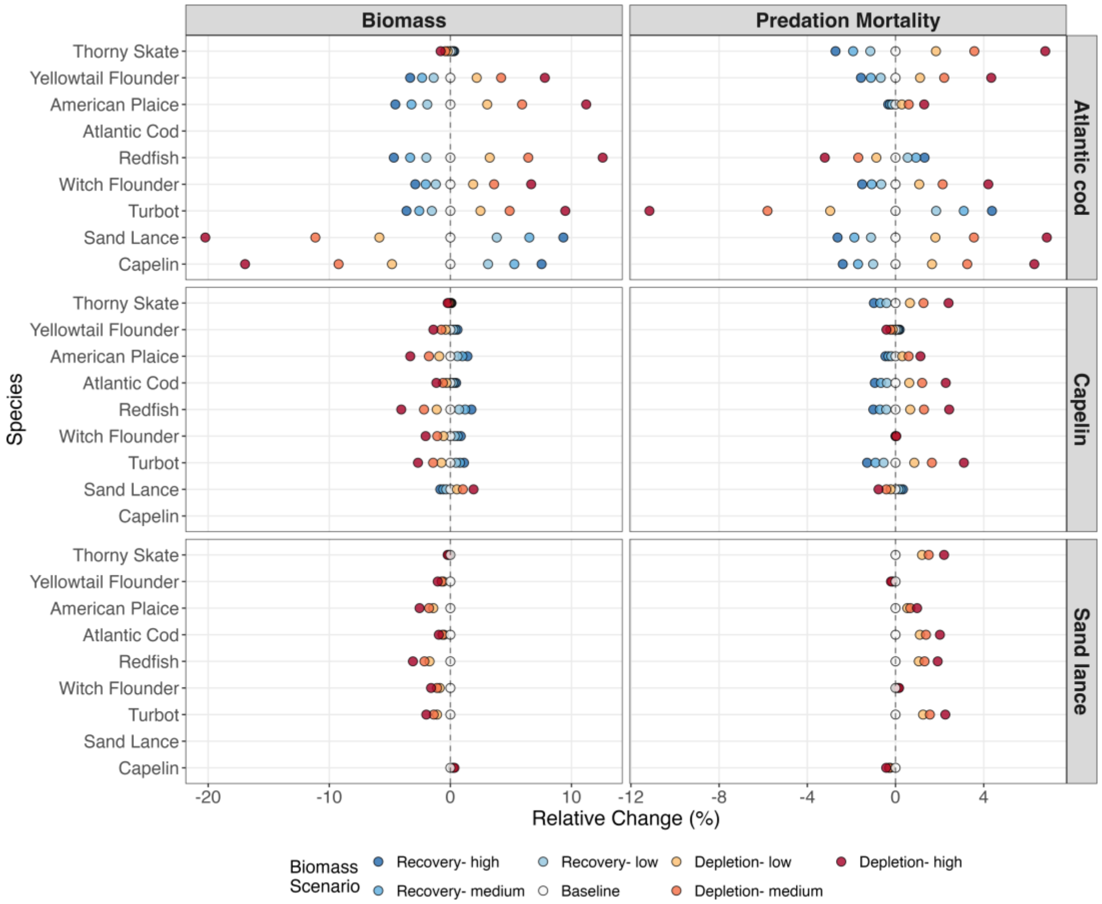

Figure 4. Population-level responses to target species biomass scenarios. Relative changes (percentage) in biomass and predation mortality under different Atlantic cod, capelin and sand lance biomass scenarios. Blue = biomass recovery, white = baseline, red = biomass depletion, with darker colors showing extreme scenarios.

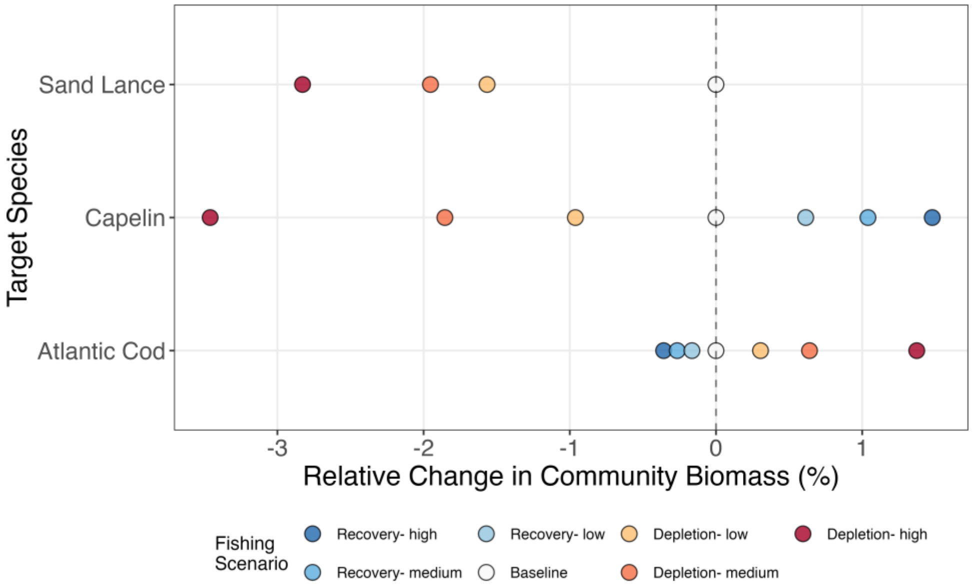

Figure 5. Community-level responses to target species biomass change scenarios. Relative changes (percentage) in total community biomass under different Atlantic cod,

capelin and sand lance biomass scenarios. Blue = biomass recovery, white = baseline, red = biomass depletion, with darker colors showing extreme scenarios.