



SOUTH ATLANTIC FISHERY MANAGEMENT COUNCIL

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POLICY CONSIDERATIONS FOR SOUTH ATLANTIC FOOD WEBS AND CONNECTIVITY AND ESSENTIAL FISH HABITATS (June 2026)

Introduction

This document provides guidance from the South Atlantic Fishery Management Council (SAFMC) on South Atlantic food webs, ecosystem connectivity, and the protection of Essential Fish Habitat (EFH) and Habitat Areas of Particular Concern (EFH-HAPCs) in support of the Council's transition to ecosystem-based fisheries management (EBFM). The guidance aligns with existing SAFMC habitat protection policies, including the Habitat Plan (SAFMC 1998a), the Comprehensive EFH Amendment (SAFMC 1998b), the Fishery Ecosystem Plan of the South Atlantic Region (SAFMC 2009a), Comprehensive Ecosystem-Based Amendments 1 and 2 (SAFMC 2009b; 2011), Fishery Ecosystem Plan II (SAFMC 2018), the Habitat Blueprint (SAFMC 2023), and the Council's Fishery Management Plans (FMPs).

For policy purposes, this document evaluates potential threats and impacts to EFH, EFH-HAPCs, and the broader South Atlantic ecosystem associated with changes in food webs and ecological connectivity. It also identifies processes that may enhance or degrade these resources. The policies and recommendations presented here are intended to address such impacts in accordance with SAFMC habitat protection mandates. This guidance may be revised in response to changing environmental conditions in the South Atlantic region, updates to applicable laws or regulations, new scientific information, or other determinations by the Council.

For clarity, the following terms are used throughout this document:

Essential Fish Habitat (EFH): Waters and substrate necessary for fish to spawn, breed, feed, and grow to maturity, including the physical, chemical, and biological properties of aquatic environments and associated benthic habitats.

Habitat Areas of Particular Concern (HAPCs): Subsets of EFH that are especially important to ecosystem function and particularly vulnerable to degradation or human impacts (e.g., spawning areas, nursery habitats, pupping grounds).

Policy Considerations

A key principle of ecosystem-based fisheries management is the explicit consideration of indirect ecological effects of fishing, particularly those mediated through food web interactions, when

developing harvest strategies and management plans. Fishing can alter trophic relationships; for example, overexploitation of predators may increase prey abundance and reduce organisms two trophic levels below them, a phenomenon known as a trophic cascade (Carpenter et al. 1985). Conversely, fishing on lower-trophic-level species such as planktivorous forage fishes may ultimately reduce predator populations through food limitation (e.g., Okey et al. 2014; Walters and Martell 2004). Competition among species for shared food resources, including during rebuilding of competing stocks or following the establishment of non-native species, can further influence ecosystem dynamics.

Food webs link multiple components of the ecosystem across habitats, depths, and regions. Movements of species between estuaries, coastal waters, and offshore environments transfer energy across ecosystems, while benthic–pelagic interactions connect production in the water column with seafloor communities. These linkages—such as those between pelagic forage fishes and their piscivorous predators or demersal carnivores—create multiple energy pathways that enhance ecosystem stability and resilience.

Environmental variability also plays an important role in shaping food webs. Changes in primary production driven by climate and oceanographic processes (e.g., precipitation, nutrient inputs, and upwelling) can propagate through the food web via bottom-up effects. Consequently, population changes for many species reflect the combined influence of fishing pressure and environmental forcing.

Food web processes can be incorporated into fisheries management through ecosystem models. Trophic-dynamic models are increasingly used by managers as ecological prediction tools because they can simulate the entire ecosystem—from primary producers to top predators and fisheries. These models help evaluate trade-offs associated with harvesting species at different trophic levels, assess ecosystem responses to environmental change, inform single-species assessments, and generate biological reference points and ecosystem-level indicators (Walters et al. 2005; Coll et al. 2006; Fulton et al. 2005).

This document provides background and context on food webs relevant to SAFMC management of the South Atlantic ecosystem. It reviews the structure and energy pathways of estuarine, nearshore, and offshore food webs; examines linkages among inshore–offshore, benthic–pelagic, and seasonal systems; and discusses key threats to food web structure and function. It also summarizes the use of food web models and ecosystem indicators in fisheries management. While examples specific to South Atlantic ecosystems are included where possible, many food web processes remain understudied in the region. This is particularly important given the strong influence of the Gulf Stream, which makes the South Atlantic ecosystem distinct from adjacent systems such as the Gulf of Mexico despite sharing many species. The document concludes with recommendations to improve understanding of food web dynamics and strengthen their integration into fisheries management.

model (SAFMC 2022). Nodes are colored based on type (see legend above). The pink nodes identify groups that include SAFMC managed species or are a managed species. The flow strength varies from Blue (weakest) to red (strongest). Each circle represents a group in the ecosystem and its size is logarithmically proportional to its biomass. Each line is a trophic interaction between two groups. The width of each line represents the flow proportion. The light grey horizontal lines indicate trophic levels. Diagram produced by Lauren Gentry, FWC-FWRI September 2024.

Threats to EFH and EFH-HAPCs from Changes in South Atlantic Food Web and Connectivity

The SAFMC finds that negative impacts to EFH and EFH-HAPCs can change South Atlantic food webs and connectivity for managed species. Table 1 following food webs and connectivity policy and research recommendations, presents a summary of South Atlantic fisheries and their designated EFH and EFH-HAPCs as presented in the SAFMC [EFH User Guide \(SAFMC 2024\)](#).

Information on Food webs was expanded upon during the development of the Fishery Ecosystem Plan II. That information was integrated into this policy as an appendix and summarized here.

Summary of the FEP 2 Appendix C

South Atlantic ecosystems are structured by a diverse mosaic of interconnected estuarine, nearshore, offshore, benthic, and pelagic habitats that support complex and tightly linked food webs. Connectivity among these systems is driven by species movements (ontogenetic, seasonal, and diel), trophic interactions, and physical oceanographic processes such as larval transport and circulation patterns. These linkages facilitate the transfer of energy and biomass across habitats, with energy derived from multiple basal sources, including marsh and seagrass detritus in nearshore systems and phytoplankton in offshore environments. Energy flows through coupled benthic (“slow”) and pelagic (“fast”) pathways, with forage species playing a central role in transferring energy to higher trophic levels.

Food web dynamics are governed by interacting bottom-up and top-down processes that vary across spatial and temporal scales. Environmental drivers such as nutrient inputs, temperature, and climate variability influence primary production and prey availability, while predation and fishing pressure shape community structure and trophic relationships. These interactions make the system highly sensitive to disturbance, where impacts from fishing, habitat degradation, invasive species, water quality changes, and climate change can propagate through the food web and alter ecosystem productivity and resilience. Connectivity further amplifies these dynamics by linking distant habitats and populations, influencing recruitment, population persistence, and the effectiveness of spatial management measures.

Despite advances in understanding, significant data gaps remain, particularly regarding offshore habitats, forage species dynamics, trophic relationships, and the effects of climate variability on ecosystem processes. Addressing these uncertainties and improving the integration of

ecosystem science into fisheries management is essential for sustaining productivity and resilience in the South Atlantic.

1. SAFMC Policies Addressing South Atlantic Food Webs and Connectivity

The SAFMC establishes the following policies to address South Atlantic food webs and connectivity, and to clarify and augment the general policies already adopted in the Habitat Plan and Comprehensive Habitat Amendment and Fishery Ecosystem Plan (SAFMC 1998a; SAFMC 1998b; SAFMC 2009a).

1.1 General Policies:

1. Forage Fisheries¹ - Managers should consider forage fish (Defined in footnote one as invertebrate and vertebrate species) stock abundances and dynamics, and their impacts on predator productivity, when setting catch limits to promote ecosystem sustainability. To do so, more science and monitoring information are needed to improve our understanding of the role of forage fish in the ecosystem. This information should be included in stock assessments, ecosystem models, and other fishery management tools and processes in order to support the development of sustainable harvest strategies that incorporate ecosystem considerations and trade-offs.

Note: Initial preliminary definition and potential list of forage species and forage fish species presented in Appendix A.

Associated Sections in Appendix C

[1. Summary of South Atlantic Food Webs](#)

[2.2. Top Down and Bottom Up Controls](#)

[2.3. Energy Pathways and Food Web Stability](#)

[2.4. Dominant Energy Pathways and Emerging Trends](#)

[4.2. Food Web Models Case Studies](#)

[5.1. Management Applications: Informing Stock Assessments](#)

[5.2. Management Applications: Evaluating Policy Options](#)

[6. Impacts of Food Webs](#)

2. Prey importance- Diet data used to describe the importance of forage species in food web models may contain certain biases depending on the metric used to inform the relative contribution to the diet, and due to other challenges involved such as varying rates of digestion for different prey (Hyslop, 1980). Therefore, the evaluation of prey importance should consider a suite of appropriate indicators including mass, occurrence,

¹ NOAA defines Fishery as “Generally, a fishery is an activity leading to harvesting of fish. It may involve capture of wild fish or raising of fish through aquaculture. A unit determined by an authority or other entity that is engaged in raising or harvesting fish. Typically, the unit is defined in terms of some or all of the following: people involved, species or type of fish, area of water or seabed, method of fishing, class of boats, and purpose of the activities. The combination of fish and fishers in a region, the latter fishing for similar or the same species with similar or the same gear types”. and fish as a “Used as a collective term, includes mollusks, crustaceans and any aquatic animal which is harvested.”(United States, 2005)

and degree of overlap as a shared resource among multiple predators. Prey that are identified as important should be recognized as ecosystem component species, and considered within the appropriate fishery-management plan.

Associated Sections in Appendix C

[2.4. Dominant Energy Pathways and Emerging Trends](#)

[3. Connectivity Among Food Webs](#)

[4.1. Food Web Models and Principles](#)

[4.3. Food Web Indicators](#)

[5.1. Management Applications: Informing Stock Assessments](#)

[5.3. Management Applications: Use of Food Web Indicators](#)

3. Food Web Indicators – Food web indicators have been employed to summarize the state of knowledge of an ecosystem or food web and could serve as ecological benchmarks to inform future actions.

Associated Sections in Appendix C

[4.3. Food Web Indicators](#)

[5.3. Management Applications: Use of Food Web indicators](#)

4. Food Web Connectivity – Separate food webs exist in the South Atlantic, for example inshore-offshore, north-south, and benthic-pelagic, but they are connected by species that migrate between them such that loss of connectivity due to habitat degradation or loss could have impacts on other components of the ecosystem that would otherwise appear unrelated and must be accounted for.

Associated Sections in Appendix C:

[1. Summary of South Atlantic Food Webs](#)

[2.3. Energy Pathways and Food Web Stability](#)

[3. Connectivity Among Food webs](#)

[4.1. Food Web Models and Principles](#)

[6. Impacts on Food webs](#)

5. Trophic Pathways – Managers should aim to understand how fisheries production is driven either by bottom-up or top-down forcing and attempt to maintain diverse energy pathways to promote overall food web stability.

Associated Sections in Appendix C:

[2. Energy Pathways](#)

[4.1. Food Web Models and Principles](#)

[4.2. Food Web Models: Case Studies](#)

[6.1. Impacts on Food Webs: Fishery Related Impacts](#)

6. Food Web Models – Food web models can provide useful information to inform stock assessments, screen policy options for unintended consequences, examine ecological and economic trade-offs, and evaluate the performance of management actions under alternative ecosystem states. A full Ecopath with Ecosim (EWE) model and a snapper grouper simplified model has been developed for the South Atlantic Region to be used as a tool for management decisions. (SAFMC, 2022)

Associated Sections in Appendix C:

[2.4. Dominant Energy Pathways and Emerging Trends](#)

[4: Food Web Models](#)

[5. Management Applications](#)

7. **Ecosystem Component Species** – Ecosystem component species are species that do not require conservation and management under a federal fishery management plan, but are included to achieve ecosystem management objectives.

Associated Sections in Appendix C:

[2.4. Dominant Energy Pathways and Emerging Trends](#)

[4.2. Food Web Model: Case Studies](#)

[5.2. Management Applications: Evaluating Policy Options](#)

[6. Impacts on Food Webs](#)

8. **Invasive Species** – Invasive species, most notably lionfish (*Pterois* spp.), are known to have negative effects on ecologically and economically important reef fish species through predation and competition and those effects should be accounted for in management actions.

Associated Sections in Appendix C:

[2.2. Energy Pathways: Top-Down and Bottom – Up Controls](#)

[3. Connectivity Among Food Webs](#)

[4.2. Food Web Models: Case Studies](#)

[6.4. Impacts on Food Webs: Invasive species](#)

9. **Contaminants** – Bioaccumulation of contaminants in food webs can have sub-lethal effects on marine fish, mammals, and birds and is also a concern for human seafood consumption.

Associated Sections in Appendix C:

[2.2. Energy Pathways: Top Down and Bottom Up Controls](#)

[6.2. Impacts on Food Webs: Water Quality](#)

2. Research and Information Needs Addressing South Atlantic Food Webs and Connectivity

2.1 Improve Data Availability and Monitoring

- Expand monitoring of:
 - Forage species abundance and dynamics
 - Plankton communities
 - Benthic prey resources
- Increase diet and trophic studies for:
 - Non-commercial species
 - Offshore and pelagic species
- Enhance fishery-independent surveys:
 - Across habitats (estuarine to offshore)
 - Across life stages

- Address foundational data gaps necessary for ecosystem-based fisheries management

2.2 *Advance Scientific Research*

- Conduct research on:
 - Species distribution and habitat use
 - Reproduction, recruitment, growth, and survival
 - Predator–prey interactions
 - Species vulnerability to environmental variability
- Characterize offshore habitats used by estuarine-dependent species
- Improve understanding of:
 - Climate variability impacts on ecosystem productivity
 - Trophic interactions and energy pathways
 - Shifts in species distributions and behavior

2.3 *Advance Ecosystem Modeling and Assessment*

- Update and refine ecosystem models (e.g., Ecopath with Ecosim) with new data
- Integrate:
 - Physical oceanographic data
 - Biological and trophic datasets
 - Fisheries information
- Use models to:
 - Evaluate management scenarios
 - Assess climate impacts
 - Analyze multispecies tradeoffs
- Link ecosystem models to management strategy evaluations (MSEs):
 - Incorporate ecological, economic, socio-cultural, and habitat considerations

2.4 *Integrate Ecosystem Information into Management*

- Incorporate ecosystem-derived parameters into stock assessments where feasible
- Apply food web indicators to:
 - Track ecosystem condition
 - Inform management decisions
- Use ecosystem models to evaluate:
 - Tradeoffs among management strategies
 - Multi-species and ecosystem-based policies
- Develop ecosystem-level reference points (ELRPs) and thresholds:
 - Identify ecosystem limits and emergent properties
 - Inform statutory reference points

2.5 *Address Emerging Stressors and Risk*

- Improve understanding of:
 - Climate-driven changes in productivity, behavior, and distributions
 - Effects of ocean warming, acidification, and circulation changes
- Develop and apply:

- Climate Vulnerability Assessments
- Regional Habitat Assessments
- Ecosystem-level risk assessments
- Evaluate species and ecosystem vulnerability:
 - Exposure and sensitivity to environmental stressors
- Continue efforts to:
 - Mitigate invasive species (e.g., lionfish)
 - Improve water quality monitoring and management
 - Address habitat degradation

2.6 Enhance Understanding of Connectivity

- Quantify:
 - Cross-habitat and cross-shelf linkages
 - Larval transport pathways
 - Migration corridors
- Evaluate the role of connectivity in:
 - Recruitment and population persistence
 - Fisheries productivity
 - Effectiveness of spatial management (e.g., MPAs)

2.7 Habitat Protection and Management (EFH and HAPCs)

- Continue refinement of:
 - Essential Fish Habitat (EFH)
 - Habitat Areas of Particular Concern (HAPCs)
- Recognize that:
 - Impacts to EFH and HAPCs can alter food webs and connectivity
 - Habitat degradation reduces ecosystem resilience and productivity

2.8 Regional Coordination and Strategic Planning

- NOAA and regional partners should:
 - Develop ecosystem-level assessment products
 - Coordinate research, monitoring, and modeling efforts
- Promote a systems-based approach to:
 - Identify overarching risks (e.g., climate change, sea level rise, circulation shifts)
 - Prioritize management and scientific needs across:
 - Habitats
 - Species and taxa
 - Ecosystem functions
 - Fisheries and dependent communities

Table 1. Habitats designated as Essential Fish Habitat (EFH), their associated managed fisheries/species, and EFH-HAPCs (Source: SAFMC EFH Users Guide 2024).

Essential Fish Habitat	Fisheries/Species	EFH- Habitat Areas of Particular Concern
<i>Wetlands</i>		
Estuarine and marine emergent wetlands	Shrimp, Snapper Grouper	Shrimp: State-designated nursery habitats; Mangrove wetlands
Tidal palustrine forested wetlands	Shrimp	State-designated nursery habitats
<i>Submerged Aquatic Vegetation</i>		
Estuarine and marine submerged aquatic vegetation	Shrimp, Snapper Grouper, Spiny lobster	Snapper Grouper; Shrimp; Spiny lobster
<i>Shell bottom</i>		
Oyster reefs and shell banks	Shrimp, Snapper Grouper	Oyster reefs (all); Shell banks (all)
<i>Coral and Hardbottom</i>		
Coral reefs, live/hardbottom, medium to high profile outcroppings from shore to at least 200 m (656 ft), where annual temperature range supports coral growth	Snapper Grouper, Spiny lobster, Coral, Coral Reefs and Live/Hardbottom Habitat	The Point; Ten Fathom Ledge; Big Rock; MPAs; Phragmatopoma (worm reefs); Nearshore hardbottom (FL east coast); Coral/hardbottom from Jupiter to Dry Tortugas; Deepwater Coral HAPCs
Rock overhangs, rock outcrops, manganese-phosphorite rock slab formations, and rocky reefs	Snapper Grouper (incl. blueline tilefish)	Associated with Deepwater Coral HAPCs
Artificial reefs	Snapper Grouper	Special Management Zones (SMZs)
<i>Soft bottom</i>		
Subtidal, intertidal non-vegetated flats	Shrimp	State-designated nursery habitats
Offshore marine habitats used for spawning and growth to maturity	Shrimp	
Sandy shoals of capes and offshore bars	Coastal Migratory Pelagics	Sandy shoals; Cape Lookout, Cape Fear, Cape Hatteras (NC); Hurl Rocks (SC)
Troughs and terraces intermingled with sand, mud, or shell hash at depths of 150–300 m	Snapper Grouper (incl. golden tilefish)	Golden tilefish HAPC
<i>Water column</i>		
Ocean-side waters from surf to shelf break, including Sargassum	Coastal Migratory Pelagics, Dolphin Wahoo	Pelagic Sargassum
All coastal inlets	Coastal Migratory Pelagics	Shrimp; Snapper Grouper
All state-designated nursery habitats of particular importance (e.g., PNA, SNA)	Coastal Migratory Pelagics	Shrimp; Snapper Grouper
High salinity bays and estuaries	Coastal Migratory Pelagics (incl. cobia, Spanish mackerel)	Spanish mackerel: Bogue Sound, New River (NC); Broad River (SC)
Pelagic Sargassum	Dolphin Wahoo	Pelagic Sargassum
Gulf Stream	Shrimp, Snapper Grouper, Coastal Migratory Pelagics, Spiny lobster, Dolphin Wahoo	Gulf Stream frontal zones
Spawning area in water column above adult habitat and associated pelagic environment	Snapper Grouper	Snapper Grouper spawning locations

3. Work Cited

- Carpenter, S.R., Kitchell, J F, Hodgson, J R. Bioscience 35.10 (1985): 634-639.
Cascading trophic interactions and lake productivity. Bioscience 35(10): 634- 639.
- Coll, M; Santojanni, A; Arneri, E; Palomera, I. 2006. An ecosystem model of the Northern and Central Adriatic Sea: analysis of ecosystem structure and fishing impacts. *Biologia marina mediterranea* 13.1: 467-471.
- Hyslop, E.J. 1980. Stomach content analysis-a review of methods and their application. *Journal of Fish Biology*. 17:411-429.
- Fulton, E., Fuller, M., Smith, A. and Punt, A. 2004. Ecological indicators of the ecosystem effects of fishing: final report. Australian Fisheries Management Authority Report R99/1546, pp. 116.
- Okey, T. A., A. M. Cisneros-Montemayor, R. Pugliese, and R. U. Sumaila. 2014. Exploring the trophodynamic signature of forage species in the U.S. South Atlantic Bight ecosystem. Fisheries Centre Working Paper 2014-14, University of British Columbia Fisheries Centre, Vancouver, Canada.
- SAFMC. 1998a. [Final Habitat Plan for the South Atlantic region: Essential Fish Habitat requirements for fishery management plans of the South Atlantic Fishery Management Council](#). South Atlantic Fishery Management Council, 1 Southpark Cir., Ste 306, Charleston, SC 29407-4699. 457 pp. plus appendices.
- SAFMC. 1998b. [Final Comprehensive Amendment Addressing Essential Fish Habitat in Fishery Management Plans of the South Atlantic Region. Including a Final Environmental Impact Statement/Supplemental Environmental Impact Statement, Initial Regulatory Flexibility Analysis, Regulatory Impact Review, and Social Impact Assessment/Fishery Impact Statement](#). South Atlantic Fishery Management Council, 1 Southpark Cir., Ste 306, Charleston, SC 29407-4699. 136pp.
- SAFMC (South Atlantic Fishery Management Council). 2009a. [Fishery Ecosystem Plan of the South Atlantic Region](#). South Atlantic Fishery Management Council, 4055 Faber Place Drive, Ste 201, North Charleston, SC 29405.
- SAFMC (South Atlantic Fishery Management Council). 2009b. [Comprehensive Ecosystem-Based Amendment 1 for the South Atlantic Region](#). South Atlantic Fishery Management Council, 4055 Faber Place Drive, Suite 201; North Charleston, SC 29405.
- SAFMC (South Atlantic Fishery Management Council). 2011. [Comprehensive Ecosystem-Based Amendment 2 for the South Atlantic Region](#). South Atlantic Fishery Management Council, 4055 Faber Place Drive, Suite 201; North Charleston, SC 29405.
- SAFMC (South Atlantic Fishery Management Council). 2018. [Fishery Ecosystem Plan II of the South Atlantic Region](#). South Atlantic Fishery Management Council, 4055 Faber Place Drive, Ste 201, North Charleston, SC 29405.
- SAFMC (South Atlantic Fishery Management Council). 2022. Ecosystem Model of

Intermediate Complexity for Snapper Grouper Complex. South Atlantic Fishery Management Council, 4055 Faber Place Drive, Ste 201, North Charleston, SC 29405.

SAFMC (South Atlantic Fishery Management Council). 2023. [South Atlantic Fishery Management Council Habitat Program Evaluation and Blueprint](#). South Atlantic Fishery Management Council, 4055 Faber Place Drive, Ste 201, North Charleston, SC 29405.

SAFMC (South Atlantic Fishery Management Council). 2024. [Users Guide to Essential Fish Habitat Designations by the South Atlantic Fishery Management Council](#). South Atlantic Fishery Management Council, 4055 Faber Place Drive, Ste 201, North Charleston, SC 29405.

Walters, Carl J et al.,2005, Possible ecosystem impacts of applying MSY policies from single-species assessment, ICES Journal of Marine Science, Volume 62, Issue 3, 2005, Pages 558–568, <https://doi.org/10.1016/j.icesjms.2004.12.005>

Walters and Mortell 2004. Fisheries Ecology And Management, Princeton University Press, Princeton, NJ 2004, ISBN 0-691-11545-1Paperback, 423 pp.

4. References

Andrews, S.N. et al. 2019. Consumption of Atlantic Salmon Smolt by Striped Bass: A Review of the Predator-Prey Encounter Literature and Implications for the Design of Effective Sampling Strategies. *Fishes* 2019, 4, 50; doi:10.3390/fishes4040050

Austin, Riley S. 2022. Age, Growth, Foraging, and Trophic Ecology of Bigeye (*Thunnus obesus*) and Yellowfin (*Thunnus albacares*) Tuna in Continental Shelf and Slope Regions of the Northeast U.S. MS Thesis, University of Maine. Electronic Theses and Dissertations. 3556.

Buchheister, A. et al. 2016. Spatial and temporal dynamics of Atlantic menhaden (*Brevoortia tyrannus*) recruitment in the Northwest Atlantic Ocean. *ICES Journal of Marine Science* (2016), 73(4), 1147– 1159. doi:10.1093/icesjms/fsv260

Grezzlik, m.t. 2021. Evaluating the effects of Atlantic menhaden management and environmental change on the northwest Atlantic ocean ecosystem. Ms thesis, Humboldt state university. 91 pp.

Krumsick, K.J. 2020. Trophic and size spectra modeling reveal key species interactions and quantify community recovery dynamics within newfoundland and labrador fisheries ecosystems. PhD dissertation, Memorial University of Newfoundland. 250 pp.

Krumsick, K.J. and J.A.D. Fisher. 2022. Spatial variation in food web structure in a recovering marine ecosystem. *PLoS ONE* 17(5): e0268440. <https://doi.org/10.1371/journal.pone.0268440>

Luckhurst, B.E. 2018. A preliminary assessment of the ecological role and importance of squid in the pelagic trophic web of the northwest atlantic ocean including the sargasso sea. *Collect. Vol. Sci. Pap. Iccat*, 74(7): 3679-3691.

Murphy, KJ, GT Pecl, JD Everett, RF Heneghan, SA Richards, AJ Richardson, JM Semmens

- and JL Blanchard. 2023 Improving the biological realism of predator–prey size relationships in food web models alters ecosystem dynamics. *Biol. Lett.* 19: 20230142. <https://doi.org/10.1098/rsbl.2023.0142>
- Nadeau, S. 2021. Evaluating the Foraging Ecology and Energetics of Atlantic Bluefin Tuna (*Thunnus thynnus*) in the Gulf of Maine. MS Thesis, University of Maine. 155 pp. Electronic Theses and Dissertations. 3534. <https://digitalcommons.library.umaine.edu/etd/3534>
- Staudinger, M.D., et al. 2020. The role of sand lances (*Ammodytes* sp.) in the Northwest Atlantic Ecosystem: A synthesis of current knowledge with implications for conservation and management. *Fish and Fisheries* 21:522–556. DOI: 10.1111/faf.12445
- Strom, J.F., et al. 2019. Ocean predation and mortality of adult Atlantic salmon. *Nature: Scientific Reports* | (2019) 9:7890 | <https://doi.org/10.1038/s41598-019-44041-5>
- Turcotte, F. et al. 2023. Atlantic bluefin tuna diet variability in the southern Gulf of St. Lawrence, Canada. *Marine Environmental Research* 187 (2023) 105949.
- United States, National Oceanic and Atmospheric Administration. "NOAA fisheries glossary" , 2005
- Varela, J.W., et al. 2020. Feeding ecology of Atlantic bluefin tuna (*Thunnus thynnus*) in the Gulf of Saint Lawrence, Canada. *Marine Environmental Research* Volume 161, October 2020, 105087. <https://doi.org/10.1016/j.marenvres.2020.105087>
- Wuenschel, Mark J., et al. 2024. Variation in energy density of northwest Atlantic forage species: Ontogenetic, seasonal, annual, and spatial patterns. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*. 2024;16:e10287. DOI: 10.1002/mcf2.10287

Appendix A. Top ten prey Items by FMP

Below are the results of one method used to determine the top ten prey items of the predator species in each SAFMC Fishery Management Plan (FMP). The “Average %” value was calculated by the percent of each prey item in the FMP’s species’ diets averaged across all diets available for the species included in the FMP. For the Coastal Migratory Pelagic, Dolphin Wahoo, and Snapper grouper FMPs the top ten species for only fish prey was also calculated. These diets were primarily calculated from adult diet information and juvenile information was integrated in when possible. Due to the variety of data sources the only species with available adult and juvenile specific diet information are Red Snapper, King Mackerel, and Spanish Mackerel.

Top 10 Prey Items: Coastal Migratory Pelagic FMP			
If in diet, what's the average % that this prey makes up of the diet?			
All prey	Average %	Fish prey	Average %
Anchovies	15.81	Anchovies	15.81
Herrings	15.23	Herrings	15.23
Mega-invertebrate predators	11.59	Sardines	10.49
Sardines	10.49	Shad	6.82
Shad	6.82	Halfbeaks	6.48
Halfbeaks	6.48	Scads	5.98
Scads	5.98	Benthic coastal invertivores	3.33
Benthic coastal invertivores	3.33	Demersal coastal invertivores	2.63
Rock shrimps	2.851	Pelagic coastal piscivores	2.40
Demersal coastal invertivores	2.63	Pelagic planktivores	1.91
Total % out of diet	81.2	Total % out of fish only diet	71.1

Dolphin Wahoo FMP			
If in diet, what's the average % that this prey makes up of the diet?			
All prey	Average %	Fish prey	Average %
Sardines	15.06	Sardines	15.06
Pelagic oceanic piscivores	14.31	Pelagic oceanic piscivores	14.31
Auxis mackerels	9.30	Auxis mackerels	9.30
Squids	8.65	Dolphinfish	6.88
Dolphinfish	6.88	Anchovies	6.25
Anchovies	6.25	Herrings	4.77
Mega-invertebrate predators	5.40	Demersal coastal omnivores	4.53
Herrings	4.77	Pelagic coastal piscivores	3.93
Demersal coastal omnivores	4.53	Blue runner	2.57
Penaeid shrimps	4.33	Pelagic planktivores	2.25
Total % out of diet	79.5	Total % out of fish only diet	69.9

Snapper Grouper FMP			
If in diet, what's the average % that this prey makes up of the diet?			
All prey	Average %	Fish prey	Average %
Mega-invertebrate predators	15.85	Benthic coastal invertivores	6.77
Benthic coastal invertivores	6.77	Demersal coastal omnivores	5.18
Echinoderms and gastropods	5.84	Herrings	4.87
Encrusting fauna	5.41	Other grunts	4.77
Squids	5.24	Benthic oceanic invertivores	3.13
Demersal coastal omnivores	5.18	Demersal coastal invertivores	1.65
Herrings	4.87	Benthic coastal piscivores	1.61
Other grunts	4.77	Scads	1.40
Bivalves/Oysters	3.32	Demersal coastal piscivores	1.18
Benthic oceanic invertivores	3.13	Other sciaenids	1.12
Total % out of diet	60.4	Total % out of fish only diet	31.7

Golden Crab FMP			
If in diet, what's the average % that this prey makes up of the diet?			
All prey	Average %	Fish prey	Average %
Bivalves/Oysters	30.3		
Dead carcasses	19.6		
Offshore infaunal crustaceans	11.4		
Offshore benthic detritus	9.09		
Octopods	9.01		
Benthic oceanic invertivores	5		
Echinoderms and gastropods	4.81		
Mega-invertebrate predators	3.36		
Squids	2.44		
Penaeid shrimps	2.44		
Total % out of diet	97.4		

Shrimp FMP			
If in diet, what's the average % that this prey makes up of the diet?			
All prey	Average %	Fish prey	Average %
Small mobile epifauna	21.95		
Mega-invertebrate predators	10		
Deep-burrowing infauna	9.79		
Bivalves/Oysters	9.75		
Offshore polychaetes	7.70		
Encrusting fauna	7.60		
Echinoderms and gastropods	6.80		
Estuarine benthic detritus	5.35		
Offshore benthic detritus	5.35		
Microphytobenthos	4.99		
Total % out of diet	89.3		

Spiny Lobster FMP			
If in diet, what's the average % that this prey makes up of the diet?			
All prey	Average %	Fish prey	Average %
Mega-invertebrate predators	20		
Offshore infaunal crustaceans	20		
Encrusting fauna	16		
Echinoderms and gastropods	10		
Bivalves/Oysters	10		
Offshore polychaetes	10		
Microbial heterotrophs	5		
Benthic macroalgae	5		
Carnivorous zooplankton	2		
Other zooplankton	2		
Total % out of diet	100		

Acknowledgement: Many thanks to FWC-FWRI and Lauren Gentry for helping update the language, providing the graphs and conducting analysis to help inform the HEAP's Food web Policy.

Appendix B: Tables cross referencing the policies and their associated management and indicator relevance

Table B1: Crosswalk of Policies to associated Appendix C Sections their key ecological concepts and their management relevance

Policy	Associated Appendix C Sections	Key Ecological Concept	Management Relevance
Forage Fisheries	1; 2.2; 2.3; 2.4; 4.2; 5.1; 5.2; 6	Forage species link primary production to predators	Incorporate forage dynamics into catch limits and assessments
Prey Importance	2.4; 3; 4.1; 4.3; 5.1; 5.3	Prey availability drives predator productivity	Use multiple diet metrics; identify key prey
Food Web Indicators	4.3; 5.3	Indicators track ecosystem structure and change	Use indicator portfolios for management
Food Web Connectivity	1; 2.3; 3, 4.1; 6	Energy transfer across habitats via species movement	Protect connectivity and EFH linkages
Trophic Pathways	2; 4.1; 4.2; 6.1	Top-down and bottom-up processes regulate ecosystems	Maintain pathway diversity for resilience
Food Web Models	2.4, 4; 5	Models simulate trophic interactions and tradeoffs	Use models to evaluate policy scenarios
Ecosystem Component Species	2.4; 4.2; 5.2; 6	Non-target species have key ecological roles	Include in ecosystem analyses
Invasive Species	2.2; 3; 4.2, 6.4	Invasive species alter trophic dynamics	Account for impacts in management
Contaminants	2.2, 6.2	Bioaccumulation affects higher trophic levels	Evaluate impacts on food webs and seafood safety

Table B2: Crosswalk of Policies to ecosystem Indicator, indicator purpose, and data required for indicator use

Policy	Relevant Indicators	Indicator Purpose	Data Requirements for Indicator
Forage Fisheries	Biomass of small pelagics; trophic level	Track energy availability to predators	Survey biomass, catch, diet
Prey Importance	Diet diversity; trophic overlap	Identify key prey roles	Diet studies
Food Web Indicators	LFI; trophic level; transfer efficiency	Assess ecosystem status	Survey biomass, models
Food Web Connectivity	Mean trophic links; connectivity indices	Measure ecosystem linkages	Diet + movement data
Trophic Pathways	Primary production; pelagic/demersal ratio	Track energy flow structure	Remote sensing, surveys
Food Web Models	Model-derived indicators	Evaluate ecosystem scenarios	Integrated datasets
Ecosystem Component Species	Guild production; functional diversity	Assess ecological roles	Survey + diet data
Invasive Species	Prey biomass; predator ratios	Detect ecosystem disruption	Survey + diet data
Contaminants	Contaminant levels; trophic magnification	Assess bioaccumulation	Tissue sampling

Appendix C: Fishery Ecosystem Plan 2

1. South Atlantic Food Web Dynamics, Description and Drivers of South Atlantic Food Webs

South Atlantic food webs span estuarine, nearshore, and offshore habitats and include diverse assemblages of flora and fauna linked through complex trophic interactions. Detailed habitat descriptions, including associated biological communities and food webs, are provided in the Fishery Ecosystem Plan II (pages 12–14).

Many species in the South Atlantic ecosystem exhibit complex life histories that involve shifts among habitats throughout their life cycles. These ontogenetic habitat transitions connect multiple food webs and facilitate the transfer of energy across ecosystem boundaries. Additionally, several diadromous species that are listed as threatened or endangered are temporary seasonal components of these food webs, including American eel and Atlantic sturgeon, which utilize estuarine and coastal habitats during key life stages.

Other species demonstrate pronounced life-stage habitat shifts that link ecosystems. For example, gag grouper are offshore piscivores as adults, while juveniles depend on estuarine nursery habitats such as oyster reefs and seagrass beds (Casey et al. 2007). Similarly, round scad exhibit spatial partitioning across life stages, with adults occupying inner and outer continental shelf habitats and juveniles occurring primarily on the mid-shelf (Hales 1987). Mangrove and marsh habitats are also critical nursery areas that support many commercially and ecologically important species and contribute significantly to regional fish production (Kimirei et al. 2011).

Species interactions within these food webs are shaped by trophic dynamics and ecosystem structure. Marine ecosystems may be particularly sensitive to perturbations such as overfishing because trophic pathways are often shorter than in other ecosystem types, allowing impacts to propagate rapidly through the food web (Dunne et al. 2004). At the same time, ecosystems with high biodiversity and complex trophic interactions may exhibit greater resilience due to functional redundancy (Martinez 1993, 1994; Saporiti et al. 2014). In the South Atlantic Bight, the standing biomass of ecologically and economically important species is relatively low compared to other U.S. marine ecosystems, likely reflecting regional oceanographic processes that lead to limitations in nutrient availability and primary productivity (Gomez et al. 2026).

Emerging ecosystem stressors may further influence food-web structure and function. Invasive species, in particular, represent a growing concern. For example, Lionfish (*Pterois* spp.) have been shown to reduce recruitment of native reef fishes and compete with native species for habitat and prey resources (Barbour et al. 2010; Albins and Hixon 2013) and the porcelain crab (*Petrolisthes armatus*), may alter predator–prey dynamics in coastal ecosystems (Hollebone and Hay 2008). Ocean acidification caused by warming waters, increased atmospheric carbon dioxide, and coastal runoff in the South Atlantic can also negatively affect calcifying organisms and larval stages of many species which may have cascading effects throughout food webs (Hall et al. 2020).

Despite advances in ecosystem research, important data gaps remain. Knowledge of South Atlantic food webs is limited for many offshore and pelagic species that are not primary fishery targets, and some trophic linkages may therefore be underrepresented in current ecosystem descriptions. Forage species are believed to play a central role in linking primary consumers to larger predators such as snappers and groupers (Sedberry 1985), and these relationships are increasingly being quantified through ecosystem modeling efforts such as the South Atlantic Bight Ecopath model (Okey et al. 2014).

2. Energy Pathways

2.1 Basal Food Web Resources

Marine and estuarine food webs derive carbon and energy from a range of basal resources, including detritus, salt marsh vegetation, seagrasses, phytoplankton, macrophytes, and filamentous algae. The relative importance of these sources varies spatially along the inshore–offshore gradient and temporally with seasonal shifts in primary production.

In estuarine systems, such as Sapelo Island, Georgia, *Spartina* detritus, phytoplankton, and benthic diatoms dominate organic matter inputs supporting secondary production, whereas offshore systems rely primarily on phytoplankton-derived carbon with minimal terrestrial influence. Seagrass habitats can also provide important localized carbon sources.

Stable isotope analysis (e.g., $\delta^{13}\text{C}$) is widely used to trace carbon flow through food webs, linking consumer biomass to primary production sources and enabling evaluation of community-level trophic structure.

2.2 Top-Down and Bottom-Up Controls

Food web dynamics are governed by interacting bottom-up (environmental) and top-down (consumer-driven) processes that vary across space, time, and trophic levels.

Bottom-up control reflects variability in primary production and resource availability driven by nutrient inputs, water quality, climate oscillations (e.g., ENSO, AMO), and oceanographic circulation. In such systems, prey availability strongly influences predator growth, survival, and reproduction (Rogers, 2024).

Top-down control arises from predation and fishing pressure. Overexploitation of predators can trigger trophic cascades, altering prey abundance and restructuring communities (Surma, 2025). Similarly, invasive species may exert strong predatory or competitive pressures. Feedbacks between trophic levels can also produce recruitment limitations (e.g., compensatory dynamics) that delay stock recovery.

In most marine ecosystems, these controls are tightly coupled rather than independent. Their relative influence depends on ecosystem productivity, fishing intensity, trophic structure, and environmental conditions. For example, highly productive upwelling systems tend to be bottom-up driven, whereas lower productivity systems are often more influenced by fishing pressure.

2.3 Energy Pathways and Food Web Stability

Energy flows through marine food webs via interconnected pelagic (“fast”) and benthic (“slow”) pathways, distinguished by differences in turnover rates and energy flux. Pelagic systems, driven by phytoplankton, exhibit rapid production and turnover, while benthic systems, based on detrital pathways, provide slower but more stable energy sources.

Stability is enhanced when consumers integrate energy from both pathways. Asynchronous and asymmetric coupling between fast and slow channels buffers ecosystems against perturbations and supports more stable recovery dynamics.

Disruptions to this balance—such as predator removal or nutrient enrichment—can destabilize food webs by decoupling pathways or synchronizing production, reducing resilience. Maintaining diversity in energy pathways is therefore critical for sustaining ecosystem stability and function.

2.4 Dominant Energy Pathways and Emerging Trends

Energy transfer from lower to higher trophic levels is strongly mediated by forage species, which serve as critical links between primary producers and top predators. In the South Atlantic, key forage groups include small pelagic fishes (e.g., sardines, anchovies, menhaden), as well as shrimp and other mid-trophic organisms (Chee 2024). These species underpin the productivity of commercially and recreationally important predators such as snapper, grouper, mackerel, tuna, and billfish, as well as marine mammals, seabirds, and sharks.

Forage species are characterized by rapid growth, high reproductive output, and short life spans, allowing quick population responses to favorable conditions. However, these same traits—combined with schooling behavior—make them highly susceptible to environmental variability and overfishing.

Emerging evidence highlights several management-relevant trends affecting energy pathways:

- Environmental change, shifting species composition, and fishing pressure are altering trophic linkages and may restructure energy flow.
- Data limitations, particularly for offshore and pelagic systems, suggest current models may underestimate key trophic interactions.

Sustaining ecosystem function requires explicitly accounting for forage species’ roles in food webs. This includes improved monitoring of forage abundance, incorporation into stock assessments and ecosystem models, and evaluation of predator-prey dynamics to better capture ecosystem-level tradeoffs.

Maintaining the integrity of energy pathways—and the connectivity between forage populations, predators, and environmental drivers—is essential for supporting resilient and productive South Atlantic marine ecosystems.

3. Connectivity among Food Webs

South Atlantic ecosystems consist of interconnected food webs spanning estuarine, nearshore, offshore, benthic, and pelagic environments. Movements of organisms across these habitats transfer energy and nutrients, linking distinct ecosystem components. Many species—particularly reef fishes—use different habitats across life stages, with estuarine or coastal nurseries supporting juveniles and offshore habitats supporting adults. As a result, disturbances such as habitat degradation, climate change, or fishing pressure in one area can propagate across the broader ecosystem.

Fish movements—daily, seasonal, and ontogenetic—are largely driven by foraging optimization, predator avoidance, and reproductive requirements. These movements connect feeding, spawning, and refuge habitats, which may differ substantially (e.g., reef vs. sand bottom, seagrass vs. water column). Mobile invertebrate feeders, including grunts, porgies, and snappers, are particularly important in the South Atlantic, linking habitats through their foraging on benthic prey and serving as prey for higher trophic levels. These interactions redistribute energy across habitats and trophic levels, effectively coupling otherwise distinct food webs (Ward et al., 2025).

Ontogenetic habitat shifts further strengthen connectivity (Mumby, 2006). Many species transition from spawning areas to productive nursery habitats and later move to adult habitats with higher-energy prey resources. These movements transfer biomass and energy across estuarine, coastal, and offshore systems, creating trophic subsidies that enhance ecosystem productivity (Preston et al., 2025). Environmental variability—including temperature, ocean chemistry, and prey availability—can alter these movement patterns and associated energy transfers, with implications for growth, survival, and trophic dynamics (Hyman et al., 2026).

3.1 Benthic–Pelagic Coupling

Benthic and pelagic systems are tightly linked through trophic interactions and physical processes that transfer energy between the water column and seafloor (Walters et al., 2025). Pelagic predators can concentrate forage fishes near reef structures, increasing their availability to demersal predators and linking midwater and benthic food webs (Auster et al., 2009).

Demersal species also directly consume pelagic prey, while many species undergo ontogenetic shifts between pelagic and benthic feeding strategies. For example, juvenile stages of species such as tomtate initially feed on plankton before transitioning to benthic prey, thereby transferring pelagic production to reef systems. Similarly, species like Vermilion Snapper feed on plankton advected onto the shelf, linking oceanic productivity to reef communities.

Physical processes such as advection and biologically mediated processes like diel vertical migration further enhance these connections by delivering planktonic prey to benthic habitats. Habitat complexity (e.g., hard-bottom reefs) supports higher biomass and diversity partly due to these trophic linkages (Gomes et al., 2024).

Emerging research highlights that variability in plankton distribution—potentially influenced by climate change—can affect foraging success and spatial dynamics of species reliant on pelagic

prey (Zhulay et al., 2023). Improved observation tools (e.g., acoustic surveys) and better characterization of prey fields are needed to refine understanding of these linkages and their implications for fisheries.

3.2 Inshore–Offshore Connections

Cross-shelf connectivity is fundamental to the life histories of many South Atlantic species. Reef fishes often migrate to specific offshore spawning sites, with larvae transported to inshore or estuarine nursery habitats via oceanographic processes. Species such as gag grouper depend on this connectivity, utilizing estuaries as juveniles before migrating offshore and returning to spawn (Keener et al, 1988).

These linkages rely on alignment between spawning behavior and ocean circulation patterns to ensure successful larval transport and settlement. Disruptions to circulation, habitat quality, or timing (e.g., due to climate variability) may reduce recruitment success (Gokturk et al., 2022).

Marine protected areas (MPAs) across estuarine, shelf, and shelf-edge habitats can function as an interconnected network when linked by larval dispersal and adult movement. Maintaining these connections is critical for sustaining populations and maximizing the ecological benefits of spatial management (Blouet et al., 2025).

3.3 Latitudinal Connections

Large-scale ocean circulation, particularly the Florida Current and Gulf Stream, facilitates long-distance transport of larvae and plankton, connecting ecosystems across the southeaster201n U.S. and beyond. Eddies and inshore transport processes promote both retention and delivery of larvae to suitable nursery habitats (Sponaugle et al., 2005, Shulzitski et al., 2016).

In addition to passive drift, many species undertake active alongshore migrations related to spawning, temperature preferences, and prey availability. Species such as king mackerel, cobia, and greater amberjack exhibit extensive seasonal movements that connect regions from the Carolinas to Florida, the Gulf of Mexico, and the Caribbean (Shepard et al., 2010; Lowerre-Barbieri et al., 2021) .

These connections also link MPAs and fishing grounds across broad spatial scales. However, geographic features such as the narrow continental shelf off Florida can concentrate both fish and fishing effort, increasing vulnerability to exploitation. Climate-driven changes in ocean circulation and temperature regimes may further alter larval transport pathways and migration patterns (Kendall et al., 2016; Young et al., 2018).

3.4 Seasonal Connectivity

Seasonal variability in oceanographic conditions drives changes in larval transport, plankton productivity, and species distributions. Cross-shelf transport of larvae varies seasonally, with features such as the Charleston Gyre enhancing connectivity between offshore spawning areas and inshore nursery habitats, particularly in winter (Sedberry et al., 2001).

Seasonal pulses in plankton and benthic invertebrate production provide critical food resources that support fish growth and reproduction, often aligning with spawning periods. Variability in these seasonal dynamics can influence recruitment success and population structure (Barth et al., 2007; Cecchetto et al., 2024).

Climate change is expected to modify these seasonal patterns by altering temperature regimes, productivity cycles, and circulation processes. Experimental studies indicate that elevated temperature and CO₂ levels can reduce foraging efficiency and increase energetic stress in juvenile fishes, potentially affecting survival and recruitment (Nowicki et al., 2012; Dye et al., 2026).

3.5 Integrated Considerations for Connectivity (Emerging Insights)

Connectivity among food webs in the South Atlantic is shaped by the interaction of species movements, habitat distribution, and oceanographic processes. Emerging evidence suggests that:

- Climate change and ocean acidification may alter foraging behavior, habitat use, and survival, particularly for early life stages.
- Variability in prey fields (planktonic and benthic) is a key but understudied driver of connectivity and energy transfer.
- Current data limitations—especially for offshore, pelagic, and prey communities—constrain the ability to fully characterize ecosystem linkages.

Addressing these gaps will require expanded monitoring of prey availability, improved integration of predator-prey dynamics into ecosystem models, and application of advanced technologies (e.g., acoustic surveys, fine-scale tracking).

A more comprehensive understanding of connectivity is essential for effective fisheries management, as it underpins species productivity, spatial management effectiveness, and ecosystem resilience.

4. Food Web Models

4.1 Models and Principles

Marine food webs, particularly in spatially complex subtropical systems, are challenging to characterize due to the large number of interacting species, diverse habitats, and variable environmental conditions. Ecosystem models provide a structured way to represent these interactions, quantify energy flow, and explore ecosystem responses to fishing, environmental variability, and management actions.

A range of modeling approaches is commonly used in marine ecology, differing in complexity, scale, and emphasis:

- **Species Distribution Models (SDMs)** relate species occurrence or abundance to environmental conditions to predict spatial distributions. These models are widely

used for habitat characterization and climate-related analyses but generally do not explicitly represent trophic interactions or population dynamics.

- **Foraging-based models** incorporate principles from behavioral ecology to describe how organisms balance energy intake, predation risk, habitat quality, and prey availability. While they can link space use to trophic interactions, these approaches rely on assumptions about optimal behavior and are difficult to parameterize for complex, multispecies systems.
- **Individual- and agent-based models**, such as OSMOSE and InVitro, simulate interactions among individual organisms and allow ecosystem patterns to emerge from these processes. These models provide strong mechanistic detail but are data- and computationally intensive, limiting their application at large spatial scales.
- At broader ecosystem scales, **trophodynamic ecosystem models** integrate species interactions, energy flow, and human impacts within a single framework.
 - **Ecopath with Ecosim (EwE)** combines a mass-balanced representation of trophic structure with time-dynamic and spatially explicit simulations. EwE has been widely applied to examine ecosystem structure, fisheries impacts, and tradeoffs among management scenarios.
 - **Atlantis** is a more complex end-to-end modeling framework that integrates trophic dynamics with physical and biogeochemical processes. Although powerful, its data and development requirements can limit routine application.

All modeling approaches involve tradeoffs among realism, data availability, computational demands, and uncertainty. Increasing complexity can improve process representation but often reduces transparency and operational flexibility. Model choice should therefore align with study objectives, available data, and the spatial and temporal scales of interest.

4.2 Case Studies

South Atlantic Ecosystem Modeling

South Atlantic Region (SAR) EwE Model: High Complexity

The South Atlantic Region (SAR) Ecopath with Ecosim (EwE) model represents the U.S. South Atlantic ecosystem from Cape Hatteras to southern Florida, spanning estuaries to the outer continental shelf and upper slope. Developed in the early 2000s to support ecosystem-based management for the Council, the model has undergone extensive refinement. The current iteration includes ~140 functional groups and has been reviewed and endorsed by the Scientific and Statistical Committee (SSC). Because of its size and complexity, the SAR model now primarily serves as a comprehensive data repository and reference system.

Key findings and applications of the SAR model include:

- Characterization of trophic structure and energy flow across the South Atlantic shelf ecosystem.
- Identification of forage species as key mediators of energy transfer to higher trophic levels.
- Evidence that relatively small changes in forage biomass can drive disproportionate ecosystem responses.
- Red snapper recruitment scenario analyses showing that sustained increases in red snapper biomass are likely to result in only modest reductions in biomass of co-occurring reef fish species (e.g., black sea bass, greater amberjack, red porgy, and some grouper age stanzas).

South Atlantic Reef Fish (SARF) EwE Model – Intermediate-Complexity

The South Atlantic Reef Fish (SARF) EwE model is a model of intermediate complexity (MICE) derived from the SAR model to address targeted ecological and management questions. The SARF model includes 41 functional groups, with an emphasis on snapper–grouper species. It has been refined through workshops and review by the SAFMC SSC Model Workgroup using the most recent stock assessment, diet, and fisheries data.

The SARF model has been expanded with an Ecospace module to incorporate spatial processes such as habitat distribution, environmental drivers, fishing effort, and species movement.

Key findings and current uses of the SARF model include:

- Reproduction of key trophic dynamics and ecosystem responses observed in the high-complexity SAR model.
- Re-evaluation of red snapper recruitment scenarios yielding ecosystem effects of similar magnitude and direction as earlier SAR analyses.
- Ongoing spatial analyses to evaluate drivers of shifting black sea bass distributions, including habitat change, productivity, competition, and predator–prey interactions.
- Development of a flexible tool for testing climate, spatial management, and species-specific hypotheses relevant to reef fish management.

Together, the SAR and SARF models form a complementary ecosystem modeling framework for the South Atlantic, with the SAR model providing a data-rich ecosystem foundation and the SARF model enabling focused, spatially explicit, and management-relevant research.

Key Findings of other regional modeling include

- Rebuilding predator populations (e.g., gag grouper) can produce strong top-down effects on prey and competing species.
- Optimal fishery outcomes (balancing biomass and economic returns) occur at higher overall stock levels than historical baselines.
- Invasive lionfish reduce biomass of small fishes and invertebrates and indirectly impact commercially important predators through competition.
- Marine protected areas (MPAs) show limited benefits at small spatial scales (<2% coverage), while larger closures (15–30%) can yield both ecological and economic gains.

4.3 Food Web Indicators

Food web indicators are used to assess ecosystem structure, function, and resilience, and to track responses to fishing and environmental change. These indicators may be:

- **Descriptive** (e.g., species abundance), or
- **Integrative** (e.g., trophic structure, energy transfer efficiency).

No single indicator is sufficient; a portfolio approach is required. Indicators vary in responsiveness, interpretability, and data requirements, with structural indicators generally more readily measurable than resilience metrics.

Common indicator categories include:

- **Energy Flow**
 - Productivity (e.g., production per unit biomass)
 - Primary production required to support fisheries
 - Trophic level indicators
 - Pelagic habitat indices (e.g., chlorophyll fronts)
- **Resilience**
 - Trophic connectivity (links per species)
 - Transfer efficiency
 - Dietary diversity indices
- **Structure**
 - Large fish indicator (LFI)
 - Biomass of small pelagic fish
 - Proportion of predatory species
 - Pelagic-to-demersal ratios

Indicator performance depends on data availability (e.g., diet composition, survey biomass, catch data) and may exhibit nonlinear or lagged responses to ecosystem change. Ongoing efforts (e.g., ICES) emphasize selecting indicators that are measurable, sensitive, theoretically sound, and relevant to management.

Indicator name	Description	Data needs
<i>Indicators Linked to Energy Flow</i>		
Productivity (production per unit biomass, including seabird breeding success)	survival and reproductive output is affected by food quantity and quality; detects gross structural changes in energy flow	nesting surveys, number offspring, pregnancy rates, spawner abundance
Primary production required to support fisheries	characterizes ecosystem production and conversion of organic matter across trophic levels; difficult to communicate; requires estimates of transfer efficiency that are not readily available	food web model
Productive pelagic habitat index (chlorophyll fronts)	chl-a fronts are areas of efficient energy transfer from low trophic levels to top predators; implications for management are unclear	satellite imagery, oceanographic models
Ecosystem exploitation (fisheries)	useful to describe harvesting patterns and pressure of the fisheries on the food web	catch
marine trophic level (TL) indicators	based on average weighted trophic levels across a suit of species; integrated across the ecosystem; most useful for assessing food web effects of fisheries	food habits data, survey time series, catch, TL estimates
<i>Indicators linked to resilience</i>		
Mean trophic links per species	reflects connectivity and stability; dependent on temporal and spatial characteristics; requires comprehensive diet data	food habits data
Ecological Network Analysis derived indicators (mean overall transfer efficiency)	a descriptor of ecosystem health; average TE varies across ecosystem types; requires comprehensive diet data	food web model
Gini-Simpson dietary diversity index	summarizes contributions of prey resources to consumers; requires comprehensive diet data	food habits data
<i>Indicators linked to structure</i>		
Guild surplus production	productivity of functional guilds	survey biomass; catch
Large fish indicator (LFI)	sensitive to fishing pressure	survey biomass
total biomass of small fish	the amount of energy transferred from zooplankton to higher trophic levels is limited by biomass of small pelagic fish	survey biomass
proportion of predatory fish	captures changes in trophic structure and functional diversity of fish due to fishing and environmental pressures	survey biomass, food habits data
pelagic to demersal ratio	describes changes in trophic energy flow and community structure	survey biomass

5. Management Applications

Fisheries management in the South Atlantic has traditionally relied on single-species stock assessments to estimate abundance and set harvest limits, with limited incorporation of food web dynamics, predator–prey interactions, or other ecosystem information. However, ecosystem and food web models can complement this existing framework by improving key inputs, evaluating tradeoffs of management decisions, and providing broader ecosystem considerations into fisheries management.

5.1 Informing Stock Assessment

Stock assessments often assume constant life-history parameters (e.g., natural mortality, growth, recruitment), despite known variability driven by environmental conditions and species interactions. Ecosystem and food web models can help address this gap by:

- Estimating time-varying **natural mortality** linked to predator abundance and prey availability
- Informing **growth and fecundity** responses to environmental and trophic conditions
- Providing ecosystem-based inputs for sensitivity analyses within assessment models

These approaches have precedent (e.g., use of multispecies mortality estimates for Atlantic menhaden and gag grouper) and are becoming increasingly feasible with modern stock assessment model platforms. Incorporating ecosystem-informed parameters can help assessment model platforms more accurately reflect the environment and reduce bias in assessment outputs.

5.2 Evaluating Policy Options

Single-species projections do not account for interactions among managed species or concurrent management actions. Ecosystem models allow managers to:

- Evaluate **multi-species tradeoffs** (e.g., competition, predation, rebuilding conflicts)
- Assess **indirect effects** of harvest policies across the food web
- Incorporate **environmental variability and uncertainty** into management decisions
- Compare outcomes against ecosystem-level reference points (e.g., biomass, productivity)

When calibrated to stock assessment outputs, ecosystem models can serve as complementary tools to test management scenarios and support more integrated decision-making.

5.3 Use of Food Web Indicators

Food web indicators provide efficient, integrative measures of ecosystem condition, capturing changes in energy flow, trophic structure, and resilience that may not be detected in single-species metrics.

While individual indicators are limited, a **portfolio approach** can:

- Track ecosystem responses to fishing and environmental change
- Provide early warning signals of structural shifts
- Support ecosystem-based management without requiring full model implementation

Indicators are particularly useful for summarizing and distilling complex dynamics into metrics that are practical for monitoring and decision-making.

6. Impacts on Food Webs

South Atlantic food webs are influenced by both direct (e.g., fishing) and indirect (e.g., environmental change) stressors. These impacts often interact, altering ecosystem structure, energy flow, and resilience.

6.1 Fishery-Related Impacts

Overfishing and Trophic Cascades

Removal of certain species can alter trophic structure and trigger cascading effects across the food web (Surma, 2025). Impacts depend on the trophic role of the species affected:

- Loss of predators → increases in prey (top-down effects)
- Reduction of forage species → decreased energy to higher trophic levels (bottom-up effects)

These changes can restructure communities and reduce ecosystem stability.

Bycatch

Non-target species mortality affects a wide range of taxa, including protected species and key functional groups. Although [mitigation measures](#) (e.g., turtle excluder devices [TEDs], bycatch reduction devices [BRDs], gear modifications) reduce impacts, bycatch can still alter food web structure and energy pathways.

Habitat Effects of Fishing

Fishing activities can modify benthic habitats (e.g., trawling impacts, gear loss, anchoring), affecting species that depend on these habitats and indirectly altering food web dynamics. Existing gear restrictions help mitigate, but do not eliminate, these effects.

6.2 Water Quality

Nutrients

Excess nutrient inputs can lead to hypoxia, algal blooms, and habitat loss (e.g., seagrass), shifting community composition and disrupting food webs.

Contaminants

Pollutants such as heavy metals and organic compounds can impair reproduction, growth, and survival. Many contaminants bioaccumulate and biomagnify through trophic levels,

disproportionately affecting predators and posing human health risks (e.g., mercury) (Oros, 2025).

Harmful Algal Blooms

Blooms can alter food web structure, reduce habitat quality, and introduce toxins that bioaccumulate through trophic pathways (e.g., ciguatera), affecting both ecosystems and human consumers.

6.3 Habitat Alteration

Loss or degradation of critical habitats (e.g., seagrass, marshes, reefs, oysters) reduces nursery areas, prey availability, and ecosystem productivity. These changes can disrupt trophic linkages and reduce resilience across estuarine, nearshore, and offshore systems.

6.4 Invasive Species

Invasive species can rapidly alter food web structure through predation, competition, and disruption of energy pathways.

The Indo-Pacific lionfish is a primary example in the South Atlantic, exhibiting (del Rio, 2023):

- Broad habitat use and rapid population growth
- High predation rates on native fishes and invertebrates
- Significant reductions in prey biomass and recruitment

Lionfish impacts are exacerbated by lack of natural predators and may be amplified by climate-driven habitat expansion. While eradication is not feasible, targeted removal and protection of native predators may help mitigate impacts.

6.5 Climate Impacts

Climate change is altering environmental conditions and food web dynamics through:

- Increasing temperatures and shifting species distributions
- Ocean acidification affecting calcifying organisms and lower trophic levels
- Changes in productivity, disease prevalence, and habitat availability
- Sea level rise impacting coastal and estuarine habitats

Large-scale climate variability (e.g., AMO) can drive regime shifts that restructure ecosystems. These changes may alter trophic interactions, reduce habitat-forming species, and affect overall ecosystem productivity and resilience.

7. References

- Acker, J.G., and G. Leptoukh. 2007. Online analysis enhances use of NASA earth science data. *Eos, Transactions American Geophysical Union* 88:14–17.
- Albins, M.A. 2013. Effects of invasive Pacific red lionfish on native Atlantic reef fish communities. *Marine Ecology Progress Series* 474:243–252.
- Albins, M.A., and M.A. Hixon. 2008. Invasive Indo-Pacific lionfish (*Pterois volitans*) reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series* 367:233–238.
- Albins, M.A., and M.A. Hixon. 2010. Worst case scenario: potential long-term effects of invasive lionfish on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes* 87:115–122.
- Albins, M.A., and M.A. Hixon. 2013. Worst case scenario revisited: impacts of lionfish on native reef fish communities. *Marine Ecology Progress Series* 474:243–252.
- Anderson, P.J., and J.F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189:117–123.
- Auster, P.J., J. Godfrey, A. Watson, A. Paquette, and G. McFall. 2009. Behavior of prey links midwater and demersal piscivorous reef fishes. *Neotropical Ichthyology* 7:109–112.
- Auster, P.J., D. Grenda, J. Godfrey, E. Heupel, S. Auscavitch, and J. Mangiafico. 2011. Behavioral observations of young-of-year *Sphyraena barracuda* at offshore subtropical reefs (NW Atlantic). *Southeastern Naturalist* 10:563–569.
- Barber, R.T., and F.P. Chavez. 1983. Biological consequences of El Niño. *Science* 222:1203–1210.
- Barbour, A.B., et al. 2010. Mangrove use by invasive lionfish (*Pterois volitans*). *Marine Ecology Progress Series* 401:291–294.
- Barth, J.A., B.A. Menge, J. Lubchenco, et al. 2007. Delayed upwelling alters nearshore coastal ocean ecosystems. *Proceedings of the National Academy of Sciences* 104:3719–3724.
- Bascompte, J., C.J. Melián, and E. Sala. 2005. Interaction strength combinations and overfishing in a marine food web. *Proceedings of the National Academy of Sciences* 102:5443–5447.
- Baumgartner, T.R., et al. 1992. Reconstruction of Pacific sardine population history. *CalCOFI Reports* 33:24–40.
- Behrenfeld, M.J., et al. 2006. Climate-driven trends in ocean productivity. *Nature* 444:752–755.

- Casey, J.P., et al. 2007. Habitat use by juvenile gag (*Mycteroperca microlepis*) in Charlotte Harbor, Florida. *Gulf and Caribbean Research* 19:1–10.
- Catano, L.B., et al. 2016. Reef fish foraging and habitat connectivity. *Coral Reefs* 35:485–495.
- Chagaris, D., and B. Mahmoudi. 2009. Food web interactions and fisheries dynamics. *Fisheries Research* 102:35–45.
- Chagaris, D., and B. Mahmoudi. 2013. Ecosystem modeling of gag grouper. NOAA Technical Report NMFS.
- Chagaris, D., et al. 2015. Ecosystem-based management in the Gulf of Mexico. *Marine and Coastal Fisheries* 7:19–33.
- Checkley, D.M., et al. 2009. Climate, anchovy, and sardine population dynamics. *Annual Review of Marine Science* 1:485–518.
- Christensen, V., and D. Pauly. 1992. ECOPATH II: balancing steady-state ecosystem models. *Ecological Modelling* 61:169–185.
- Chee, C., R.T. Leaf, and K.S. Dillon. 2024. Combining biotracer and stomach content analyses for trophic dynamics. *Ecological Informatics* 82:102746.
<https://doi.org/10.1016/j.ecoinf.2024.102746>
- Cisneros-Mata, M.A., et al. 1995. Population dynamics of small pelagic fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 52:120–134.
- Cowen, R.K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1:443–466.
- Cury, P.M., et al. 2005. Trophodynamic indicators for ecosystem-based fisheries. *ICES Journal of Marine Science* 62:430–442.
- Cury, P.M., et al. 2011. Global forage fish and predator dependence. *Science* 334:1703–1706.
- Dahl, K.A., and W.F. Patterson. 2014. Habitat-specific impacts of invasive lionfish. *Marine Ecology Progress Series* 512:1–14.
- Delorenzo, D.M., D.M. Bethea, and J.K. Carson. 2015. Diet and trophic level of Atlantic sharpnose shark (*Rhizoprionodon terraenovae*). *Journal of Fish Biology* 86:385–391.
- del Río, L., et al. 2023. Biology and ecology of lionfish as invasive species. *PeerJ* 11:e15728.
<https://doi.org/10.7717/peerj.15728>
- Dunne, J.A., R.J. Williams, and N.D. Martinez. 2004. Network structure and robustness of marine food webs. *Marine Ecology Progress Series* 273:291–302.

- Dye, B., M.A. Peck, K.E. van de Wolfshaar, and A. van Leeuwen. 2026. Resource level and temperature effects on fish guild performance. *Conservation Physiology* 14:coag005.
- Essington, T.E., et al. 2015. Fishing impacts on forage fish and ecosystems. *Proceedings of the National Academy of Sciences* 112:6648–6652.
- Estes, J.A., et al. 2009. Marine mammal declines and food-web consequences. *Philosophical Transactions of the Royal Society B* 364:1647–1658.
- Farmer, N.A., et al. 2013. Reef fish spawning aggregations. *Marine Ecology Progress Series* 485:233–245.
- Farmer, N.A., et al. 2017. Connectivity of reef fish spawning sites. *Fisheries Oceanography* 26:123–138.
- Ferrier, S. 1984. Status of the Rufous Scrub-bird. PhD Dissertation. University of New England.
- Frank, K.T., et al. 2005. Trophic cascades in cod-dominated ecosystems. *Science* 308:1621–1623.
- Frederiksen, M., et al. 2006. Bottom-up control of marine food webs. *Journal of Animal Ecology* 75:1259–1268.
- Fry, B., and P.L. Parker. 1979. $\delta^{13}\text{C}$ evidence of benthic plant importance in seagrass systems. *Estuarine and Coastal Marine Science* 8:499–509.
- Fulton, E.A., et al. 2004. Atlantis ecosystem model. *ICES Journal of Marine Science* 61:171–188.
- Fulton, E.A., et al. 2005. Indicators of ecosystem health. *ICES Journal of Marine Science* 62:518–527.
- Garrison, L.P., et al. 2010. MSVPA predator-prey modeling expansion. *ICES Journal of Marine Science* 67:856–870.
- Gentry, L. et.al., 2025, Addition of Ecospace Module to the South Atlantic Reef Fish (SARF) Model: Report to SAFMC SSC April 2025. .
https://safmc.net/documents/8b_ecospace_report_for_ssc_april_2024_v1-pdf/
- Goldman, S.F., and G.R. Sedberry. 2010. Trophic linkages in deep reef systems. *Marine Biology* 157:123–135.
- Goldman, S.F., and G.R. Sedberry. 2011. Feeding habits of demersal fishes on the Charleston Bump. *ICES Journal of Marine Science* 68:390–398.

- Gomez, F.A., et al. 2026. Wind control of ocean-biogeochemical variability in the South Atlantic Bight. *Journal of Geophysical Research: Oceans*.
- Govoni, J.J., et al. 2009. Cyclonic eddies as larval fish habitat. *ICES Journal of Marine Science* 67:403–411.
- Green, S.J., et al. 2012. Invasive lionfish drive reef fish declines. *PLoS ONE* 7:e32596.
- Grober-Dunsmore, R., et al. 2008. Vertical zoning in marine protected areas. *Fisheries* 33:598–610.
- Haines, E.B. 1976. Stable carbon isotopes in salt marsh ecosystems. *Estuarine and Coastal Marine Science* 4:609–616.
- Hare, J.A., et al. 2009. Climate impacts on marine fish distributions. *ICES Journal of Marine Science* 66:1490–1497.
- Hilborn, R., et al. 2017. Forage fish management and ecosystems. *Fish and Fisheries* 18:1–17.
- Hoegh-Guldberg, O., and J.F. Bruno. 2010. Climate change impacts on marine ecosystems. *Science* 328:1523–1528.
- Houde, M., et al. 2011. Bioaccumulation in marine food webs. *Environmental Science & Technology* 45:1135–1141.
- Hughes, T.P. 1994. Phase shifts in coral reef ecosystems. *Science* 265:1547–1551.
- ICES. 2014. Food web indicator workshop report (WKFooWI). ICES CM 2014/ACOM:48.
- Jakimska, A., et al. 2011. Heavy metals in marine environments. *Environmental Reviews* 19:204–226.
- Jørgensen, S.E., F. Xu, and R. Costanza (eds). 2010. *Handbook of Ecological Indicators*. CRC Press.
- Kendall, M.S., M. Poti, and K.B. Karnauskas. 2016. Climate change and larval transport. *Global Change Biology* 22:1532–1547.
- Kimirei, I.A., et al. 2011. Ontogenetic habitat use in reef fishes. *Estuarine, Coastal and Shelf Science* 92:47–58.
- Layman, C.A., et al. 2012. Stable isotope tools for food web analysis. *Biological Reviews* 87:545–562.
- Link, J.S. 2010. *Ecosystem-Based Fisheries Management*. Cambridge University Press.

- MacArthur, R., and E. Pianka. 1966. Optimal use of patchy environments. *The American Naturalist* 100:603–609.
- Mackinson, S., et al. 2009. Ecosystem model forcing factors. *Ecological Modelling* 220:2972–2987.
- Methot, R.D., and C.R. Wetzel. 2013. Stock synthesis framework. *Fisheries Research* 142:86–99.
- Morris, J.A., and J.L. Akins. 2009. Lionfish biology and impacts. NOAA Technical Report.
- NMFS. 2011. *U.S. National Bycatch Report*. NOAA.
- Okey, T.A., and R. Pugliese. 2001. Ecopath model of the southeastern U.S. shelf. Fisheries Centre Research Reports.
- Oros, A. 2025. Heavy metal trophic transfer in marine fish. *Journal of Xenobiotics* 15:59.
- Orr, J.C., et al. 2005. Ocean acidification impacts. *Nature* 437:681–686.
- Paerl, H.W., et al. 1998. Nutrient loading and hypoxia. *Marine Ecology Progress Series* 166:17–25.
- Peterson, B.J., and R.W. Howarth. 1987. Isotope tracing in salt marsh food webs. *Limnology and Oceanography* 32:1195–1213.
- Pikitch, E.K., et al. 2012. Forage fish conservation. *Science* 338:117–118.
- Plagányi, É.E. 2007. Ecosystem-based fisheries models. FAO Fisheries Technical Paper.
- Polovina, J. 1984. Coral reef ecosystem modeling. *Coral Reefs* 3:1–11.
- Power, M.E. 1992. Top-down vs bottom-up forces. *Ecology* 73:733–746.
- Randall, J.E. 1967. Food habits of reef fishes. *Studies in Tropical Oceanography* 5:665–847.
- Rogers, T.L., et al. 2024. Drivers of pelagic food web dynamics. *Ecology* 105:e4274.
- Rooney, N., et al. 2006. Stability of food webs. *Nature* 442:265–269.
- Saponari, F., et al. 2014. Food web overlap in disturbed ecosystems. *PLoS ONE* 9:e103132.
- Sedberry, G.R., J.C. McGovern, and O. Pashuk. 2001. Charleston Bump as essential fish habitat. *American Fisheries Society Symposium* 25:3–24.

- Shin, Y.-J., et al. 2012. Indicators for marine ecosystems. *ICES Journal of Marine Science* 69:1–12.
- Smith, A.D.M., et al. 2011. Impacts of fishing on ecosystems. *Science* 333:1147–1150.
- Sponaugle, S., et al. 2005. Frontal eddies and reef fish settlement. *Limnology and Oceanography* 50:1033–1048.
- Steneck, R.S. 2012. Apex predators and trophic cascades. *PNAS* 109:7953–7954.
- Surma, S., E.A. Pakhomov, and T.J. Pitcher. 2025. Trophic cascades and top-down control. *Frontiers in Ecology and Evolution* 13:1587171.
- Trites, A.W., and C.P. Donnelly. 2003. Forage fish and predator dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 60:123–132.
- Vinueza, L.R., et al. 2014. Climate-driven trophic coupling. *Ecological Monographs* 84:411–434.
- Walters, C., V. Christensen, and D. Pauly. 1997. Dynamic ecosystem models. *Reviews in Fish Biology and Fisheries* 7:139–172.
- Wanless, S., et al. 2005. Seabirds and forage fish interactions. *Marine Ecology Progress Series* 285:259–271.
- Ware, D.M., and R.E. Thomson. 2005. Bottom-up control of fish production. *Science* 308:1280–1284.
- Weaver, D.C., and G.R. Sedberry. 2001. Trophic subsidies at the Charleston Bump. *American Fisheries Society Symposium* 25:137–152.
- Young, E.F., et al. 2018. Climate impacts on connectivity. *Evolutionary Applications* 11:978–994.
- Zhulay, I., et al. 2023. Reduced pelagic–benthic coupling in Arctic ecosystems. *Scientific Reports* 13:6739.