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An Investigation of the Fisheries Ecosystem Dynamics in Rhode Island's Nearshore Waters

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AN INVESTIGATION OF THE FISHERIES ECOSYSTEM DYNAMICS IN RHODE ISLAND'S NEARSHORE WATERS

BY

ANNA J. MALEK

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
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DOCTOR OF PHILOSOPHY DISSERTATION

OF

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ABSTRACT:

This research was developed in response to recent interest in offshore wind energy development and the ongoing need for ecosystem-based spatial management planning in Rhode Island's nearshore waters. Despite heavy use and close proximity to a number of marine science institutions, Rhode Island and Block Island Sounds have been neglected in terms of scientific research, resulting in a poor understanding of the fisheries ecosystem in this area. This research aimed to address this knowledge gap by assessing the biogeography, trophic dynamics and habitat associations of the fish and invertebrate communities in this region. Specifically, the goals of this research were to: 1) Evaluate the fine-scale spatial structure of the demersal fish and invertebrate community, 2) Assess the dietary guild structure and the flow of energy through the fisheries food web, and 3) Investigate the relationship between the fish community and benthic habitat.

Otter trawls and beam trawls were used to sample fish and invertebrates throughout Rhode Island and Block Island Sounds from 2009 to 2012. Field work was conducted in collaboration with two commercial fishing vessels, the *F/V Darana R* and *F/V Mister G*, and the Northeast Area Monitoring and Assessment Program. During otter trawl surveys, stomach and white tissue samples were taken from 25 species for analysis of diet composition and nitrogen and carbon stable isotope signatures. A combination of site-specific water column profiles, high resolution acoustic surveys, and seafloor video surveys were used for habitat characterization.

Regionally-grouped abundance, biomass, diversity, and size spectra were used to assess spatial patterns in the aggregate fish community, and nonparametric hierarchical cluster analysis was used to determine species assemblages. Analyses revealed coherent gradients in fish community biomass, diversity and species composition extending from inshore to offshore waters, as well as patterns related to the differing bathymetry of Rhode Island and Block Island Sounds. Species assemblages were characterized by a combination of piscivores (silver hake, summer flounder), benthivores (American lobster, black sea bass, little skate, scup) and planktivores (sea scallop), and exhibited geographic patterns that were persistent from year to year, yet variable by season. Such distributions reflect the cross-shelf migration of fish and invertebrate species in the spring and fall, highlighting the importance of considering seasonal fish behavior when planning construction schedules for offshore development projects.

Stomach content analysis was used to define trophic structure according to dietary guilds, while nitrogen and carbon stable isotopes were used to determine the trophic position of fish and invertebrate species and to assess the relative importance of benthic and pelagic production in supporting the fisheries food web. Results suggest that the fisheries food chain in Rhode Island and Block Island Sounds consists of four trophic levels and six distinct dietary guilds (planktivores, benthivores, shrimp and amphipod eaters, crab eaters, small fish and shrimp eaters, piscivores). Inter-species isotopic and dietary overlap within guilds was high, suggesting that resource partitioning plays a major role in structuring the fish community in this region. Furthermore, carbon isotopes indicate that most fish are supported by pelagic phytoplankton, although there is evidence that benthic production also plays a role, particularly for obligate benthivores such as skates.

Multivariate analysis of otter and beam trawl catch data and acoustic, videographic, and oceanographic benthic habitat parameters suggest that the fish communities in Rhode Island and Block Island Sounds are structured by both permanent (i.e. depth, habitat type) and transient (i.e. bottom water temperature) habitat characteristics. As such, otter trawl and beam trawl species assemblages can be explained by a suite of seafloor and oceanographic habitat parameters, including mean depth, surface and bottom water temperature, standard deviation of benthic surface roughness, minor grain size, mean slope, and surface salinity. Furthermore, spatial patterns in diet composition indicate habitat-specific feeding by demersal fish species, such as winter flounder and silver hake. Feeding on benthic prey is, therefore, an important link between demersal fish assemblages and their habitats in this region. The results of this work not only provide valuable insight into fisheries ecosystem dynamics in a temperate nearshore environment, but will also inform spatial management plans for Rhode Island and Block Island Sounds. Furthermore, the methods for this study are consistent with European guidelines for assessing the impacts of offshore wind turbines on the marine environment and could provide a baseline for measuring the cumulative effects of offshore development projects within Rhode Island and Block Island Sounds.

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I am deeply thankful to the many Collie Lab members, faculty mentors, undergraduate assistants, graduate students, captains, crews, family, and friends, without whom this work would not have been possible. A special thank you to my major professor, Dr. Jeremy Collie, for his advice and support from the first day of otter trawling to the last day of analysis. I am also grateful to my doctoral committee members, John King, Jon Hare, David Taylor, and Peter August, whose guidance improved the quality of this dissertation. In addition to my academic mentors, I owe many thanks to Margaret Petruny-Parker and the Commercial Fisheries Research Foundation (CFRF) for the opportunity to work with a keen group of commercial fishermen, who shared many helpful insights throughout the course of this work.

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DEDICATION:

This work is dedicated to my grandmother, Ethel Thelma Hutton, whose ancestors relied on the robust fisheries resources of Newfoundland to feed their family, their communities, and their souls.

PREFACE:

This doctoral dissertation is presented in manuscript format, and is subdivided into five chapters. Chapter one is a general introduction that describes the motivation for this research and as how it contributes to the advancement of ecosystem based fisheries science. Chapter two is a manuscript titled “Fine scale spatial patterns in the demersal fish and invertebrate community in a northwest Atlantic ecosystem” that was published in *Estuarine, Coastal, and Shelf Science* in June 2014. Chapter three is a manuscript titled “Dietary guilds and trophic structure of the fish community in Rhode Island Sound and Block Island Sound, USA” that has been prepared for submission to the *Canadian Journal of Fisheries and Aquatic Sciences*. Chapter four is a manuscript titled “Habitat associations of the demersal fish and invertebrate community in a nearshore northwest Atlantic ecosystem” that has been prepared for submission to *Marine Ecology Progress Series*. Chapter five is a speculative discussion that explores topics not covered in the manuscripts, including the implications of this work for local marine spatial planning efforts. In addition to these chapters, this dissertation also includes an appendix containing supplementary data and maps that were prepared for, but not included in, the manuscripts.

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similar habitats appearing close together. Each point represents the habitat features at one otter trawl station. Symbols represent habitat group, as defined by BIOENV and LINKTREE analysis. Dashed contours represent species assemblage groups as defined by CLUSTER analysis. Analysis of similarity indicates that there are significant differences in habitat characteristics between otter trawl species assemblage groups (R=0.475, p=0.001).

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otter trawl station. Symbols represent habitat group, as defined by BIOENV and LINKTREE analysis. Dashed contours represent species assemblage groups as defined by CLUSTER analysis. Analysis of similarity indicated that there were significant differences in habitat characteristics between beam trawl species assemblage groups (R=0.506, p=0.001).

Figure 3.16. Map depicting the spatial patterns in beam trawl habitat and species assemblage groups in Rhode Island and Block Island Sounds. Color coded symbols represent habitat group, as defined by BIOENV and LINKTREE analysis. Dashed contours represent species assemblage groups, as defined by CLUSTER analysis.

CHAPTER 1

Introduction and Review of the Problem

By

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Introduction:

Recent interest in offshore energy development combined with the ongoing need to assess the status of overfished groundfish species has focused attention on ecosystem-based spatial management planning in Rhode Island's offshore waters. An ecosystem-based approach to management is essential to attain system-wide sustainability and to ensure the continued availability of marine resources that humans want and need (McLeod et al. 2005, Pauly & Chuenpagdee 2007). A core challenge of developing an ecosystem-based approach to management is the acquisition of knowledge concerning the distributions, population structure, interactions and trends of key species and communities. Such data are also essential to investigate changes in biological community structure (Collie et al. 2008) and shifts in the distributions of demersal species associated with global climate change (Nye et al. 2009). To address this challenge, my dissertation research aims to assess the distribution and dynamics of the fish and invertebrate community in the nearshore waters of Rhode Island Sound and Block Island Sound, USA. By illuminating the spatial dynamics and trophic structure of the fish community and the basis of fish-habitat relationships in Rhode Island's nearshore waters, this work will help guide the zoning of novel ocean uses, such as offshore wind energy, sand extraction, and blue water aquaculture.

Ecosystem based fisheries management (EBFM) is an approach to fisheries management that explicitly considers ecosystem components, such as species interactions, habitat, and environmental variability, as well as the impacts of fishing on protected species, habitat, and non-target species (Crowder & Norse 2008). In addition, EBFM recognizes other ocean use sectors, such as mineral/energy extraction, tourism, recreation, and transport, and involves stakeholders in the fisheries management process (Pikitch et al. 2004). The EBFM process is designed to be more transparent than traditional fisheries management, so as to reduce stakeholder frustrations and ensure management accountability. While considering the human dimension of the fisheries ecosystem is not a new concept (the goal has been to manage for maximum yield/profit for many years), the cooperation of stakeholders from assessment to application is novel to EBFM (Link 2010).

Two key components of EBFM that are central to my dissertation research are the trophic dynamics and habitat requirements of the fish community. Traditionally, the fisheries management system has focused on single-species assessments and policies, with little acknowledgement of species and ecosystem interactions (Link 2010). Conversely, EBFM has a distinct multispecies focus for assessments and policies, which over time, will progress to an ecosystem focus, incorporating, not only species interactions, but also climate and habitat (Johnson & Welch 2009).

Dietary guild analysis and stable isotope analysis are two common approaches for assessing the trophic structure in a fisheries ecosystem, with each technique providing a unique ecological perspective (Fry 1988, Wilson 1999). Fish stomach content analysis, upon which dietary guild analysis is based, provides a direct measure of predator consumption (Hyslop 1980). A unique and powerful attribute of stomach content and dietary guild analysis is their utility in identifying specific trophic linkages (i.e. predator-prey relationships), which is critical for developing multispecies models and, thus, an ecosystem based approach to fisheries management (Fogarty 2013). Stomach content analysis, however, does not take into account temporal variation in predator diets, as stomach contents represent a snapshot of fish feeding behavior. Furthermore, stomach content analysis is often ineffective for planktivorous species, due to the size and digestive state of prey. Nonetheless, stomach content and dietary guild analysis are valuable approaches to assessing the trophic structure of fisheries ecosystems, as the resulting classification of species into functional groups, assessment of resource partitioning, and identification of competitive interactions enables the progression of multispecies models and ecosystem-based fisheries management (Auster & Link 2009, Garrison & Link 2000).

Stable isotope analysis is also a powerful tool for assessing trophic dynamics in fisheries ecosystems, with nitrogen stable isotopes ($\delta^{15}N$) indicating the time-integrated feeding histories and trophic positions of consumer species, and carbon stable isotopes ($\delta^{13}C$) revealing the relative importance of different basal resources in supporting fish production (France 1993, Hobson et al. 1995, Post 2002, Mackenzie et al. 2011). Stable isotopes are assimilated in fish tissue over weeks to months, and thus reflect the time-integrated feeding history of consumer species (Peterson & Fry 1987). As such, in contrast to gut content analysis, stable isotopes are an effective means to assess temporal variability in fish feeding behaviors, which arguably, is equally important as identifying specific predator-prey relationships. Given the temporal integration of stable isotopes, $\delta^{15}N$ and $\delta^{13}C$ often reflect feeding behavior in different locations and ecosystems (i.e. estuaries v. continental shelf). This discrimination can be a useful tool for describing the movement patterns and habitat use of fish species, but can also confound analytical interpretation if baseline isotopic signatures are not known for different locations (Abrantes & Barnett 2011, Mackenzie et al. 2011, Dixon et al. 2015). Overall, $\delta^{15}N$ and $\delta^{13}C$ analysis is a useful tool for developing an ecosystem-based approach to management, as it identifies species that act as direct links to basal resources as well as species that share trophic roles.

With regards to the habitat, traditional and ecosystem-based management tools for characterizing and protecting fish habitat have been similar (marine protected areas and rotating closures) (Gleason et al. 2010). As habitat mapping capabilities have improved over the last 10 years, however, EBFM has begun to consider habitat in a more process-oriented manner (Johnson et al. 2012). More specifically, EBFM has begun to consider the role that habitat plays in not only the distribution of marine species, but also the productivity of the ecosystem (Erikkson et al. 2006).

A final and key component of EBFM that is particularly pertinent in Rhode Island’s nearshore waters is that EBFM identifies and incorporates other ocean use sectors from the outset (Hall & Mainprize 2004). Perhaps the best example of this is marine spatial planning (Douvere 2008, Ehler & Douvere 2009). The purpose of marine spatial planning is to minimize conflicts between competing ocean uses and preserve ecosystem services by allocating the spatial and temporal distribution of human activities in marine areas (Beck et al. 2009, Foley et al. 2010). Many ocean uses impact benthic habitat (mineral/energy extraction, fishing, dredge disposal), and thus, it is an essential consideration in the marine spatial planning process (Gilliland & Laffoley 2008).

Areas that are targeted by fishing often have particular environmental and biological conditions that contribute to the productivity of an ecosystem (e.g. George's Bank, Cox's Ledge) (Jennings et al. 2009). Benthic habitat maps, particularly those that incorporate oceanographic features and benthic biota, are essential to understanding the relationship between fishing effort, fish production, and ecosystem services (Williams & Bax 2001, Freidlander & Brown 2003). An example of such an application is Cordell Bank, where a combination of habitat maps and submersible surveys has led to the development of closed areas to protect sensitive rockfish (*Sebastes* spp.) habitat (Iampietro et al. 2008, Anderson et al. 2009). A similar case is evident in the Gulf of Alaska, where the designation of closed areas for the protection of young halibut, *Hippoglossus stenolepis*, has been based on the distribution of benthic habitat maps (Witherell et al. 2000). And in our own backyard, the designation of essential fish habitat on Stellwagen Bank has been based on benthic habitat maps (Auster et al. 2001). Thus, fine-scale fish biogeography characterizations and biologically relevant habitat maps are essential data for the development of effective marine spatial plans. Overall, making tradeoffs between habitat protection, fisheries extraction, and other ocean uses will become increasingly important as our continental shelves get more crowded with offshore energy ventures (Link 2010).

A common motivator of marine spatial planning worldwide has been the development of offshore wind energy (Jay 2010). An example of this is in Danish waters, where thousands of offshore turbines are operational (Douvere & Ehler 2009). Without a thorough understanding of the fine-scale distribution and significance of benthic habitat to fish and other benthic biota, however, the sustainability of offshore wind farm development is debatable (Punt et al. 2009). Ideally, managers direct developers to construct turbines in areas that will have the least negative impact on particular species or communities (e.g. scallop beds, cerianthid anemone aggregations), but the data required to make such recommendations are often lacking. Thus, my dissertation research aims to address this need in the first area in US territorial waters being planned for offshore wind energy development, Rhode Island and Block Island Sounds.

Rhode Island Sound and Block Island Sound separate the estuaries of Narragansett Bay and Long Island Sound from the outer continental shelf. As such, they provide important linkages between nearshore and offshore processes, including nutrient fluxes, larval transport, and migration of the adult stages of resource species, such as the American lobster (*Homarus americanus*) and winter flounder (*Pseudopleuronectes americanus*) (Costa-Pierce 2010). Furthermore, Rhode Island and Block Island Sound support a variety of commercial and recreational fishing activities, such as scallop dredging, otter trawling, long-lining and gill-netting, producing over $60 million in seafood landings every year (Hasbrouk et al. 2011). Despite their heavy use and close proximity to a number of marine science institutions, Rhode Island and Block Island Sounds are neglected in terms of scientific research, resulting is a poor understanding of the distribution and dynamics of the fisheries resources in this area. My dissertation research seeks to fill this data gap through cooperative research and interdisciplinary collaborations.

Studies to support the management of Rhode Island's offshore waters have become a priority since 2000, when interest in developing artificial reefs, aquaculture sites, and offshore wind turbines emerged in this region. Combined with traditional fisheries and existing dredge-disposal sites, these multiple uses require integrated spatial management planning to site activities in appropriate habitats that will minimize, to the extent possible, the cumulative impacts on resident species and the ecological and economic services derived from this near-shore region (Crowder & Norse 2008, Gilliland & Laffoley 2008, Foley et al. 2010). Since 2008, the Rhode Island Coastal Resources Management Council has led the charge to develop a spatial management plan for Rhode Island Sound and Block Island Sound (RI SAMP 2010). Although a general understanding of the ecology of Rhode Island Sound and Block Island Sound exists, there is a lack of site-specific data to guide spatial management planning (Mahon et al. 1998, Costa-Pierce 2010, Hale et al. 2010).

My dissertation research aims to address this need by conducting comprehensive sampling of the demersal fish and invertebrate community and their associated habitats in Rhode Island Sound and Block Island Sound. Specifically, the goals of my doctoral research are to: 1) Evaluate the fine-scale spatial structure of the demersal fish and invertebrate community, 2) Assess the dietary guild structure and the flow of energy through the fisheries food web, and 3) Investigate the relationship between fish species assemblages and benthic habitat.

The results of this work will not only provide valuable insight into fisheries ecosystem dynamics in a temperate coastal environment, but will also guide spatial management plans for Rhode Island and Block Island Sounds. The products of this research will be immediately available to state and federal management agencies to help guide the sustainable location of renewable energy structures within the Rhode Island's nearshore waters. Furthermore, the methods for this study are consistent with European guidelines for assessing the impacts of offshore wind turbines on the marine environment and could provide a baseline for measuring the cumulative effects of offshore development projects within Rhode Island and Block Island Sounds (CEFAS 2004, BSH 2007). In the end, the incorporation of this research into marine spatial planning efforts will help to conserve and protect the ecological resiliency of Rhode Island's coastal waters and the variety of uses they support.

Literature Cited:

Abrantes, K., and Barnett, A. 2011. Intrapopulation variations in diet and habitat use in a marine apex predator, the broadnose sevengill shark, *Notorynchus cepedianus*. Marine Ecology Progress Series 442: 133–148.

Anderson, T. J., Syms, C., Roberts, D. A., Howard, D. F., 2009. Multi-scale fish–habitat associations and the use of habitat surrogates to predict the organization and abundance of deep-water fish assemblages. Journal of Experimental Marine Biology and Ecology 379: 34–42.

Auster, P.J., Joy, K., and Valentine, P.C. 2001. Fish species and community distributions as proxies for seafloor habitat distributions: the Stellwagen Bank National Marine Sanctuary example (Northwest Atlantic, Gulf of Maine). Environmental Biology of Fishes 60 (4): 331-346.

Auster, P.J., and Link, J. 2009. Compensation and recovery of feeding guilds in a northwest Atlantic shelf fish community. Marine Ecology Progress Series 382: 163–172.

Beck, M.W., Ferdaña, Z., Kachmar, J., Morrison, K.K., Taylor P. 2009. Best Practices for Marine Spatial Planning. The Nature Conservancy, Arlington, VA.

Bundesamt für Seeschifffart unh Hydrologie (BSH). 2013. Investigation of the impacts of offshore wind turbines on the marine environment. Federal Maritime and Hydrographic Agency, Hamburg, Germany, 87 pp.

The Centre for Environment, Fisheries, and Aquaculture Science (CEFAS). 2004. Offshore Wind Farms: Guidance Note for Environmental Impact Assessment in Respect of FEPA and CPA Requirements, Version 2. Lowestoft, United Kingdom, 44 pp.

Collie, J.S., Wood, A.D., Jeffries, H.P., 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences 65: 1352-1365.

Costa-Pierce, B., 2010. Ecology of the SAMP. Chapter #2 in Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Crowder, L., Norse, E., 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. Marine Policy 32: 772-778.

Douvere, F. 2008. The importance of marine spatial planning in advancing ecosystem-based sea use management. Marine Policy 32: 762-771.

Douvere, F., Ehler, C. N., 2009. New perspectives on sea use management: initial findings from European experience with marine spatial planning. Journal of Environmental Management 90: 77–88.

Dixon, H.J., Dempson, J.B., and Power, M. 2015. Assessing the use of different marine growth zones of adult Atlantic salmon scales for studying marine trophic ecology with stable isotope analysis. Fisheries Research 164: 112-119.

Ehler, C., and Douvere, F. 2009. Marine Spatial Planning: A Step-by-step Approach toward Ecosytem-based Management. UNESCO Intergovernmental Oceanographic Commission, Paris, France.

Eriksson, B.K., Ruback, A., and Hillebrand, H. 2006. Biotic habitat complexity controls species diversity and nutrient effects on net biomass production. Ecology 87: 246-254.

Fogarty, M.J. 2013. The art of ecosystem-based fishery management. Canadian Journal of Fisheries and Aquatic Sciences 71 (3): 479-490.

Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.R., Prahler, E., Rohr, N., Sivas, D.,Beck, M.W., Carr, M.H., Crowder, L.B., Duffy, J.E., Hacker, S.D., McLeod, K.L., Palumbi, S.R., Peterson, C.H., Regan, H.M., Ruckelshaus, M.H., Sandifer, P.A., and Steneck, R.S. 2010. Guiding ecological principles for marine spatial planning. Marine Policy 35: 955-966.

France, R.L. 1993. Carbon-13 enrichment in benthic compared to planktonic algae: food web implications. Marine Ecology Progress Series 124: 307-312.

Friedlander, A.M., and Brown, E. 2003. Fish Habitat Utilization Patterns and Evaluation of the Efficacy of Marine Protected Areas in Hawaii: Integration and Evaluation of NOS Digital Benthic Habitats Maps and Reef Fish Monitoring Studies. Final Report to NOAA Ocean Service Biogeography Program, 1-78.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography 33 (5): 1182-1190.

Garrison, L., and Link, J. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202: 231–240.

Gilliland, P. M., Laffoley, D., 2008. Key elements and steps in the process of developing ecosystem- based marine spatial planning. Marine Policy 32: 787–796.

Gleason, M., McCreary, S., Miller-Henson, M., Ugoretz, J., Fox, E., Merrifiend, M., McClintock, W., Serpa, P., and Hoffman, K. 2010. Science-based and stakeholder-driven protected area network planning: as successful case study from north central California. Ocean and Coastal Management 53: 52-68.

Hale, S., 2010. Biogeographical patterns of marine benthic macroinvertebrates along the Atlantic coast of the northeastern USA. Estuaries and Coasts 33: 1039–1053.

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

Hasbrouck, E.C, Scotti, J., Stent, J., Gerbino, K., 2011. Rhode Island commercial fishing and seafood industries: The development of an industry profile. Commercial Fisheries Research Foundation, Kingston, Rhode Island, 124 pp.

Hobson, K.A., Ambrose, W.G., and Renaud, P.E. 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya : insights from delta13C and delta15N analysis. Marine Ecology Progress Series 128: 1–10.

Hyslop, E. J. 1980. Stomach contents analysis-a review of methods and their application. Journal of Fish Biology 17 (4): 411–429.

Iampietro, P.J.,Young, M.A., and Kvitek, R.G. 2008. Multivariate prediction of rockfish habitat suitability in Cordell bank national marine sanctuary and Del Monte Shalebeds, California, USA. Marine Geodesy 31 (4): 359-371.

Jay, S. 2010. Planners to the rescue: Spatial planning facilitating the development of offshore wind energy. Marine Pollution Bulletin 60 (4): 493-499.

Jennings, S., Kaiser, M., and Reynolds, J.D. 2009. Marine Fisheries Ecology. John Wiley & Sons.

Johnson, A., Jenkins, S., Hiddink, J.G., and Hinz, H. 2012. Linking temperate demersal fish species to habitat: scales, patterns, and future directions. Fish and Fisheries 14 (3): 256-280.

Johnson, J.E., and Welch, D.J. 2009. Marine fisheries management in a changing climate: a review of vulnerability and future options. Reviews in Fisheries Science 18 (1): 106-124.

Link, J.S., 2010. *Ecosystem-based Fisheries Management: Confronting Tradeoffs*. Cambridge University Press, New York, USA.

MacKenzie, K.M., Palmer, M.R., Moore, A., Ibbotson, A.T., Beaumont, W.R., Poulter, D.J., and Trueman, C.N. 2011. Locations of marine animals revealed by carbon isotopes. Scientific reports 1: 21.

Mahon, R., Brown, S. K., Zwanenburg, K. C., Atkinson, D. B., Buja, K. R., Claflin, L., Howell, G. D., Monaco, M.E., O'Boyle, R.N., Sinclair, M., 1998. Assemblages and biogeography of demersal fishes of the east coast of North America. Canadian Journal of Fisheries and Aquatic Sciences 55: 1704–1738.

McLeod, K.L., Lubchenko, J., Palumbi, S.R.,Rosenberg, A.A., 2005. Scientific consensus statement on marine ecosystem-based management. Communication Partnership for Science and the Sea. Available: http://www.compassonline.org/.

Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series 393: 111-129.

Pauly, D., Chuenpagdee, R., 2007. Fisheries and coastal ecosystems: the need for integrated management in sustainable resource management. Edward Elgar Publishing, Surrey, UK, 14 pp.

Peterson, B., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annual review of ecology and systematics 18: 293–320.

Pikitch, E., Santora, E.A., Babcock, A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heheman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., and Sainsbury, K. 2004. Ecosystem-based fishery management. Science 305: 346-347.

Post, D.M. 2002. Using stable isotopes to estimate trophic positions: Models, methods, and assumptions. Ecology 83: 703-718.

Punt, M.J., Groeneveld, R. A., van Ierland, E. C., Stel, J. H., 2009. Spatial planning of offshore wind farms: A windfall to marine environmental protection? Ecological Economics 69: 93–103.

Rhode Island Special Area Management Plan (RI SAMP), 2010. Coastal Resources Management Council, Wakefield, Rhode Island.

Williams, A., and Bax, N.J. 2001. Delineating fish-habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. Marine and Freshwater Research 52 (4): 513-536.

Wilson, J.B. 1999. Guilds, functional types and ecological groups. Oikos 86: 507-522.

Witherell, D., Pautzke, C., and Fluharty, D. 2000. An ecosystem-based approach for Alaska groundfish fisheries. ICES Journal of Marine Science 57 (3): 771-77

CHAPTER 2

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Fine-scale Spatial Patterns in the Demersal Fish and Invertebrate Community in a Northwest Atlantic Ecosystem

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Abstract:

The abundance, biomass, diversity, and species composition of the demersal fish and invertebrate community in Rhode Island Sound and Block Island Sound, an area slated for offshore renewable energy development, were evaluated for spatial and seasonal structure. We conducted 58 otter trawls and 51 beam trawls in the spring, summer and fall of 2009-2012, and incorporated additional data from 88 otter trawls conducted by the Northeast Area Monitoring and Assessment Program. We used regionally-grouped abundance, biomass, diversity, and size spectra to assess spatial patterns in the aggregate fish community, and hierarchical cluster analysis to evaluate trends in species assemblages. Our analyses revealed coherent gradients in fish community biomass, diversity and species composition extending from inshore to offshore waters, as well as patterns related to the differing bathymetry of Rhode Island and Block Island Sounds. The fish communities around Block Island and Cox's Ledge are particularly diverse, suggesting that the proximity of hard bottom habitat may be important in structuring fish communities in this area. Species assemblages in Rhode Island and Block Island Sounds are characterized by a combination of piscivores (silver hake, *Merluccius bilinearus*, summer flounder, *Paralichthys dentatus*, and spiny dogfish, *Squalus acanthias*), benthivores (American lobster, *Homarus americanus*, black sea bass, *Centropristis striata, Leucoraja* spp. skates, and scup, *Stenotomus chrysops*) and planktivores (sea scallop, *Placopecten magellanicus*), and exhibit geographic patterns that are persistent from year to year, yet variable by season. Such distributions reflect the cross-shelf migration of fish and invertebrate species in the

spring and fall, highlighting the importance of considering seasonal fish behavior when planning construction schedules for offshore development projects. The fine spatial scale (10s of km) of this research makes it especially useful for local marine spatial planning efforts by identifying local-scale patterns in fish community structure that will enable future assessment of the ecological impacts of offshore development. As such, this knowledge of the spatial and temporal structure of the demersal fish community in Rhode Island and Block Island Sounds will help to guide the placement of offshore structures so as to preserve the ecological and economic value of the area.

Introduction:

An ecosystem-based approach to management is essential to attain system-wide sustainability and to ensure the continued availability of marine resources that humans want and need (McLeod et al. 2005, Pauly & Chuenpagdee 2007). Designing an effective ecosystem-based management plan requires a comprehensive understanding of the distributions, population structures, interactions and trends of local fish and invertebrate species. Such detailed information, however, is rarely available even in the most well-studied ecosystems (Cury et al. 2005).

Recent interest in offshore energy development combined with the ongoing need to assess the status of overfished groundfish species has focused attention on ecosystem-based spatial management planning in Rhode Island’s offshore waters. The broad-scale (100s of km) distribution of fish species in this area is well-known from standardized trawl surveys (Gabriel 1992, Jordaan et al. 2010). However, spatial management is often implemented at smaller scales (Collie et al. 2013), requiring knowledge of fish distributions and fish-habitat associations at 10-km scales (Smith et al. 2013). Thus, when developing spatial management plans, targeted fisheries surveys should be employed to fully assess fine-scale fish community dynamics and potential ecological impacts of offshore energy development.

Rhode Island Sound and Block Island Sound separate the estuaries of Narragansett Bay and Long Island Sound from the outer continental shelf (Figure 1.1). As such, they provide important linkages between near-shore and offshore processes, including nutrient fluxes, larval transport, and migration of the adult stages of resource species, such as the American lobster (*Homarus americanus*) and winter flounder (*Pseudopleuronectes americanus*) (Costa-Pierce 2010). Furthermore, Rhode Island Sound and Block Island Sound support a variety of commercial and recreational fishing activities, such as scallop dredging, otter trawling, long-lining and gill-netting, producing over $60 million in seafood landings in Rhode Island every year (Smythe & Beutel 2010, Hasbrouck et al. 2011). Despite their heavy use and close proximity to a number of marine science institutions, Rhode Island and Block Island Sounds have been neglected in terms of scientific research, resulting in a poor understanding of the distribution and dynamics of the fisheries resources in this area.

Studies to support the management of Rhode Island’s offshore waters have become a priority since 2000, when interest in developing artificial reefs, aquaculture sites, and offshore wind turbines emerged in this region. Combined with traditional fisheries and existing dredge-disposal sites, these multiple uses require integrated spatial management planning to site activities in appropriate habitats that will minimize, to the extent possible, the cumulative impacts on resident species and the ecological and economic services derived from this near-shore region (Crowder & Norse 2008, Gilliland & Laffoley 2008, Foley et al. 2010). Since 2008, the Rhode Island Coastal Resources Management Council has led the charge to develop a spatial management plan for Rhode Island and Block Island Sounds (RI SAMP 2010). But, while a general understanding of the ecology of Rhode Island Sound and Block Island Sound exists, there is a lack of site-specific data to guide spatial management planning (Mahon et al. 1998, Costa-Pierce 2010, Hale 2010). Compounding the challenge, this spatial planning process is being conducted against a background of changing coastal climate (Nixon et al. 2009, Nye et al. 2009). As a result, historical baseline data may no longer represent current conditions (Collie et al. 2008).

We aimed to address these challenges by conducting comprehensive sampling of the demersal fish and invertebrate community in Rhode Island Sound and Block Island Sound. In particular, we sought to: 1) Evaluate the spatial structure of the demersal fish community in Rhode Island and Block Island Sounds, and 2) Determine whether intra- or inter-annual variations in the composition of these communities exist. With this information, we will then begin to assess the potential impacts of offshore development and climate change in Rhode Island's offshore waters (Punt et al. 2009, BSH 2013).

Methods:

Study Area

The study area, encompassing Rhode Island Sound and Block Island Sound, is located on the inner continental shelf in the northwest Atlantic (Figure 1.1). This area is seasonally dynamic, with sea surface temperatures ranging from 2°C in the winter to 25°C in the summer, and primary production ranging from 59 mg C m^{-2} d^{-1} in the winter to 1738 mg C m^{-2} d^{-1} in the spring (Nixon et al. 2010, Ullman & Codiga 2010). There are three major bathymetric features in Rhode Island Sound and Block Island Sound: 1) Block Island, a 25 km^2 island that lies in the center of Block Island Sound, 2) Cox's Ledge, an expansive rocky shelf in southeast Rhode Island Sound, and 3) Southwest Ledge, an abrupt rocky shoal southwest of Block Island (Figure 1.1). Water depth ranges from 0-65 meters, with this work sampling from 20 meters depth inshore and around Block Island to 55 meters depth offshore. Rhode Island and Block Island Sounds fall within the Northeast Shelf Large Marine Ecosystem, and mark the biogeographic boundary between Virginean and Acadian regions (Cook & Auster 2007, Costa-Pierce 2010). As such, Rhode Island and Block Island Sounds are included in the home range of both Mid-Atlantic and North-Atlantic species. Thus, the species assemblage in this area is highly dynamic and likely to reflect changes in ocean climate.

Field Methods

We used otter trawls and beam trawls to sample the demersal fish and invertebrate communities throughout Rhode Island and Block Island Sounds in spring, summer and fall 2009-2012. This dual-gear sampling approach was employed to attain a more holistic assessment of the macrofaunal communities in our study area than could be achieved with one gear type alone. The distinct sampling efficiencies of the two types of gear were recognized at the beginning of the project, and thus otter trawl and beam trawl data were treated separately, then explored in a complimentary manner. Given the limitations of individual sampling gears (i.e. otter trawl, fixed gear, beam trawl), multi-gear approaches are frequently used to achieve more complete evaluations of coastal ecosystems (Franco et al. 2012).

As such, we used otter trawls to sample soft-bottom habitats (sand, mud, clay) and beam trawls to sample fish and invertebrate populations in areas that were too rough for otter trawls (gravel, cobble, moraine). We selected otter trawl stations to achieve maximum coverage of the study area and beam trawl stations to target hard bottom habitats. We also conducted beam trawls at 10 of the otter trawl stations to provide direct gear comparisons. A total of 58 otter trawls were conducted between 2009 and 2011, with 42 trawls in the fall of 2009, 2010, and 2011, and 16 trawls in the spring of 2011 (Figure 1.1). A total of 51 beam trawls were conducted in 2010, 2011, and 2012, with 13 trawls in the winter of 2010 and 38 trawls in the summer of 2011 and 2012 (Figure 1.1).

Otter trawls were performed aboard the 90’ *F/V Darana R* using the sampling gear and vessel crew of the Northeast Area Monitoring and Assessment Program (NEAMAP) (http://www.vims.edu/fisheries/neamap). Each tow was conducted with a 400 x 12-cm, three-bridle, four-seam otter trawl, coupled with a pair of Thyboron, Type IV 66” trawl doors. The cod-end was made of double 12-cm stretch mesh (knot to knot) with a 2.43 cm knotless nylon liner. All tows were 20 minutes in duration with a target tow speed of 1.5 m s^{-1}, resulting in a tow distance of approximately 1.8 km.

Beam trawls were conducted on the 55’ *F/V Mister G*, using a 3-m beam trawl, with cod-end mesh equivalent to that of the NEAMAP otter trawl. All tows were 20 minutes in duration with a target tow speed of 2.0 m s^{-1}, resulting in a tow distance of approximately 2.4 km.

After each trawl, we recorded aggregate wet weights (kg), counts, and individual length measurements (Fish: Fork length, Squid: Mantle length, Lobster: Carapace length, Crab: Carapace width) for all species collected (Table 1.1). We measured temperature, salinity, and dissolved oxygen profiles at each trawl station and recorded weather conditions and sea-state.

Data from additional otter trawls conducted independently by NEAMAP were later incorporated into the data set to increase sampling coverage in inshore waters, which were sparsely sampled by our field work (Figure 1.1). A total of 88 NEAMAP otter trawls were conducted within our study area between 2009 and 2011, with 63 trawls during the fall of 2009, 2010, and 2011, and 25 trawls during the spring of

2011.The NEAMAP survey targets the coastal zone, and thus all NEAMAP trawls were conducted between 6 and 27 meters water depth. The sampling gear and catch-processing protocol used by NEAMAP are identical to that of our work, allowing NEAMAP data to be appended without transformation.

Statistical Methods - Univariate Analyses

We accounted for the different gear configurations and catchabilities of beam trawls and otter trawls by excluding pelagic species, sand dollars, and sea stars, and standardizing catch data by the area swept (otter trawl area swept = 0.022 – 0.031 km^2; beam trawl area swept = 0.0066 - 0.0076 km^2). The following pelagic species were excluded: American shad (*Alosa sapidissima*), Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), Atlantic menhaden (*Brevoortia tyrannus*), Atlantic moonfish (*Selene setapinnis*), bay anchovy (*Anchoa mitchilli*), blue runner (*Caranx crysos*), blueback herring (*Alosa aestivalis*), butterfish (*Peprilis triacanthus*), crevalle jack (*Caranx hypos*), northern kingfish (*Menticirrhus saxatilis*), northern puffer (*Sphoeroides maculatus*), northern sennet (*Sphyraena borealis*), rough scad (*Trachurus lathami*), round herring (*Etrumeus teres*), and round scad (*Decapterus punctatus*). Standardized catch data were used to calculate aggregate fish community abundance, biomass and diversity at each trawl site. We used Shannon-Weiner's *H* as a diversity index because it is sensitive to changes in rare species (Hill 1973). While insufficient field calibrations prevented full integration of otter trawl and beam trawl data, results were interpreted simultaneously to provide a comprehensive evaluation of the aggregate demersal fish and invertebrate community.

Prior to analysis, all data were tested for normality and homogeneity of variance. Data were log transformed before analysis to achieve a normal distribution.

Univariate Analyses - Seasonality & Geography

We used 2-way analysis of variance (ANOVA) models and posthoc pairwise comparisons to test for the effect of season (spring, summer, fall, winter) and trawl type (otter, beam) on fish community abundance, biomass, and diversity. ANOVAs were followed by multiple comparison tests. To facilitate spatial analysis, we combined site-specific abundance, biomass, diversity, and length frequency into six subsections: Inshore West (IW), Inshore East (IE), Nearshore West (NW), Nearshore East (NE), Offshore West (OW), and Offshore East (OE) (Figure 1.1). Subsections were delineated by water depth and position within Rhode Island and Block Island Sounds. Inshore, Nearshore and Offshore zones are characterized by water depths of 20-30 meters, 30-40 meters, and greater than 40 meters, respectively (Figure 1.1). The boundary between Rhode Island Sound and Block Island Sound, extending southward from the mouth of Narragansett Bay, was used to demarcate eastern and western regions.

We used 2-way ANOVA models to test for the effects of geographic position (region, zone, subsection) on total fish community abundance, biomass, and diversity. Data were tested for normality and homogeneity of variance. Data were log transformed before analysis to achieve a normal distribution. Tukey Honest Significant Difference tests (Tukey HSD) were used to make pairwise comparisons between subsections, as well as to assess broader-scale spatial patterns in fish community abundance, biomass, and diversity between inshore (IW, IE), nearshore (NW, NE) and offshore zones (OW, OE), as well as eastern (IE, NE, OE) and western regions (IW, NW, OW).

Univariate Analyses - Size Spectra

We constructed aggregate length-frequencies for each trawl site to assess trends in overall community structure, using length data from all fish and invertebrates that were measured. Length frequencies were generated by pooling across species and plotting logarithmic frequency against geometric length class (Warwick 1984). These specifications reduced noise in the length-frequency distributions and facilitated ecological interpretation (White et al. 2007).

Statistical Methods - Multivariate Analyses

In contrast to the univariate analyses described above, all demersal species were included in multivariate analyses to fully resolve spatial patterns in species composition. We used the Plymouth Routines In Multivariate Ecological Research (PRIMER), version 6.0, for all multivariate analyses (Clark & Gorley 2006). Species-specific fish abundance data from each site were fourth-root transformed to reduce the influence of highly abundant species and a Bray-Curtis similarity index was used to measure the similarity in fish community composition between sites. The Bray-Curtis measure is widely used and has properties that are desirable for ecological studies, such as complementarity, localization, and dependence on totals (Clarke et al. 2006). A multi-dimensional scaling plot (MDS plot) was derived from the similarity matrix to ordinate the sites in two dimensions such that the relative distances apart of all points are in the same rank order as the dissimilarities of the study sites (Kruskal & Wish 1978). Accordingly, points that are close together represent sites that have very similar species assemblages and points that are far apart represent sites that have highly dissimilar species assemblages. We used MDS plots to visualize between-site similarity in fish community compositions.

Multivariate Analyses – Seasonality & Geography

We performed an analysis of similarity (ANOSIM) on the Bray-Curtis similarity matrix of species-specific fish abundance using season (spring, summer, fall, winter) as a factor. ANOSIM tests the null hypothesis that there are no differences between groups of samples (the fish abundance Bray-Curtis similarity matrix) when examined in the context of an *a priori* factor (season) (Clarke 1993). An R value of 0 indicates there are no differences between groups, while an R value greater than 0 reflects the degree of the differences. The test was permuted 999 times to generate a significance level ($p<0.05$ used here).

Permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008) was used to test for geographic differences in species composition. For these tests the factors were zone (inshore, nearshore, offshore) and east-west region, corresponding to Rhode Island Sound and Block Island Sound. Permutations of the residuals (9999) were used to test main effects of zone and region and their interactions. Pair-wise contrasts were made between zones.

Multivariate Analyses - Species Assemblage Analysis

We used hierarchical clustering analysis with a group-average linking algorithm to divide trawl sites into groups based on the similarity of fish community composition. The cluster analysis was carried out with the SIMPROF routine, which determines statistically significant station clusters within an *a priori* ungrouped set of stations (Clarke 1993). We used the SIMPER function to determine the group of species that characterized each species assemblage group.

Results:

A total of 101 fish and invertebrate species were caught during otter trawl and beam trawl surveys, of which 25 species were consistently prevalent (Table 1.1). Scup, *Stenotomus chrysops*, little skate, *Leucoraja erinacea*, and silver hake, *Merluccius bilinearis*, were the most abundant species caught in otter trawls. Together, these species accounted for 93.2% of otter trawl catch. Sand dollars, *Echinarachnius parma*, sea stars, *Astropecten* sp. and *Asterias* sp., and sea scallops, *Placopecten magellanicus*, were the most abundant species caught in beam trawls. These species accounted for 98.5% of beam trawl catch. Species are referred to by common name for the remainder of the results and discussion (refer to Table 1.1 for scientific names).

Univariate Analyses

Univariate Analyses - Seasonality & Geography

Both season and trawl type had a significant effect on fish community abundance, biomass and diversity (ANOVA $p<0.05$). Thus, otter trawl and beam trawl data were considered separately for the remainder of the analyses. Furthermore, spring otter trawls and winter beam trawls were excluded from analysis due to low sample sizes and limited temporal and spatial coverage. As such, the following results reflect 105 otter trawls conducted in the fall of 2009, 2010, and 2011, and 38 beam trawls conducted in the summer of 2011 and 2012 (Figure 1.1).

We identified both regional (East-West) and zonal (Inshore-Nearshore-Offshore) patterns in demersal fish and invertebrate community abundance, biomass, and diversity throughout Rhode Island and Block Island Sounds (Figure 1.2). Spatial trends in fish community abundance were primarily regional, with higher fish abundance in the western region around Block Island (otter trawl: $p=0.03$; beam trawl: $p=0.08$). Zonal trends in fish community abundance were not significant. Fish community biomass, however, exhibited a distinct gradient from inshore to offshore, with the greatest fish biomass in the offshore zone (otter trawl: $p=0.004$). This zonal trend was most pronounced in Block Island Sound, but was persistent throughout the study area. Fish community diversity exhibited similar spatial patterns as biomass, with the highest diversity in the offshore zone (otter trawl: p<0.001; beam trawl: p=0.01). Pairwise comparison of subsections further identified two areas of particularly high biodiversity: 1) North of Cox's ledge (NE) and, 2) South of Block Island (OW) (otter trawl: p=0.003; beam trawl: p=0.04; Figures 1 and 2).

Univariate Analyses - Size Spectra

Considered together, beam trawls and otter trawls sampled a broad size spectrum of the demersal fish and invertebrate community in Rhode Island and Block Island Sounds (Figure 1.3). The beam trawl captured a higher number of smaller individuals and the otter trawl captured more larger individuals with good overlap at intermediate lengths. Small individuals (<20 cm) were more prevalent in the western region of the study area, whereas larger individuals (>60 cm) were more abundant offshore. These spatial patterns in length frequencies reflect the presence of ultra-abundant species, such as spiny dogfish and *Cancer* spp. crabs.

Multivariate Analyses

Despite catch data standardization by area towed, we found that otter trawls and beam trawls caught different species assemblages (ANOSIM: R=0.925, p=0.001). For this reason, we conducted separate multivariate analyses for otter trawl and beam trawl catch data.

Multivariate Analyses - Seasonality & Geography

Our analyses revealed a strong seasonal signal in demersal fish community composition (ANOSIM: Otter Trawl - R=0.722, p=0.001; Beam Trawl - R=0.349, p=0.001). Abundant black sea bass and winter flounder characterized spring catches, whereas abundant silver hake and summer flounder characterized fall catches. This seasonal signal reflects the inshore-offshore migration of demersal fish species in the spring and fall. To facilitate spatial analysis of species assemblages and clarify ecological interpretations, we excluded spring otter trawls and winter beam trawls from cluster analysis. Thus, the following results reflect 105 otter trawls conducted in the fall of 2009, 2010, and 2011, and 39 beam trawls conducted in the summer of 2011 and 2012 (Figure 1.1).

Permutational MANOVA revealed significant differences in fish species composition by zone (otter trawl: p<0.001; beam trawl: p=0.001). The demersal fish assemblage offshore was more distinct than those in nearshore and inshore zones. There were also significant interactions between zone and region. For the otter trawl data, the inshore-offshore gradient was stronger in Rhode Island Sound than Block Island Sound. For the beam trawl data, the inshore-offshore gradient was more pronounced in Block Island Sound, because there were few shallow beam trawl stations in Rhode Island Sound.

Multivariate Analyses - Otter Trawl Species Assemblages

Hierarchical cluster analysis of the species abundance data from each otter trawl revealed five species assemblage groups in Rhode Island and Block Island

Sounds (Figure 1.4). Of the 105 sites sampled, the majority (80 of 105) were characterized by scup and summer flounder. Of the remaining sites, 17 were characterized by spiny dogfish and sea scallops, three were characterized by silver hake and summer flounder, two were characterized by black sea bass and sea scallops, and two were characterized by silver hake and American lobster. One otter trawl site had a unique fish community structure, reflecting an overall low abundance and diversity.

Otter trawls clustered primarily by location and in some cases by year, reflecting both permanent (i.e. depth) and transient (i.e. bottom temperature) habitat characteristics. When examined spatially, the clusters indicate geographic grouping of species assemblages (Figure 1.5). For example, there are assemblages associated with deeper waters, shallow waters, and the northern extent of Cox's Ledge. More specifically, we found higher densities of scup, summer flounder, skates (*Leucoraja* spp.), and lobster inshore and around Block Island, and higher densities of spiny dogfish and sea scallops offshore (Figure 1.5). Many sites sampled in different years fell into the same cluster, which indicates that the species composition at these sites is stable from year to year.

Multivariate Analyses - Beam Trawl Species Assemblages

Cluster analysis of the species abundance data from each beam trawl revealed six distinct species assemblage groups in Rhode Island and Block Island Sounds (Figure 1.6). Of the 38 sites sampled, 14 were characterized by *Leucoraja* spp.

skates and *Cancer* spp*.* crabs, nine were characterized by sea scallops and sand dollars, six were characterized by sea scallops and sea stars, five were characterized by silver hake and American lobster, and three were characterized by yellowtail flounder and sea scallops. One beam trawl site, located just east of Montauk Point, supports a particularly unique demersal community (Figure 1.6 & 7). Many species caught were unique to that site, such as white sea cucumbers (*Pentamera* sp.), short-browed mud shrimp (*Callianassa atlantica*), mantis shrimp (*Squilla empusa*), and clearnose skate (*Raja eglanteria*).

When examined spatially, the clusters indicate geographic grouping of species assemblages (Figure 1.7). For example, species assemblages characterized by sea scallops, sand dollars, and yellowtail flounder are associated with flat, sandy seafloor found offshore, while species assemblages characterized by silver hake and lobster are associated with shallow, irregular seafloor found north of Block Island (Figure 1.7). Overall, we found higher densities of skates (*Leucoraja* spp.), crabs (*Cancer* spp*.*), and lobster inshore and around Block Island and higher densities of sea scallops, yellowtail flounder, sea stars, and sand dollars offshore.

Discussion:

This study suggests that the spatial structure of the demersal fish and invertebrate community in Rhode Island and Block Island Sounds is persistent from year to year, yet distinct by season. We found pronounced gradients in fish community biomass, diversity and species composition extending from inshore to offshore waters, as well as patterns related to the differing bathymetry of Block Island Sound and Rhode Island Sound. Cluster analysis revealed geographically distinct species assemblages, which appear to be shaped by a combination of physical, oceanographic and biological factors.

Data from other trawl surveys conducted throughout Rhode Island and Block Island Sounds (National Marine Fisheries Service Bottom Trawl Survey, Rhode Island Department of Environmental Management Trawl Survey, University of Rhode Island Graduate School of Oceanography Fish Trawl Survey) corroborate this interannual consistency and seasonal variability of the demersal fish community (Bohaboy et al. 2010). These trends reflect the temperate nature of the ecosystem as well as the seasonal migrations of fish and invertebrate species, such as winter flounder and lobster (Deegan 1993, Oviatt 2004, Scopel et al. 2009, Wuenschel et al. 2009). In ecosystems such as this, where sub-annual climactic cues determine species distributions, it is essential to incorporate seasonal dynamics in spatial management plans so as to account for potential impacts to all life stages and species present throughout the year.

The geographic patterns in fish community abundance, biomass, diversity, and species assemblage within Rhode Island and Block Island Sounds may be influenced by a variety of factors, including primary production, water depth and benthic habitat (Gratewick & Speight 2005, Bosman et al. 2011, Planque et al. 2011). Spatial patterns of demersal fish community abundance are often related to trends in primary production (Iverson 1990), which preliminary studies have found to be higher in Block Island Sound than in Rhode Island Sound during summer months (Nixon et al. 2010). If the typical bottom-up ecological model is followed, this pattern in primary production would lead to increased fish abundance in Block Island Sound, which we document here (McQueen et al. 1989, Hunter & Price 1992). As such, this study provides initial evidence for the coupling of chlorophyll and fish production in Rhode Island's coastal waters. Ongoing studies that directly link primary production to fish community dynamics, however, are crucial to understanding the strength of bottom-up forcing in Rhode Island and Block Island Sounds (Friedland et al. 2012). This mechanism is particularly important to understand prior to offshore development, as the distribution and quantity of primary production may be altered by new ocean uses (Lindeboom et al. 2011, Chassot et al. 2007).

In addition to the bottom-up effects of regional-scale spatial variability in primary production, the megafaunal community in Rhode Island and Block Island Sounds may also be influenced by top-down predation pressure, operating at finer scales. Top-down control posits that consumer species structure the ecological community via predation, such that an increase in predator populations (i.e. spiny dogfish, summer flounder, black sea bass) leads to a decrease in prey abundance (i.e. scup, butterfish, lobster, crabs) (Carpenter et al. 1985). In Rhode Island and Block Island Sounds, offshore development will likely alter benthic habitat, which may enhance predator populations, and thus impact demersal fish and invertebrate community structure (Boehlert & Gill 2010). Furthermore, previous work has shown that, even in the absence of habitat alteration, predation pressure influences the distribution and recruitment patterns of various species that inhabit the study area (Levin et al. 1997, Garrison et al. 2000, Lough 2010). Thus, local-scale predation pressure may play an important role in structuring the demersal species assemblage in Rhode Island and Block Island Sounds. However, further research is needed to fully understand the interacting effects of bottom-up and top-down trophic forces in this dynamic area.

The affinity of demersal fish assemblages for specific depth ranges has been observed in a variety of ecosystems (Persohn et al. 2009, Sonntag et al. 2009). Relationships between fish community biomass and water depth are also apparent in other bottom trawl surveys conducted in this area (Bohaboy et al. 2010). While water depth was a significant determinant of fish community composition within Rhode Island and Block Island Sounds, our work suggests that fish species assemblages are also shaped by the physical features of the surrounding seafloor and the proximity to hard-bottom habitat (i.e. Cox's Ledge, Southwest Ledge, Block Island). Thus, depth-based ecosystem classifications that have been widely used in marine spatial planning may, in themselves, not be sufficient for Rhode Island and Block Island Sounds (Douvere & Ehler 2009).

A general paradigm about marine benthic communities is that, as bottom complexity increases from smooth sand and mud to rock and cobble, ecological complexity and species diversity increase (Salomon et al. 2010). The presumed relationship is that the more heterogeneous the habitat, the more species it can support because more niches are available (Guegan et al. 1998, Levin et al. 2001, Eriksson et al. 2006). This pattern appears to hold true in Rhode Island's offshore waters, where the more complex seafloor (i.e. more habitat diversity) around Block Island and Cox's Ledge supports more diverse fish communities than the less complex seafloor found inshore (LaFrance et al. 2010). However, a detailed analysis that couples site-specific benthic habitat parameters and demersal fish community metrics is needed to fully understand the fish-habitat relationship in Rhode Island and Block Island Sounds (Anderson et al. 2009, 2013). This relationship is particularly important to understand in order to site offshore development activities in appropriate habitats that will minimize the impacts on resident species (Cogan et al. 2009).

A core challenge of developing an ecosystem-based spatial management plan is selecting species or species-groups to serve as ecological indicators (Methratta & Link 2006). In systems such as Rhode Island and Block Island Sounds, where a wide variety of species constitute the fish community, ecological indicator species should represent all functional groups present (i.e. piscivore, benthivore, planktivore). In this way, management plans will be sensitive to: 1) species that structure the ecological community via predation (piscivores), 2) species that are most sensitive to changes in the physical features of the seafloor (benthivores), and 3) species that respond rapidly to changes in primary production (planktivores) (Carpenter et al. 1985, Lindeboom et al. 2011). Thus, we propose the following indicator species for Rhode Island and Block Island Sounds: summer flounder, silver hake, black sea bass, American lobster, and sea scallop. These species were selected based upon the aforementioned criteria as well as to their significance in structuring the aggregate fish community and otter trawl and beam trawl species assemblage groups. Carefully selecting indicator species to track ecosystem change, as outlined above, provides essential insight into the structure and function of complex fisheries food webs in highly dynamics areas, such as Rhode Island and Block Island Sounds.

Many spatial management plans suffer from a lack of information at an appropriate spatial scale (Gilliland & Laffoley 2008, Douvere & Ehler 2009). The spatial coverage and sampling densities of federal trawl surveys, such as the Northeast Fisheries Science Center's Bottom Trawl Survey (~1 station per 687 km^2), and inshore trawl surveys, such as NEAMAP (~1 station per 130 km^2), are insufficient for assessing the small-scale patterns in fish and invertebrate communities that is necessary for local marine spatial planning (Stauffer 2004, Bonzek et al. 2011). The sampling density of the work presented here (~1 station per 20 km^2), however, enables the identification of fine-scale spatial trends in demersal fish assemblages, thus providing a scientific foundation for spatial management planning for Rhode Island and Block Island Sounds. Furthermore, the methods for this study are consistent with European guidelines for assessing the impacts of offshore wind turbines on the marine environment, and as such provide a baseline for measuring the cumulative effects of offshore development projects within Rhode Island and Block Island Sounds (CEFAS 2004, BSH 2013). Thus, the incorporation of this research into marine spatial planning efforts will help to conserve and protect the ecological resiliency of Rhode Island's coastal waters and the variety of uses it supports (Gilliland & Laffoley 2008).

Ultimately, this work provides a novel description of the spatial structure of the demersal fish and invertebrate community in Rhode Island and Block Island sounds, serving as a microcosm for similar fish biogeography studies along the Atlantic coast of North America and other continental shelves around the world. Furthermore, the species assemblage characterization established by this work provides a baseline against which to measure the impacts of imminent climate change in the highly dynamic southern New England region. Moreover, by sampling areas slated for offshore development as well as suitable control sites, this research facilitates future efforts to understand the severity and extent of the ecological impacts from offshore wind farm development. The spatial scale (10s of km) of this work makes it particularly useful for spatial management planning, as ~10 km is likely to be the minimum scale for development activities and their associated management, as well as the smallest scale at which we can detect differences in habitat use by demersal fish (Jay 2010, Collie et al. 2013). Thus, our approach serves as a model for other fisheries surveys that aim to inform marine spatial planning in nearshore ecosystems.

Literature Cited:

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd., Plymouth, UK, 214 pp.

Anderson, T. J., Syms, C., Roberts, D. A., Howard, D. F., 2009. Multi-scale fish–habitat associations and the use of habitat surrogates to predict the organization and abundance of deep-water fish assemblages. Journal of Experimental Marine Biology and Ecology 379: 34–42.

Anderson, T.J. McArthur, M.A., Syms, C., Nichol, S., Brooke, B., 2013. Infaunal biodiversity and ecological function on a remote oceanic island: The role of biogeography and bio-physical surrogates. Estuarine, Coastal and Shelf Science 117: 227-237.

Boehlert, G. W., and, Gill, A.B. 2010. Environmental and ecological effects of ocean renewable energy development: a current synthesis. Oceanography 23 (2): 68-81.

Bohaboy, E.C., Malek, A.J., Collie, J.S., 2010. Baseline characterization: data sources, methods, and results. Technical Report #13 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island

Bonzek, C.F., Garland, J., Lange, J.D. Jr., Latour, R.J., 2010. Northeast Area Monitoring and Assessment Program Final Report Fall 2007 - Fall 2010. Virginia Institute of Marine Science, 220 p. Accessed at http://www.neamap.net/publications/NEAMAP_Data%20Report_Fall07-Fall2011.pdf

Bosman, S. H., Methven, D.A., Courtenay, S. C., Hanson, J. M., 2011. Fish assemblages in a north Atlantic coastal ecosystem: Spatial patterns and environmental correlates. Estuarine, Coastal and Shelf Science 92: 232–245.

Bundesamt für Seeschifffart unh Hydrologie (BSH), 2013. Investigation of the impacts of offshore wind turbines on the marine environment. Federal Maritime and Hydrographic Agency, Hamburg, Germany, 87 pp.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. Bioscience 35: 634-639.

The Centre for Environment, Fisheries, and Aquaculture Science (CEFAS), 2004. Offshore Wind Farms: Guidance Note for Environmental Impact Assessment in Respect of FEPA and CPA Requirements, Version 2. Lowestoft, United Kingdom, 44 pp.

Chassot, E., Melin, F., Le Pape, O., Gascuel, D., 2007. Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. Mar Ecology Progress Series 343: 45–55.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd., Plymouth, UK, 190 pp.

Clarke, K.R., Somerfield, P.J., Chapman, M.G., 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. Journal of Experimental Marine Biology and Ecology 330: 55–80.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Cogan, C. B., Todd, B. J., Lawton, P., Noji, T. T., 2009. The role of marine habitat mapping in ecosystem-based management. ICES Journal of Marine Science 66: 2033–2042.

Collie, J.S., Wood, A.D., Jeffries, H.P., 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences 65: 1352-1365.

Collie, J.S., Adamowicz, W.L., Beck, M.W., Craig, B., Essington, T.E., Fluharty, D., Rice, J., Sanchirico, J.N., 2013. Marine spatial planning in practice. Estuarine, Coastal and Shelf Science 117: 1-11.

Costa-Pierce, B., 2010. Ecology of the SAMP. Chapter #2 in Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Crowder, L., Norse, E., 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. Marine Policy 32: 772-778.

Cury, P.M., Mullon, C., Garcia, S.M., Shannon, L.J., 2005. Viability theory for an ecosystem approach to fisheries. ICES Journal of Marine Science 62: 577–584.

Deegan, L. A., 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. Canadian Journal of Fisheries and Aquatic Science 50: 74-79.

Douvere, F., Ehler, C. N., 2009. New perspectives on sea use management: initial findings from European experience with marine spatial planning. Journal of Environmental Management 90: 77–88.

Eriksson, B.K. , Ruback, A., Hillebrand, H., 2006. Biotic habitat complexity controls species diversity and nutrient effects on net biomass production. Ecology 87**:** 246-254.

Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.R., Prahler, E., Rohr, N., Sivas, D.,Beck, M.W., Carr, M.H., Crowder, L.B., Duffy, J.E., Hacker, S.D., McLeod, K.L., Palumbi, S.R., Peterson, C.H., Regan, H.M., Ruckelshaus, M.H., Sandifer, P.A., Steneck, R.S., 2010. Guiding ecological principles for marine spatial planning. Marine Policy 35: 955-966.

Franco, A., Pérez-Ruzafa, A., Drouineau, H., Franzoi, P., Koutrakis, E.T., Lepage, M., Verdiell-Cubedo, D., Bouchoucha, M., López-Capel, A., Riccato, F., Sapounidis, A., Marcos, C., Oliva-Paterna, F.J., Torralva-Forero, M., Torricelli, P., 2012. Assessment of fish assemblages in coastal lagoon habitats: Effect of sampling method. Estuarine, Coastal and Shelf Science 112: 115-125.

Friedland, K. D., Stock, C., Drinkwater, K. F., Link, J. S., Leaf, R. T., Shank, B. V, Rose, J. M., Pilskaln, C.H., Fogarty, M.J., 2012. Pathways between primary production and fisheries yields of large marine ecosystems. PloS ONE 7, e28945.

Gabriel, W.L., 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, Northwest Atlantic. Journal of Northwest Atlantic Fisheries Science 14: 29-46.

Gilliland, P. M., Laffoley, D., 2008. Key elements and steps in the process of developing ecosystem- based marine spatial planning. Marine Policy 32: 787–796.

Gratewick, B., Speight, M.R., 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66: 650-667.

Guegan, J.F., Lek, S., Oberdorff, T., 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. Nature 391: 382-384.

Hale, S. S., 2010. Biogeographical patterns of marine benthic macroinvertebrates along the Atlantic coast of the northeastern USA. Estuaries and Coasts 33, 1039–1053.

Hill, M.O., 1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54: 327- 432.

Hasbrouck, E.C, Scotti, J., Stent, J., Gerbino, K., 2011. Rhode Island commercial fishing and seafood industries: The development of an industry profile. Commercial Fisheries Research Foundation, Kingston, Rhode Island, 124 pp.

Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724-732.

Iverson, R.L., 1990. Control of marine fish production. Limnology and Oceanography 35, 1593-1604.

Jay, Stephen. 2010. Planners to the rescue: Spatial planning facilitating the development of offshore wind energy. Marine pollution bulletin 60 (4): 493-499.

Jordaan, A.,Chen, Y., Townsend, D.W., Sherman, S., 2010. Identification of ecological structure and species relationships along an oceanographic gradient in the Gulf of Maine using multivariate analysis with bootstrapping. Canadian Journal of Fisheries and Aquatic Sciences 67: 701-719.

Kruskal, J.B., Wish, M., 1978. Multidimensional Scaling. Sage Publications, Beverly Hills, California, 92 pp.

LaFrance, M., Shumchenia, E., King, J., Pockalny, R., Oakley, B., Pratt, S., Boothroyd, J., 2010. Benthic habitat distribution and subsurface geology at selected sites from the Rhode Island Ocean Special Area Management Study Area. Technical Report #4 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Ecology, Evolution and Systematics 32: 51-93.

Lindeboom, H. J., Kouwenhoven, H. J., Bergman, M. J. N., Bouma, S., Brasseur, S., Daan, R., Fijn, R. C., de Haan, D., Dirksen, S., van Hal, R., Hille Ris Lambers, R., ter Hofstede, R., Krijgsveld, K.L., Leopold, M., Scheidat, M., 2011. Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. Environmental Research Letters 6: 035101.

Mahon, R., Brown, S. K., Zwanenburg, K. C., Atkinson, D. B., Buja, K. R., Claflin, L., Howell, G. D., Monaco, M.E., O'Boyle, R.N., Sinclair, M., 1998. Assemblages and biogeography of demersal fishes of the east coast of North America. Canadian Journal of Fisheries and Aquatic Sciences 55: 1704–1738.

McLeod, K.L., Lubchenko, J., Palumbi, S.R.,Rosenberg, A.A., 2005. Scientific consensus statement on marine ecosystem-based management. Communication Partnership for Science and the Sea. Available: http://www.compassonline.org/.

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J., Lean, D.R.S., 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59: 289–309.

Methratta, E., Link, J., 2006. Evaluation of quantitative indicators for marine fish communities. Ecological Indicators 6: 575–588.

Nixon, S. W., Fulweiler, R. W., Buckley, B. A., Granger, S. L., Nowicki, B. L., Henry, K. M., 2009. The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay. Estuarine, Coastal and Shelf Science 82: 1–18.

Nixon, S., Granger, S., Oviatt, O., Fields, L., Mercer, J., 2010. Spatial and temporal variability of surface chlorophyll, primary production, and benthic metabolism in Rhode Island and Block Island Sounds. Technical Report #9 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series 393: 111-129.

Oviatt, C. A., 2004. The changing ecology of temperate coastal waters during a warming trend. Estuaries, 27: 895–904.

Pauly, D., Chuenpagdee, R., 2007. Fisheries and coastal ecosystems: the need for integrated management in sustainable resource management. Edward Elgar Publishing, Surrey, UK, 14 pp.

Persohn, C., Lorance, P., Trenkel, V.M., 2009. Habitat preferences of selected demersal fish species in the Bay of Biscay and Celtic Sea, North-East Atlantic. Fisheries Oceanography 18: 268-285.

Planque, B., Loots, C., Petitgas, P., Lindstrøm, U., Vaz, S., 2011. Understanding what controls the spatial distribution of fish populations using a multi-model approach. Fisheries Oceanography 20: 1–17.

Punt, M.J., Groeneveld, R. A., van Ierland, E. C., Stel, J. H., 2009. Spatial planning of offshore wind farms: A windfall to marine environmental protection? Ecological Economics 69: 93–103.

Rhode Island Special Area Management Plan (RI SAMP), 2010. Coastal Resources Management Council, Wakefield, Rhode Island.

Salomon, A.K., Gaichas, S.K., Shears, N.T., Smith, J.E., Madin, E.M.P., Gaines, S.D., 2010. Key features and context-dependence of fishery-induced trophic cascades. Conservation Biology 24: 382-394.

Scopel, D.A., Golet, W.J., Watson, W.H., 2009. Home range dynamics of the American lobster, *Homarus americanus*. Marine and Freshwater Behavior and Physiology 42: 63-80.

Smith, B., Collie, J.S., Lengyel, N.L., 2013. Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fish on northern Georges Bank. Marine Ecology Progress Series 472: 199-217.

Sonntag, N., Garthe, S., Adler, S., 2009. A freshwater species wintering in a brackish environment: Habitat selection and diet of Slavonian grebes in the southern Baltic Sea. Estuarine, Coastal and Shelf Science 84: 186-194.

Smythe, T., Beutel, D., 2010. Fisheries activity maps: methods and data sources. Technical Report #15 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Stauffer, Gary (compiler). 2004. NOAA Protocols for Groundfish Bottom Trawl Surveys of the Nation's Fishery Resources. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-F/SPO-65, 205 p.

Ullman, D.S., Codiga, D.L., 2010. Characterizing the physical oceanography of coastal waters off Rhode Island, Part 2: New observations of water properties, currents and waves. Technical Report #3 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, RI.

Warwick, R.M., 1984. Species size distributions in marine benthic communities. Oecologia 61: 32-41.

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., Enquist, B. J., 2007. Relationships between body size and abundance in ecology. Trends in Ecology and Evolution 22: 323–330.

Wuenschel, M.J., Able, K.W., Byre, D., 2009. Seasonal patterns of winter flounder *Pseudopleuronectes americanus* abundance and reproductive condition on the New York Bight continental shelf. Journal of Fish Biology 74: 1508-1524.

Table 1.1. Mean abundance and biomass of the 25 most common species caught in otter trawls and beam trawls from 2009-2012. All data are standardized by area swept.

		OTTER TRAWL		**BEAM TRAWL**	
Common Name	Scientific Name	Mean Abundance (number/km^2)	Mean Biomass (kg/km^2)	Mean Abundance (number/km^2)	Mean Biomass (kg/km^2)
American lobster	*Homarus americanus*	111.7	32.4	148.2	36.5
Atlantic torpedo	*Torpedo nobiliana*	5.8	139.0	2.6	200.5
Black seabass	*Centropristis striata*	77.8	60.6	38.3	0.5
Clearnose skate	*Raja eglanteria*	20.2	27.3	5.1	6.7
Fourspot flounder	*Paralichthys oblongus*	192.0	31.5	1,052.7	155.0
Jonah/Rock crab	*Cancer spp.*	54.7	6.3	10,519.2	1,272.2
Little skate	*Leucoraja erinacea*	6,198.7	3,609.7	11,722.6	6,349.4
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	1.3	0.2	337.3	7.9
Monkfish	*Lophius americanus*	6.1	19.1	145.6	260.9
Northern searobin	*Prionotus carolinus*	324.1	12.3	281.1	55.4
Ocean quahog	*Arctica islandica*	14.7	3.2	275.9	56.4
Red hake	*Urophycis chuss*	129.9	14.3	523.8	50.9
Sand dollar	*Echinarachnius parma*	0.6	0.0	2,540,851.3	1,391.9
Scup	*Stenotomus chrysops*	89,954.5	2,207.9	235.1	8.2
Sea scallop	*Placopecten magellanicus*	350.4	24.9	25,665.6	4,226.5
Sea star	*Asterias & Astropecten spp.*	437.4	3.5	152,915.5	1,266.8
Silver hake	*Merluccius bilinearis*	2,765.9	190.2	641.3	87.6
Spiny Dogfish	*Squalus acanthias*	1,511.0	4,017.9	7.7	20.5
Spotted hake	*Urophycis regius*	313.6	47.4	235.1	29.6
Striped searobin	*Prionotus evolans*	133.8	51.8	35.8	7.2
Summer flounder	*Paralichthys dentatus*	248.9	266.6	86.9	83.4
Windowpane flounder	*Scophthalmus aquosus*	322.5	53.8	457.4	109.7
Winter flounder	*Pseudopleuronectes americanus*	984.9	319.0	416.5	127.6
Winter skate	*Leucoraja ocellata*	878.7	1,009.9	5,475.5	2,838.1
Yellowtail flounder	*Limanda ferruginea*	28.2	8.7	255.5	76.8

Figure 1.1. Map of the study area showing the location of otter and beam trawls conducted from 2009-2012 and delineation of subsections. IW = Inshore West, IE = Inshore East, NW = Nearshore West, NE = Nearshore East, OW = Offshore West, OE = Offshore East. The red boundary delimits the extent of the Rhode Island Ocean Special Area Management Plan.

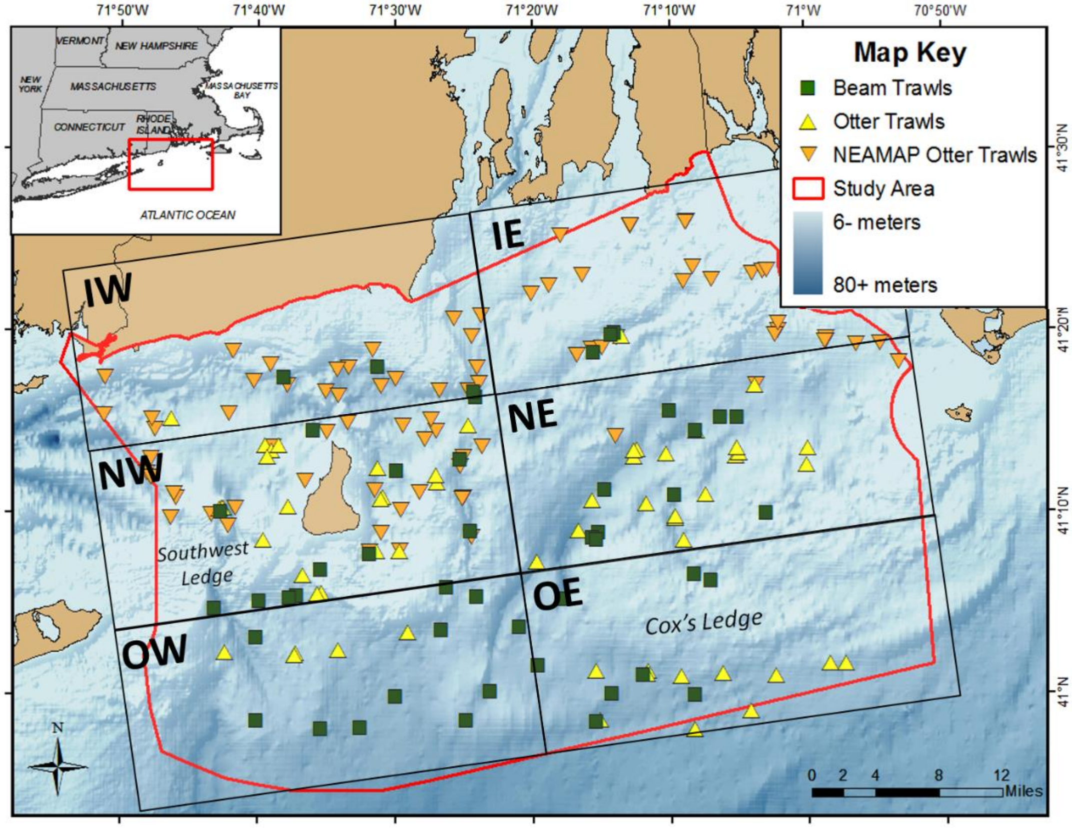


Figure 1.2. Aggregate abundance (number per km^2), biomass (kg per km^2), and diversity (Shannon Weiner H') of otter trawls and beam trawl catch in each subsection (Figure 1.1). All data were standardized by area swept. Pelagic species, sand dollars and sea stars were excluded due to differences in capture efficiency between beam trawls and otter trawls. All metrics are represented as proportions of the maximum. The error bars are standard error.

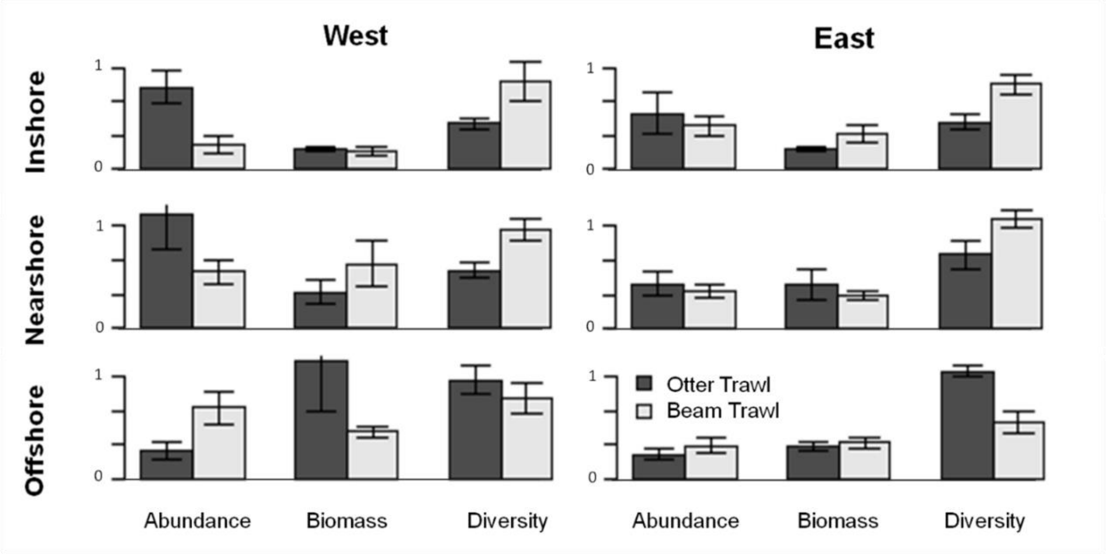


Figure 1.3. Aggregate size spectra of the demersal fish and invertebrate community within each subsection of Rhode Island and Block Island Sounds (Figure 1.1). Size spectra were generated by pooling across species and merging by subsection.

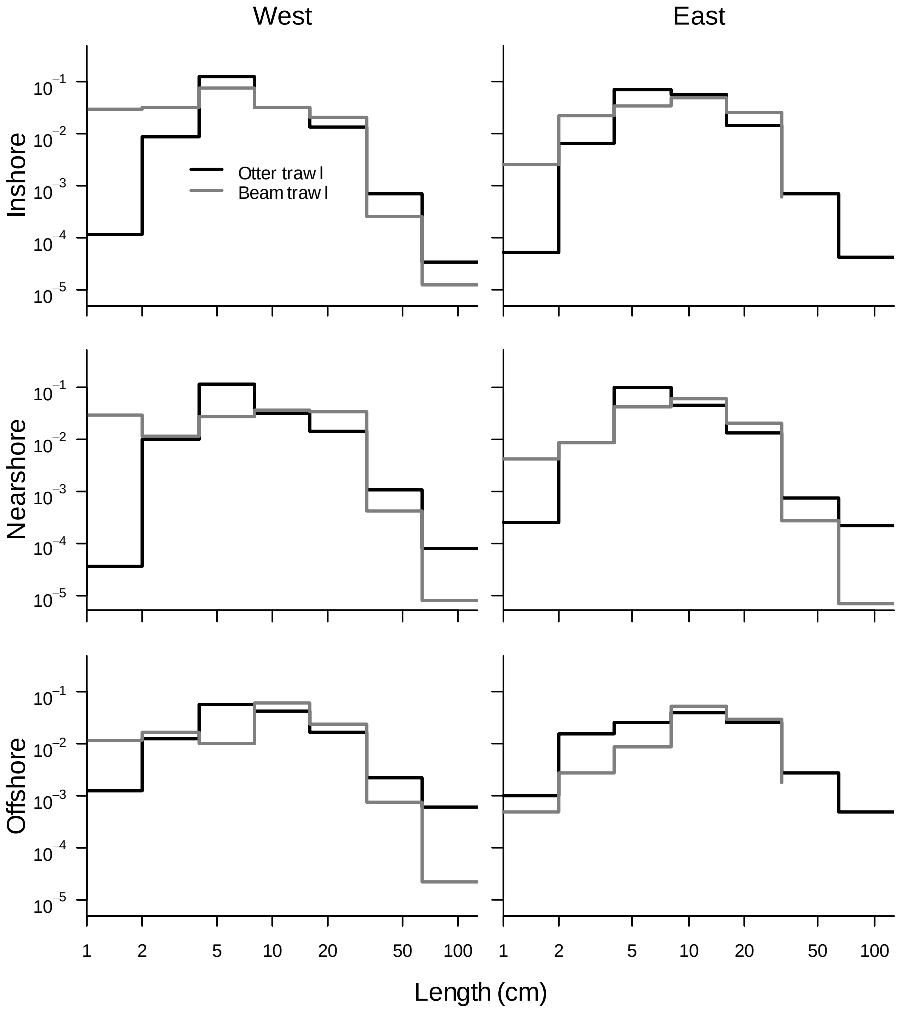


Figure 1.4. Ordination of the abundances of demersal fish and invertebrate species sampled with otter trawls within Rhode Island Sound and Block Island Sound. This non-metric multidimensional scaling plot (MDS) depicts the pattern in fish and invertebrate species composition, with similar species compositions close together. Each point represents one trawl. Symbols represent species assemblage groups, which are defined by characteristic species.

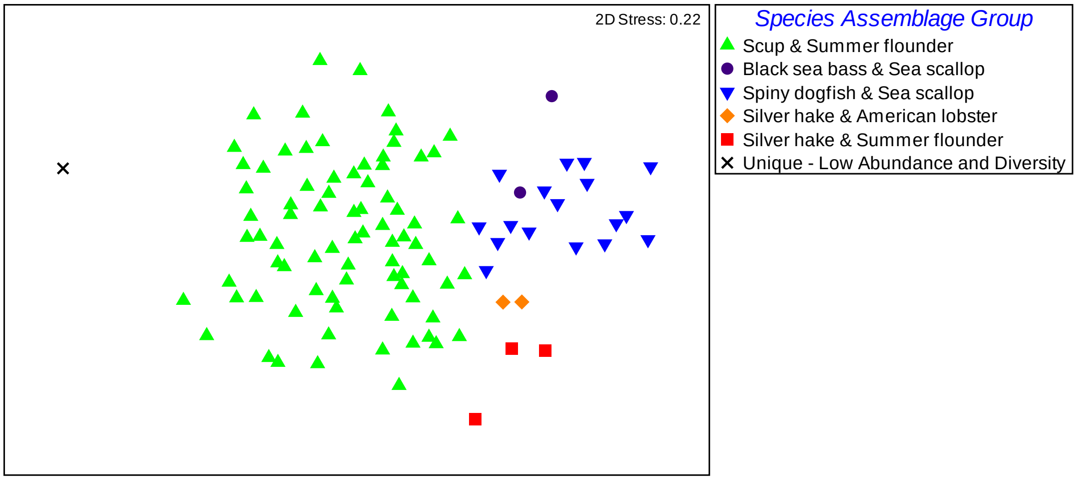


Figure 1.5. Distribution of demersal fish and invertebrate species assemblages sampled with otter trawls within Rhode Island Sound and Block Island Sound. Symbols represent species assemblage groups, defined by characteristic species (Figure 1.4).

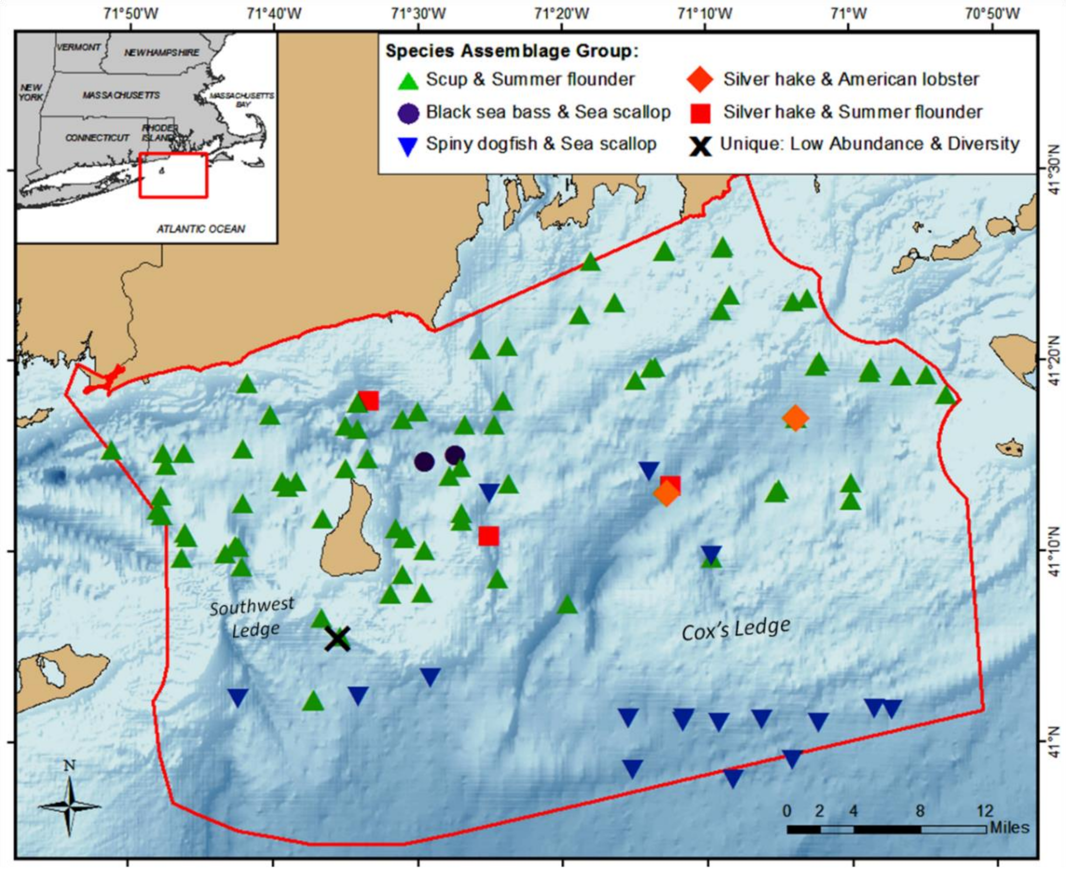


Figure 1.6. Multidimensional scaling plot depicting the abundances of demersal fish and invertebrate species sampled with beam trawls within Rhode Island Sound and Block Island Sound. Each point represents one beam trawl. Symbols represent species assemblage groups, which are defined by characteristic species.

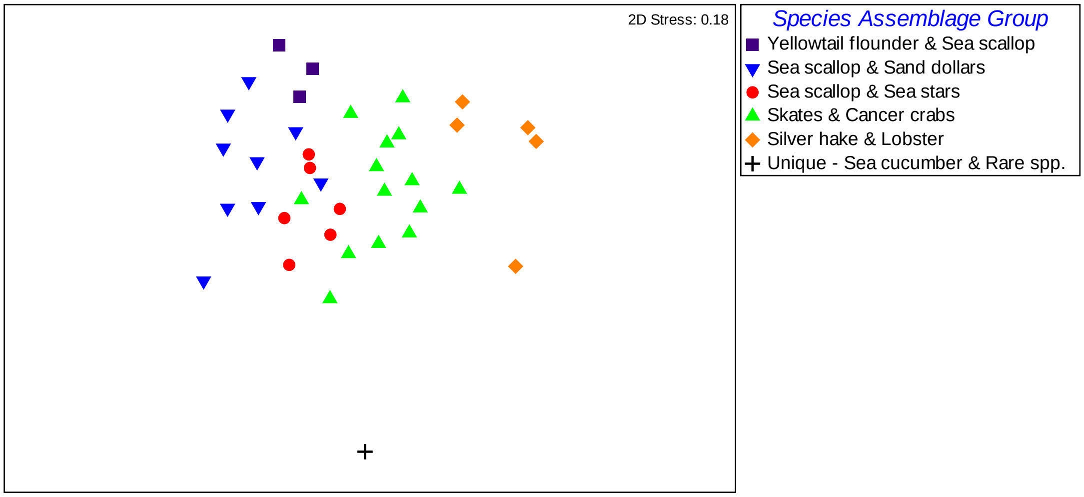
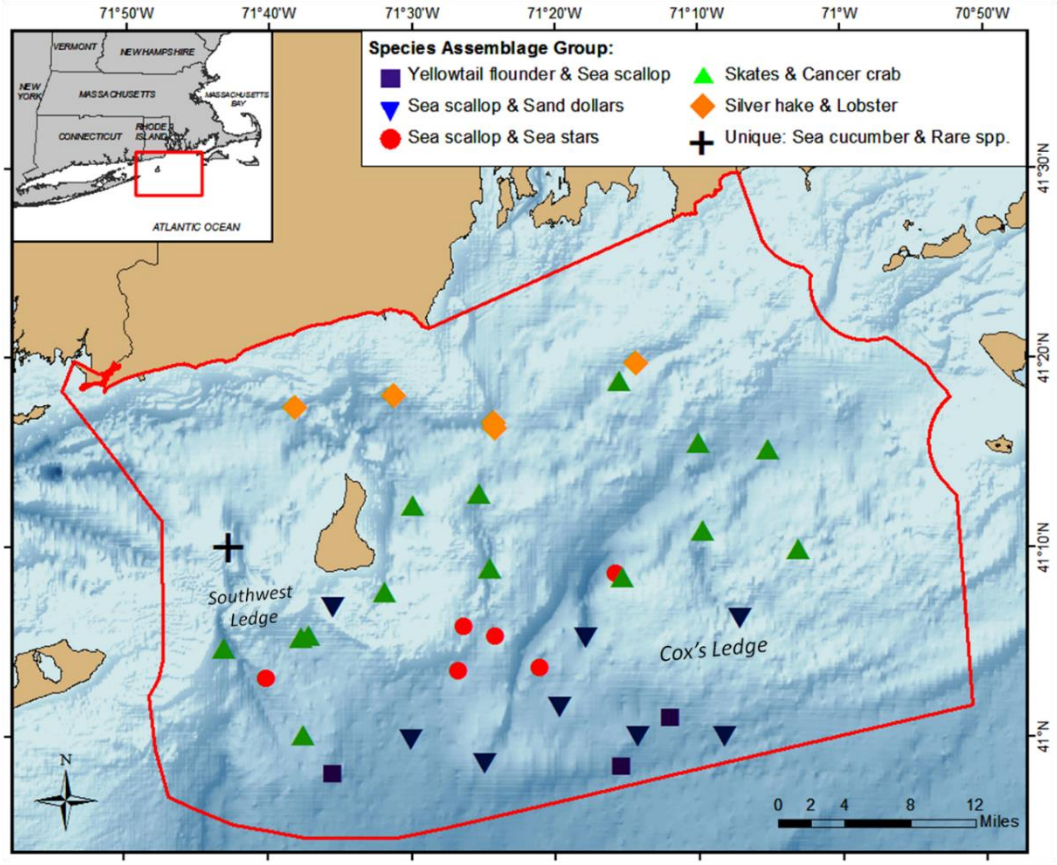


Figure 1.7. Distribution of demersal fish and invertebrate species assemblages sampled with beam trawls within Rhode Island Sound and Block Island Sound. Symbols represent species assemblage groups, defined by characteristic species (Figure 1.6).



CHAPTER 3

A manuscript prepared for submission to the Canadian Journal of Fisheries and Aquatic Sciences

Dietary Guilds and Trophic Structure of the Fish Community in Rhode Island Sound and Block Island Sound, USA

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Abstract:

In this study, we used a combination of dietary guild analysis and nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotope analysis to assess the trophic structure of the fish community in Rhode Island and Block Island Sounds, an area slated for offshore wind energy development. Between 2009 and 2011, stomach and tissue samples were taken from 20 fish and invertebrate species for analysis of diet composition and $\delta^{15}N$ and $\delta^{13}C$ signatures. Stomach content analysis was used to define trophic structure according to dietary guilds, while $\delta^{15}N$ and $\delta^{13}C$ stable isotopes were used to determine the trophic position of fish and invertebrate species and the relative importance of benthic and pelagic production in supporting the marine food web. The food chain in Rhode Island and Block Island Sounds consists of approximately four trophic levels. Within these trophic levels, the fish community is divided into distinct dietary guilds, including planktivores, benthivores, crustacean-eaters, and piscivores. Within these guilds, inter-species isotopic and dietary overlap is high, suggesting that resource partitioning or competitive interactions play a major role in structuring the fish community of this area. Carbon isotopes indicate that most fish are supported by pelagic phytoplankton, although there is evidence that benthic production also plays a role, particularly for obligate benthivores such as skates (*Leucoraja* spp.). This type of analysis is useful for developing an ecosystem-based approach to management, as it identifies species that act as direct links to basal resources as well as species groups that share trophic roles.

Introduction:

Globally, fisheries scientists and managers have asserted the need for an ecosystem-based approach to fisheries management to better account for the interactions among commercially harvested species and their prey, predators, and habitat (Pauly & Chuenpagdee 2007, Link 2010, Fogarty 2013). Development of ecosystem-based fisheries management, however, requires a thorough understanding of the trophic structure of the fisheries ecosystem of interest (Latour et al. 2003, Smith et al. 2007, Gilliland & Laffoly 2008). Such knowledge can be challenging to ascertain and apply, particularly in biologically and oceanographically complex ecosystems such as the northwest Atlantic continental shelf (Smith & Link 2010, Fogarty & Rose 2013). To address this challenge, methods such as dietary guild analysis and stable isotope analysis have been used to simplify the structure and function of highly complex ecosystems and examine the flow of energy through food webs (Fry 1988, Wilson 1999, Metcalf et al. 2008). We sought to apply these approaches to a nearshore Northwest Atlantic fisheries ecosystem, where recent interest in offshore energy development has focused attention on ecosystem-based spatial management planning (RI SAMP 2010, Malek et al. 2014).

Dietary guild analysis is a common approach for assessing the trophic structure of fisheries ecosystems (Hawkins & Macmahon 1989, Pasquaud et al. 2008, Reum & Essington 2008). By definition, a guild is “a group of species that exploit the same class of environmental resources in a similar way, and thus overlap significantly in their niche requirements” (Root 1967). As such, dietary guild analysis can be used to identify group of species with similar functional roles, and assess resource partitioning and competitive interactions within an ecosystem (Garrison & Link 2000). Theoretically, fisheries ecosystems are more stable when within-guild functional redundancy is high, as ecosystem function is maintained despite fluctuations in the abundance of individual guild members (Bell et al. 2014). The classification of species into dietary guilds enables the progression of ecosystem-based fisheries management, as species are assessed as functional groups, rather than individual species (Auster & Link 2009).

Nitrogen and carbon stable isotope analysis are also valuable tools in understanding the trophic structure of fisheries ecosystems (Peterson & Fry 1987, Hobson & Welch 1992, Layman et al. 2007). Specifically, nitrogen stable isotopes ($\delta^{15}N$) describe the time-integrated feeding history of a consumer and can be used to identify the trophic position of a species. The $\delta^{15}N$ content of a consumer's tissue is enriched approximately 3.4‰ relative to that of its diet due to trophic fractionation, thus reflecting the species' role in the marine food chain (Post 2002). Carbon stable isotopes ($\delta^{13}C$) are used to investigate the relative importance of different basal resources in supporting fish production (France 1993, Post 2002, Hobson et al. 1995, Mackenzie et al. 2011). Boundary layer effects lead to differential uptake of ^{13}C by pelagic phytoplankton and benthic macroalgae, such that the average $\delta^{13}C$ of pelagic phytoplankton is -22‰, while the average $\delta^{13}C$ of benthic macroalgae is -17‰ (Peterson & Fry 1987, France 1995). This disparity in the $\delta^{13}C$ of benthic and pelagic carbon sources is reflected in marine consumers, with benthic-feeding animals enriched approximately 5‰ compared to pelagic-feeding animals (Hobson & Welch 1992). In this way, the $\delta^{13}C$ of resident fish species reflect the initial carbon sources to the food web, thus allowing for the differentiation between pelagic and benthic food webs.

Although previous work has assessed the trophic structure of fish communities in the northwest Atlantic, the transitional seas of Rhode Island Sound and Block Island Sound have not been adequately sampled by routine state and federal surveys (Garrison & Link 2000, Jordaan et al. 2010, Smith et al. 2010). The fish community in Rhode Island Sound and Block Island Sound, however, is highly complex, both in terms of spatial distribution and seasonal patterns (Mahon et al. 1998, Hale 2010, Malek et al. 2014). Furthermore, Rhode Island and Block Island Sounds are an important migratory pathway for many fish species moving into and out of Narragansett Bay and Long Island Sound, and host commercial and recreational fishing activities that produce over $60 million in seafood landings annually (Costa-Pierce 2010, Smythe & Beutel 2010, Hasbrouck et al. 2011). Finally, offshore wind energy development is planned to begin in this area in the near future (RI SAMP 2010). Thus, it is essential that scientists and managers understand the trophic dynamics of this ecosystem, so as to be able to detect changes related to offshore development and other anthropogenic stressors.

In this study, we used a combination of fish stomach content and stable isotope analyses to assess the dietary guild structure and flow of energy through the fisheries food web in Rhode Island and Block Island Sounds. More specifically, we aimed to determine the relative importance of benthic and pelagic production in supporting the fisheries food web, whether species within the same dietary guilds maintain consistent trophic positions, and whether silver hake, scup, or winter flounder exhibit spatial patterns in foraging behaviors. These analyses are useful for developing an ecosystem-based approach to management, as they identify species that act as direct links to basal resources as well as species groups that share trophic roles.

Methods:

We assessed the diet compositions and trophic interactions of 20 fish species using stomach content analysis and stable isotope analysis (Table 2.1). Stomach and white tissue samples were collected for analysis of diet composition and nitrogen and carbon stable isotope signatures, respectively, during bottom trawl surveys conducted throughout Rhode Island and Block Island Sounds in September 2009-2011 (Figure 2.1).

Dietary Guild & Niche Breadth Analysis:

Stomach content analysis was used to define dietary guilds, which represent functionally similar species within the fish community. For highly abundant species, a random sub-sample of five fish per target species per station was selected for diet analysis. For less abundant species (< five individuals per station), all specimens were used for diet analysis. Fish stomachs were extracted immediately after capture and preserved in Normalin, a non-toxic preservative. In the laboratory, the contents of preserved stomachs were extracted and the total weight (mg wet weight) measured with an analytical balance (Bowman et al. 2000). All recovered prey items were identified to the lowest practical taxon with the aid of stereomicroscopes, and their contribution to overall diet was measured as percent of total stomach content weight (Hyslop 1980).

Data from 20 predator species and 1,762 stomach samples were used in the dietary guild analysis (Table 2.1). Stomach samples from an additional five species were collected and processed, but the sample sizes were not sufficient for inclusion in the guild analysis (>10 stomachs). Prey items were grouped based on dietary prevalence (by weight) and digestive state (fresh, partially digested, or well digested). Abundant prey items were grouped at lower taxonomic levels, while less abundant items were grouped at higher levels. The resulting prey classification consisted of 47 categories (Table 2.2).

A cluster sampling design was used to calculate the contribution of each prey type to the diet of individual predator species (Buckel et al. 1999). The mean proportional contribution of a prey type by weight was calculated using the following formula for each predator species.

$$W_k = \frac{\sum q_{sk} * M_s}{\sum M_s}, where \ q_{sk} = \frac{w_{sk}}{w_s}$$

where W_k is the proportional contribution of prey type *k* to the diet of a given predator species weighted by the number of that predator species caught at each station, q_{sk} is the proportional contribution of prey type *k* to the diet of a given predator species pooled over predator samples at station *s*, M_s is the number of a given predator species captured in a trawl at station *s*, w_s is the total weight of all prey for a given predator species from station *s*, and w_{sk} is the weight of prey type *k* for a given predator species at station *s*.

Levins (1968) standardized index of niche breadth was used to assess the dietary specialization of each predator species (Colwell & Futuyma 1971, Hulbert 1978), as follows.

$$B_i = \frac{\left(\frac{1}{\sum {p_{ik}}^2} - 1\right)}{N_i - 1}$$

where, (B_i) is the standardized index of niche breadth for predator species *i*, p_{ik} is the proportional contribution of prey type *k* to the diet of predator species *i* (W_k for predator *i*), and N_i is the total number of prey categories consumed by predator species *i* (Table 2.1). B_i ranges between 0 and 1, with a value of zero indicating maximum dietary specialization (i.e. a single prey type comprising a predator's diet) and 1 indicating nondiscrimination among prey (i.e. each prey type contributes the same proportion to a predator's diet).

The Schoener (1970) similarity index was used to assess the dietary overlap, D_{ij}, between predator category pairs (Garrison & Link 2000):

$$D_{ij} = 1 - 0.5 \left(\sum | p_{ik} - p_{jk} |\right)$$

where D_{ij} is the dietary overlap between predator *i* and predator *j*, p_{ik} is the mean proportional weight of prey *k* in predator *i (*W_k *for predator i*), and p_{jk} is the mean proportional weight of prey *k* in predator *j (*W_k *for predator j*). The statistical software package PRIMER 6.0 was used to create a resemblance matrix containing the dietary similarity (D_{ij}) of each predator pair.

Hierarchical clustering was used to group species into dietary guilds based on similarity of diet composition. The cluster analysis was carried out with the SIMPROF (similarity profiling) routine, which defines statistically significant groups among samples (Clarke & Gorley 2006). A dendrogram was derived from the cluster analysis to visualize the dietary similarities and dissimilarities between species and the resulting dietary guilds. Finally, a multi-dimensional scaling plot was derived from the dietary resemblance matrix to ordinate species-specific diet compositions in two dimensions, such that the relative distance between points represents the degree of dietary similarity between species (Kruskal & Wish 1978). A SIMPER (similarity percentages) analysis was further used to identify prey types that primarily account for the differences between dietary guilds.

Stable Isotope Analysis:

In addition to stomach content analysis, we used nitrogen (δ^{15}N) and carbon (δ^{13}C) stable isotopes to investigate the trophic positions and basal energy sources of the fish and invertebrate community in Rhode Island and Block Island Sounds. A total of 875 tissue samples were collected during bottom trawl surveys (n = 9-91 per species) (Table 2.1). The target was to collect five tissue samples per species per station, but this was achievable only for highly abundant species. In the lab, tissue samples were freeze-dried for 48 hr and homogenized with stainless steel spatulas. Sub-samples of fish tissue (~1 mg dry weight) were analyzed for nitrogen and stable isotopes at the Boston University Stable Isotope Laboratory with an automated continuous-flow isotope ratio mass spectrometer (Preston & Owens 1983). Isotopic ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ are expressed in delta notation (δ) as the relative per mil (‰) difference between the sample and international standards (i.e. atmospheric nitrogen, Vienna Pee Dee Belemnite), and are calculated using the following equation:

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1000$$

where $X = {}^{15}N$ or ^{13}C, and $R = {}^{15}N/^{14}N$ or $^{13}C/^{12}C$.

Given that a consumer's tissue is enriched approximately 3.4‰ relative to that of its diet, the trophic position (TP) of consumer species can be calculated with the following equation (Post 2002, equation modified from Piraino & Taylor 2009):

$$Trophic\ Position\ (TP) = 2 + \frac{(\delta^{15}N_{consumer} - \delta^{15}N_{scallop})}{3.4}$$

where, "2" is the trophic level of the Atlantic sea scallop (*Placopecten magellanicus*), $\delta^{15}N_{consumer}$ and $\delta^{15}N_{scallop}$ are the respective nitrogen isotope signatures of a consumer of interest and the sea scallop, and "3.4" is the $\delta^{15}N$ enrichment per trophic level (Post 2002). The sedentary and phytoplanktivorous nature of the Atlantic sea scallop makes this species a suitable benchmark organism for nitrogen stable isotope analysis (Naidu 1991, Black et al. 1993). The δ^{15}N of sea scallops sampled for this study (7.3‰), further confirmed its primary consumer trophic positioning in the food web, as it was approximately 3.4‰ lower than the zooplanktivorous species sampled.

Trophic fractionation of carbon was assumed to be 0.5‰ δ^{13}C, and was accounted for using the following formula for each species (Deniro & Epsten 1977, Post 2002, McCutcheon et al. 2003).

$$\delta^{13}C_{corrected} = \delta^{13}C_{raw} - [(TP - 1) * 0.5]$$

where, $\delta^{13}C_{corrected}$ is the carbon isotopic signature corrected for trophic fractionation, $\delta^{13}C_{raw}$ is the raw carbon isotopic signature, TP is species-specific trophic position derived from δ^{15}N, 1 is the difference between the trophic level of the benchmark species (Atlantic sea scallop) and the base of the food web (phytoplankton), and 0.5 is the rate of trophic fractionation of carbon (Post 2002).

Isotopic turnover rates of nitrogen and carbon are directly related to growth rate, with faster growing animals exhibiting shorter turnover rates (Hesslein et al. 1993). For marine fish species, previous studies have found that stable isotope signatures in white muscle tissue have isotopic turnover rates ranging from a few months to over a year (Hesslein et al. 1993, MacNeil et al. 2006). Thus, the isotopic signatures of small, fast growing fish, such as herring, reflect diets integrated over few months, whereas the isotopic signatures of large, slow growing elasmobranchs, such as smooth dogfish, reflect diets integrated over 11-14 months (MacAvoy &

Macko 2001, Miller 2006, Logan & Lutcavage 2010). The implications of such temporal isotopic integration will be discussed with respect to migratory species and habitat use.

Cluster sampling techniques were used to calculate the mean δN^{15}, trophic position, and δC^{13} for each species included in the dietary guild analysis, and one-way analysis of variance (ANOVA) models were used to test for differences in mean δN^{15} and δC^{13} between guilds. Tukey's post-hoc multiple comparison tests were used to assess pair-wise differences in δN^{15} and δC^{13} between dietary guilds.

Spatial and Annual Analysis:

Spatial analysis of fish diet composition and stable isotope signatures were conducted for silver hake, scup, and winter flounder. These species had sufficient stomach and isotope sample coverage from across the study area to enable spatial analysis (Smith 2009, Table 2.1). Species-specific diet and stable isotope data were divided into four regions for spatial analysis, based on their proximity to shore (Inshore, Offshore) and location within Rhode Island Sound and Block Island Sound (RIS, BIS). This delineation resulted in four regions: Inshore RIS, Offshore RIS, Inshore BIS, and Offshore BIS.

A multivariate Analysis of Similarity (ANOSIM) was used to test for differences in fish diet between regions (Inshore RIS, Offshore RIS, Inshore BIS, Offshore BIS) and years (2009, 2010, 2011). Multidimensional scaling plots were used to visualize the results of regional and annual ANOSIMS. Site-specific diet compositions were also projected in ArcGIS and used to visualize spatial patterns in species-specific diet composition.

Bivariate plots of species-specific $\delta^{15}N$ and $\delta^{13}C$ were used to visualize patterns in trophic position and basal carbon sources by region and year. ANOVA models and post-hoc Tukey Honest Significant Difference (Tukey HSD) tests were used to test for regional and annual differences in mean species-specific $\delta^{15}N$ and $\delta^{13}C$ values.

Results:

Dietary Guilds & Niche Breadth:

Niche breadth (B_i) ranged from 0.02 to 0.52, with 17 out of 20 species having niche breadths less than 0.3 (Table 2.1). Alewife, smooth dogfish, and weakfish exhibited the most specialized feeding behavior, with niche breadths of 0.02, 0.07, and 0.08, respectively (Table 2.1). Conversely, striped bass, monkfish, and little skate exhibited the most opportunistic feeding behavior, with niche breadths of 0.52, 0.49, and 0.36, respectively (Table 2.1).

The CLUSTER and SIMPROF analyses identified four major groups of predators with significant dietary overlap, and three species with unique dietary compositions. The predator groups were categorized based on the dominant prey types and foraging strategies of the guild members (Table 2.3, Figures 2.2 & 2.3).

The planktivore guild consisted of American shad, alewife, and butterfish and exhibited 55.4% dietary similarity (SIMPROF: $\pi = 1.85$, $p = 0.536$, Figure 2.3). The diets of these species were characterized by high proportions of unidentified animal remains, which likely represent well-digested zooplankton (Table 2.4, Figure 2.4). The dietary composition of Atlantic herring, a known planktivore, was significantly different than American shad, alewife, and butterfish, due to higher abundances of gammarid amphipods and cumaceans (Bigelow & Schroeder 2002, Table 2.4, Figure 2.4).

The benthivore guild was split into two groups, based upon prey diversity. The first benthivore group consisted of scup, winter flounder, winter skate, and little skate, and exhibited 52.4% dietary similarity (SIMPROF: $\pi = 1.96$, $p = 0.185$, Figure 2.3). These species fed upon a wide variety of prey, representing 46 of the 47 prey categories used in this study (Tables 2.4 & 2.5). The most common prey types were amphipods, polychaete worms, and unidentified animal remains (Figure 2.4). The second benthivore group consisted of yellowtail flounder and haddock, and exhibited 75.5% dietary similarity (SIMPROF: $\pi = 2.80$, $p = 0.530$). These species fed primarily on gammarid amphipods, which accounted for 51% of these species' diets (Tables 2.4 & 2.5).

The crustacean-eater guild consisted of black sea bass and smooth dogfish, and exhibited 41.3% similarity (SIMPROF: $\pi = 2.77$, $p = 0.824$, Figure 2.3). Crabs accounted for 54% of the diets of these species, while shrimp accounted for nearly 10% (Figure 2.4, Tables 2.4 & 2.5). Silver hake were also consumers of decapod crustaceans, but their diets were characterized by higher prevalence of shrimp (67%) and fish (12%), and thus were classified as a unique group (Table 2.5).

The piscivore guild consisted of bluefish, summer flounder, spiny dogfish, and striped bass, and exhibited 59.8% dietary similarity (SIMPROF: π = 2.23, p = 0.463, Figure 2.3). Fish and squid accounted for 72% and 21% of the diets of these species' diets, respectively (Figure 2.4, Tables 2.4 & 2.5). Weakfish also exhibits piscivorous feeding behavior, with fish accounting for 78% if its diet, but the high abundance of crustacean prey (15%) led to a unique dietary classification (Figure 2.4, Table 2.5).

Stable Isotopes:

Nitrogen stable isotope analysis indicates that the species sampled for this work represent two major trophic groups in the fisheries food web, secondary consumers (i.e. foragers) and tertiary consumers (i.e. predators) (Figure 2.5). Contrary to the dietary guild classification, spiny dogfish was found to exhibit the lowest trophic position of all species sampled (TP = 3.30), suggesting that stomach contents did not accurately classify the trophic role of this species. This result is likely due to the consumption of ctenophores, which are difficult to assess via stomach content analysis(Smith & Link 2010). The highest trophic position in the fisheries food was occupied by striped bass (TP = 4.42).

Within dietary guilds, inter-species isotopic overlap was high (Figure 2.5). The planktivore, benthivore, and crustacean-eater guilds all fell within trophic level 3, while the piscivore guild fell into trophic level 4. The planktivore and benthivore guilds exhibited the lowest trophic positions (3.60 ± 0.15 and 3.57 ± 0.13, respectively), while the crustacean-eater and piscivore guilds maintained the highest trophic positions (3.78 ± 0.17 and 4.06 ± 0.52, respectively). While an initial ANOVA analysis suggested that dietary guilds maintained distinct trophic positions (ANOVA p=0.031), post-hoc pairwise tests indicated that only the piscivore guild was significantly unique.

Carbon isotopic analysis indicates that most fish in Rhode Island and Block Island Sounds are supported by pelagic phytoplankton, with an aggregate carbon isotopic signature of -19.37 (± 0.13). There is also evidence, however, that benthic production plays a role, particularly for obligate benthivores, such as skates and flatfish (little skate $\delta^{13}C = -17.63$; yellowtail flounder $\delta^{13}C = -18.98$; Figure 2.5). Dietary guilds did not exhibit unique $\delta^{13}C$ signatures (ANOVA p=0.199), but the foraging strategies of planktivores and benthivores were apparent.

Spatial and Annual Analysis:

ANOSIM results suggest that silver hake and winter flounder exhibit spatial patterns in dietary composition (Region ANOSIMs: Silver Hake R=0.297, p=0.002; Winter Flounder R=0.122, p=0.029, Figures 2.6 & 2.7), while scup does not (Region ANOSIM: R=0.046, p=0.201, Figure 2.8). Overall, spatial patterns in silver hake diet were characterized by an inshore-offshore gradient, with fish dominating silver hake diet in inshore waters and shrimp dominating silver hake diet in offshore waters. Statistically, however, silver hake diet was only significantly different between the Inshore Rhode Island Sound and Offshore Rhode Island Sound regions (R=0.239, p=0.013). Winter flounder diet, on the other hand, was primarily distinguished by an east-west gradient, with amphipods dominating winter flounder diet in Block Island Sound and polychaete worms dominating winter flounder diet in Rhode Island Sound. Statistically, winter flounder diet in the Offshore Rhode Island Sound region was significantly different than winter flounder diet in both the Inshore Block Island Sound and Offshore Block Island Sound regions (R=0.118, p=0.041 and R=0.325, p=0.024, respectively). Winter flounder diet in the Inshore Rhode Island Sound region was also significantly different from winter flounder diet in the Offshore Block Island Sound region (R=0.396, p=0.013).

Silver hake, scup, and winter flounder all exhibited significant dietary differences between years (ANOSIM: Silver hake R=0.297, p=0.002; Scup R=0.463, p=0.001; Winter Flounder R=0.239, p=0.001). For all species, dietary compositions in 2011 were significantly different than dietary compositions in 2009 and 2010, but dietary compositions in 2009 were not significantly different than dietary compositions in 2010. These interannual differences were due to the high contributions of unidentified animal remains and unidentified crustaceans to dietary compositions in 2009 and 2010.

Silver hake exhibited significant spatial patterns in isotopic composition, characterized by an inshore-offshore gradient, with higher $\delta^{15}N$ and less negative $\delta^{13}C$ signatures inshore and lower $\delta^{15}N$ and more negative $\delta^{13}C$ signature offshore (ANOVA: $\delta^{13}C$ $p<0.001$; $\delta^{15}N$ $p<0.001$, Figure 2.9). These results suggest that silver hake feeds higher in the food chain and derives more energy from benthic production in inshore waters. Silver hake also exhibited interannual trends in $\delta^{13}C$

(ANOVA: p=0.017), with more negative $\delta^{13}C$ in 2011 than in 2009 and 2010. Silver hake, however, did not exhibit interannual trends in nitrogen isotopic signatures (ANOVA: p=0.412).

Scup and winter flounder did not exhibit spatial patterns or interannual trends in carbon and nitrogen isotopic signatures (Region ANOVAs – Scup: $\delta^{15}N$ p=0.553, $\delta^{13}C$ p=0.661; Winter flounder: $\delta^{15}N$ p=0.111, $\delta^{13}C$ p=0.887; Year ANOVAs – Scup: $\delta^{15}N$ p=0.689, $\delta^{13}C$ p=0.833; Winter Flounder: $\delta^{15}N$: p=0.975, $\delta^{13}C$ p=0.076; Figures 2.10 & 2.11).

Discussion:

This work highlights the complex interactions of the fish community on the northwest Atlantic continental shelf and provides details on the trophic structure of the nearshore fish community in Rhode Island and Block Island Sounds. The dietary guilds classified by this research are consistent with previous studies conducted in the region (Garrison & Link 2000). The spatial scale of this work, however, provides a unique perspective on the trophic structure of the fisheries ecosystem that is applicable to local-scale management efforts (Langton et al. 1995, Moore & Sowles 2010, RISAMP 2010).

On a regional scale in the northwest Atlantic, competition for food resources is typically not an important factor in structuring the fish community, as prey resources are consistently abundant and diverse (Auster & Link 2009, Hale 2010). Furthermore, many species exhibit opportunistic feeding behavior and are able to switch prey resources as they are available (Garrison & Link 2000, Link et al. 2000). In areas where preferred habitats constrict species distributions or in ecosystems where highly competitive species are increasing, however, competition for food may become limiting (Warwick 1984, Vinagre et al. 2014). Thus, given the diverse habitats and spatial and temporal overlap of species distributions in Rhode Island and Block Island Sounds, species classified into the same dietary guild may exhibit competitive interactions at local scales (LaFrance et al. 2010, LaFrance et al. 2014, Malek et al. 2014). The high frequency of narrow niche breadths (<0.3) further suggests that dietary specialization is an important aspect of the fish community in this area (Novakowski et al. 2008).

When discussing resource partitioning in a changing coastal ecosystems, it is important to consider trends in population growth and decline for guild-sharing species, such as winter flounder and scup (Smith et al. 2010, Bell et al. 2014). Winter flounder is classified as a benthivore, and thus exhibits significant dietary overlap with scup, winter skate, and little skate. Over the past decade, the scup population has been growing, while the winter flounder population has been declining (NEFSC 2008, Terceiro 2012). While the decline in winter flounder has not been attributed to increased competition for resources, it is important to keep this factor in mind when designing fishery management plans (Nye et al. 2009, Link & Auster 2013, Able et al. 2014). Similarly, the functional overlap between black sea bass and smooth dogfish, both members of the crustacean-eater guild, should be considered when assessing the drivers and consequences of species range expansion and population growth

(Bell et al. 2014). As such, the trophic analysis presented here contributes to our understanding of the factors impacting species population size and distribution, and highlights a potential limiting factor in stock recovery efforts.

Nitrogen isotope analysis suggest that the fisheries food chain in Rhode Island and Block Island Sounds consists of approximately four trophic levels, with primary producers occupying the first trophic level, zooplankton and filter feeders occupying the second trophic level, opportunistic foragers occupying the third trophic level, and predators occupying the fourth trophic level. The majority of the fish community sampled by this work fell into the third trophic level, including herring, butterfish, flatfish, skates, and dogfish. Such trophic redundancy suggests that resource partitioning is an important process structuring the fish community of Rhode Island and Block Island Sounds, with similar species using limiting resources in different ways (Hahm & Langton 1984, Ross 1986, Garrison 2000, Plattel & Potter 2001, Carrassón & Cartes 2002, Matthews 2004, Costa-Pierce 2010). This effective use of the available food supply may contribute to the high fish community diversity in this area (Malek et al. 2014).

Despite unique dietary guilds and foraging strategies, carbon isotope analysis indicates that most of the fish species in Rhode Island and Block Island Sounds rely on pelagic phytoplankton as a basal energy resource (Hobson et al. 1995). There is, however, evidence that benthic production also plays a role, particularly for obligate benthivores such as skates and flounder (Vander & Vadeboncoeur 2002). Such isotopic analyses are useful for developing an ecosystem-based approach to management, as they identify species that act as direct links to basal resources as well as species groups that share trophic roles (Marasco et al. 2007, Crowder & Norse 2008, Foley et al. 2010).

While the results from our work are generally consistent with previous, large-scale studies, a few discrepancies are worthy of discussion (Smith & Link 2000, Link et al. 2000). First, a number of planktivore species, including American shad and alewife, exhibit higher $\delta^{15}N$ signatures (as high as 13.30‰) than would be expected for species of their feeding ecology (Garrison & Link 2000, Trenkel et al. 2014). By comparison, silver hake, which primarily feeds upon fish and shrimp and should thus exhibit a higher $\delta^{15}N$ than planktivores, has a lower $\delta^{15}N$ signature (12.98‰) and trophic position. The enriched signals exhibited by American shad and alewife may reflect their anadromous life histories or recent estuarine foraging, as $\delta^{15}N$ increases markedly in coastal environments were the enriched $\delta^{15}N$ signal of human sewage and other terrestrial nutrient sources is persistent throughout the food web (Cabana & Rasmussen 1996, Hansson et al. 1997, McKinney et al. 2010). In general, the isotopic signatures of migratory species often reflect feeding in multiple areas and habitats (Clément et al. 2014, Dixon et al. 2015). As such, one must interpret the isotopic signatures of highly mobile species, which integrate multiple months of feeding behavior, with care (Hobson 1999, Abrantes & Barnett 2011).

Ontogenetic diet shifts have been shown to be an important for a number of the species sampled as part of this work, including silver hake, bluefish, and spiny dogfish (Buckel 1999, Garrison 2000, Garrison & Link 2000). Unfortunately, the sampling carried out for this study was insufficient for a robust comparison of species trophic roles between size classes. Preliminary analyses, however, indicate that there are no differences in the diet or isotopic signatures between different size classes for most of the species sampled. There was, however, a trend toward increasing $\delta^{15}N$ and $\delta^{13}C$ signatures with increasing spiny dogfish size (data not shown).

The results of dietary and isotopic analyses are generally consistent, except in the case of spiny dogfish. Our dietary guild analysis classified spiny dogfish as a piscivore, yet its $\delta^{15}N$ and corresponding trophic position was the lowest of all species sampled (11.7‰ $\delta^{15}N$, 3.30 TP). One explanation for this inconsistency is spiny dogfish's tendency to feed on ctenophores, a low trophic level prey which are difficult to detect in stomach samples, but would drive $\delta^{15}N$ and trophic position down (Smith & Link 2010). Spiny dogfish consumption of butterfish would also deplete $\delta^{15}N$ signatures, given that butterfish are phytoplanktivorous. Spiny dogfish has been characterized as a planktivore in other systems in the northwest Atlantic, but there is ongoing debate as to its role in the food web (Garrison & Link 2000, Alonso et al. 2002, Smith et al. 2010, Taylor et al. 2014). Due to a predominance of large spiny dogfish in our trawl survey catch, the dietary and isotopic characterizations presented here represent spiny dogfish between 50 cm and 80 cm. This limited size range may contribute to our classification of spiny dogfish as a piscivore (Monroe et al. 2014, Carlisle et al. 2015). Nonetheless, stomach and isotope samples were collected from the same individuals, and thus, one would expect diet results to reflect the trophic position derived from nitrogen stable isotope analysis.

One explanation for the dietary guild-trophic position dichotomy is that spiny dogfish exhibits net feeding behavior (i.e. rapid consumption of fish while the trawl is being hauled back), which could lead to an overestimation of the proportion of fish in spiny dogfish diet and, thus, a misclassification into the piscivore guild (Hopkins & Baird 1975). Another confounding detail of the trophic structure of spiny dogfish is the highly negative carbon isotopic signature (-23.0 ‰ $\delta^{13}C$), which is more negative than the pelagic phytoplankton in this region (-20 ‰ $\delta^{13}C$, EPA unpublished data). The low $\delta^{13}C$ signature of spiny dogfish may be a result of feeding offshore or in deep waters, where the planktonic community is super-depleted in $\delta^{13}C$, but further investigation is needed to fully understand his unique trophic process (Ostrom et al. 1997).

In a spatial context, this work suggests that silver hake and winter flounder exhibit distinct patterns in their feeding behaviors, while scup does not. More specifically, isotopic analyses indicate that silver hake occupies a higher trophic position (i.e. feeds higher in the food chain) and derives more energy from benthic production in inshore waters. The dietary patterns of silver hake corroborate these findings, with small fish dominating silver hake's diet inshore and shrimp dominating silver hake's diet offshore. These results suggest that the reduced depth and estuarine outflow in Rhode Island and Block Island Sound's inshore waters concentrate small fish prey and increase benthic-pelagic coupling. Spatial patterns in winter flounder diet also appear to be associated with prey availability, as winter flounder diet is dominated by amphipods in Block Island Sound, where amphipod tube mats are abundant (LaFrance et al. 2014). In the case of scup, a lack of spatial dietary pattern could be a result of its narrow niche breadth, which may prevent this species from readily switching prey despite spatially distinct availability. It is important to consider that factors such as offshore wind energy development will likely shift prey availability and distribution in this region.

In conclusion, application of trophic structure analyses, such as those presented here, to the development of ecosystem-based fisheries management will help to preserve the balance between trophic components and maintain a productive fisheries ecosystem. A specific application of this work is to the modelling of species as functional groups (Link 2010, Latour et al. 2003). Furthermore, it is particularly important to consider this type of work in the management of species that have specific habitat requirements and highly specialized diets, such as yellowtail flounder and black sea bass. Management of migratory predators, such as striped bass, on the other hand, may not require consideration of prey availability as they are able to integrate resources regionally. The results of this work not only provide valuable insight into fisheries ecosystem dynamics in a temperate coastal environment, but also inform spatial management plans for Rhode Island and Block Island Sounds (RI SAMP 2010). Furthermore, the methods for this study are consistent with European guidelines for assessing the impacts of offshore wind turbines on the marine environment and could provide a baseline for measuring the effects on local-scale trophic dynamics from offshore development projects (BSH 2013). Future work will focus on developing an understanding of the seasonal trends in trophic structure and the impacts of planned offshore wind energy development.

Literature Cited:

Able, K. W., Grothues, T. M., Morson, J. M., and Coleman, K. E. 2014. Temporal variation in winter flounder recruitment at the southern margin of their range: is the decline due to increasing temperatures? ICES Journal of Marine Science 71 (8): 2186-2197.

Abrantes, K., and Barnett, A. 2011. Intrapopulation variations in diet and habitat use in a marine apex predator, the broadnose sevengill shark, *Notorynchus cepedianus*. Marine Ecology Progress Series, 442: 133–148.

Alonso, M.K., Crespo, E.A., Garcia, N.A., Pedraza, S.N., Mariotti, P.A., and Mora, N.J. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environmental Biology of Fishes 63: 193–202.

Auster, P.J., and Link, J. 2009. Compensation and recovery of feeding guilds in a northwest Atlantic shelf fish community. Marine Ecology Progress Series 382: 163–172.

Bell, R.J., Fogarty, M.J., Collie, J.S. 2014a. Stability in marine fish communities. Marine Ecology Progress Series 504: 221-239.

Bell, R.J., Richardson, D.E., Hare, J.A., Lynch, P.D., and Fratantoni, P.S. 2014b. Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. ICES Journal of Marine Science: Journal du Conseil, fsu217.

Black, G.A.P., Mohn, R.K., Robert, G., and Tremblay, M.J. 1993. Atlas of the biology and distribution of the sea scallop, *Placopecten magellanicus*, and Iceland scallop, *Chlamys islandica*, in the Northwest Atlantic. Canadian Technical Report of Fisheries and Aquatic Sciences 1915.

Bowman, R.E., Stillwell, C.E., Michaels, W.L., and Grosslein, M.D. 2000. Food of northwest Atlantic fishes and two common species of squid. NOAA Tech. Memo. NMFS-NE-155, Woods Hole, MA.

Buckel, J.A., Conover, D.O., Steinberg, N.D., and McKown, K.A. 1999. Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependent loss of juvenile striped bass (*Morone saxatilis*). Canadian Journal of Fisheries and Aquatic Sciences 56 (2): 275-287.

Bulman C.M., Althaus, F., He, X., Bax, N.J., and Williams, A. 2001. Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. Marine and Freshwater Research 52: 537–548.

Bowman, I.R., Craig, N., & Drew, C. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography 33 (5): 1182–1190.

Bundesamt für Seeschifffart unh Hydrologie (BSH). 2013. Investigation of the Impacts of Offshore Wind Turbines on the Marine Environment. Federal Maritime and Hydrographic Agency, Hamburg, Germany, 87 pp.

Cabana, G., and Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences of the United States of America, 93(20): 10844–10847.

Carlisle, A.B., Goldman, K.J., Litvin, S.Y., Madigan, D.J., Bigman, J.S., Swithenbank, A.M., Kline, T.C., and Block, B.A. 2015. Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. Proceedings of the Royal Society of London B: Biological Sciences 282 (1799): 20141446.

Carrassón, M., & Cartes, J.E. 2002. Trophic relationships in a Mediterranean deep-sea fish community: partition of food resources, dietary overlap and connections within the benthic boundary layer. Marine Ecology Progress Series 241: 41-55.

Clarke, K.R., and Gorley, R.N. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Clément, M., Chiasson, A.G., Veinott, G., and Cairns, D.K. 2014. What otolith microchemistry and stable isotope analysis reveal and conceal about anguillid eel movements across salinity boundaries. Oecologia: 1-11.

Colwell, R.K. and Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Costa-Pierce, B. 2010. Chapter 2: Ecology of the SAMP *in* Rhode Island Ocean Special Area Management Plan, Volume 1. Accessed at: <http://seagrant.gso.uri.edu/oceansamp/ pdf/samp_approved/ 200_Ecol_OCRMchanges_5.4_Clean.pdf>

Crowder, L., and Norse, E. 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. Marine Policy. 32 (5): 772-778.

DeNiro, M.J., and Epstein, S. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197: 261–263.

Dixon, H.J., Dempson, J.B., and Power, M. 2015. Assessing the use of different marine growth zones of adult Atlantic salmon scales for studying marine trophic ecology with stable isotope analysis. Fisheries Research 164: 112-119.

Estrada, J.A., Rice, A.N. Lutcavage, M.E., and Skomal, G.B. 2003. Predicting trophic position in sharks of the northwest Atlantic Ocean using stable isotope analysis. Journal of the Marine Biological Association of the UK, 83: 1347-1350

Fogarty, M.J. 2013. The art of ecosystem-based fishery management. Canadian Journal of Fisheries and Aquatic Sciences 71 (3): 479-490.

Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.R., Prahler, E., Rohr, N., Sivas, D.,Beck, M.W., Carr, M.H., Crowder, L.B., Duffy, J.E., Hacker, S.D., McLeod, K.L., Palumbi, S.R., Peterson, C.H., Regan, H.M., Ruckelshaus, M.H., Sandifer, P.A., and R.S. Steneck. 2010. Guiding ecological principles for marine spatial planning. Marine Policy, 35 (5): 955-966.

France, R.L. 1993. Carbon-13 enrichment in benthic compared to planktonic algae: food web implications. Marine Ecology Progress Series 124: 307-312.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and oceanography, 33 (5): 1182-1190.

Garrison, L.P. 2000. Spatial and dietary overlap in the Georges Bank groundfish community. Canadian Journal of Fisheries and Aquatic Sciences 57 (8): 1679–1691.

Garrison, L., and Link, J. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202: 231–240.

Gilliland, P.M., and Laffoley, D. 2008. Key elements and steps in the process of developing ecosystem-based marine spatial planning. Marine Policy 32 (5): 787–796.

Hahm, W., and Langton, R.W. 1984. Prey selection based on predator/prey weight ratios for some Northwest Atlantic fish. Marine Ecology Progress Series 19 (1-2):1-5.

Hale, S.S. 2010. Biogeographical patterns of marine benthic macroinvertebrates along the Atlantic coast of the northeastern USA. Estuaries and Coasts 33 (5): 1039–1053.

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

Hansson, S., Hobbie, J.E., Ragnar, E., Larsson, U., Fry, B., and Johansson, S. 1997. The stable nitrogen isotope ratio as a marker of food-web. Ecology 78 (7): 2249–2257.

Hasbrouck, E.C., Scotti, J., Stent, J. and Gerbino, K. 2011. Rhode Island commercial fishing and seafood industries: The development of an industry profile. 124 pp.

Hawkins, C.P., and MacMahon, J.A. 1989. Guilds: the multiple meanings of a concept. Annual Review of Entomology 34: 423-451.

Hesslein, R. H., Hallard, K. A., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen, in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$. Canadian Journal of Fisheries and Aquatic Sciences 50: 2071-2076.

Hobson, K.A and Welch, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{14}N$ analysis. Marine Ecology Progress Series 84: 9-18.

Hobson, K.A., Ambrose, W.G., and Renaud, P.E. 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya : insights from delta13C and delta15N analysis. Marine Ecology Progress Series 12*8*: 1–10.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120 (3): 314–326.

Hopkins, T.L., and Baird, R.C. 1975. Net feeding in mesopelagic fishes. Fishery Bulletin 73 (4): 908-914.

Hulbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Hyslop, E. J. 1980. Stomach contents analysis-a review of methods and their application. Journal of Fish Biology 17 (4): 411–429.

Jordaan, A., Chen, Y., Townsend, D.W., and Sherman, S. 2010. Identification of ecological structure and species relationships along an oceanographic gradient in the Gulf of Maine using multivariate analysis with bootstrapping. Canadian Journal of Fisheries and Aquatic Sciences 67 (4): 701–719.

Kruskal, J.B., and Wish, M. 1978. Multidimensional Scaling. Sage Publications, Beverley Hills, California.

LaFrance, M., King, J.W., Oakley, B.A., and Pratt, S. 2014. A comparison of top-down and bottom-up approaches to benthic habitat mapping to inform offshore wind energy development. Continental Shelf Research 83: 24-44.

LaFrance, M., Shumchenia, E., King, J., Pockalny, R., Oakley, B., Pratt, S. and Boothroyd, J. 2010. Benthic habitat distribution and subsurface geology at selected sites from the Rhode Island Ocean Special Area Management Study Area. Rhode Island Ocean Special Area Management Plan, Volume 2, Technical Report #4.

Langton, R.W., Auster, P.J., and Scheider, D.C. 1995. A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. Review in Fisheries Science 3 (3): 201-229

Latour, R.J, Brush, M.J., and Bonzek, C.F. 2003. Toward ecosystem-based fisheries management: strategies for multispecies modeling and associated data requirements. Fisheries 28 (9): 10-22.

Layman, C.A., Arrington, D.A., Montana, C.G., and Post, D.M. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88: 42–48.

Levins, R. 1968: Evolution in Changing Environments: Some Theoretical Explorations. Princeton, NJ: Princeton University Press.

Link, J.S., and Auster, P.J. 2013. The challenges of evaluating competition among marine fishes: who cares, when does it matter, and what can one do about it? Bulletin of Marine Science 89 (1): 213-247.

Link, J.S., Bolles, K., and Milliken, C.G. 2000. The Feeding Ecology of Flatfish in the Northwest Atlantic. Journal of Northwest Atlantic Fisheries Science 30: 1-17.

Link, J.S. 2010. Ecosystem-Based Fisheries Management: Confronting Tradeoffs. Cambridge University Press, Cambridge, UK.

Logan, J., Haas, H., Deegan, L., and Gaines, E. 2006. Turnover rates of nitrogen stable isotopes in the salt marsh mummichog, *Fundulus heteroclitus*, following a laboratory dietswitch. Oecologia 147 (3): 391-395.

Logan, J.M., and Lutcavage, M.E. 2010. Stable isotope dynamics in elasmobranch fishes. Hydrobiologia 644: 231-244.

MacAvoy, S.E., Macko, S.A., and Garman, G.C. 2001. Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. Canadian Journal of Fisheries and Aquatic Sciences 58 (5): 923-932.

MacKenzie, K.M., Palmer, M.R., Moore, A., Ibbotson, A.T., Beaumont, W.R., Poulter, D.J., and Trueman, C.N. 2011. Locations of marine animals revealed by carbon isotopes. Scientific reports 1: 21.

MacNeil, M.A., Drouillard, K.G., and Fisk, A.T. 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. Canadian Journal of Fisheries and Aquatic Sciences 63: 345-353.

Mahon, R., Brown, S.K., Zwanenburg, K.C., Atkinson, D.B., Buja, K.R., Claflin, L., Howell, G.D., Monaco, M.E., O'Boyle, R.N, and Sinclair, M. 1998. Assemblages and biogeography of demersal fishes of the east coast of North America. Canadian Journal of Fisheries and Aquatic Sciences 55 (7): 1704–1738.

Malek, A.J., Collie, J.S., and Gartland, J. 2014. Fine-Scale Spatial Patterns in the Demersal Fish and Invertebrate Community in a Northwest Atlantic Ecosystem. Estuarine, Coastal and Shelf Science 147: 1-10.

Marasco, R.J., Goodman, D., Grimes, C.B., Lawson, P.W., Punt, A.E., and Li, T.J.Q. 2007. Ecosystem-based fisheries management : some practical suggestions. Canadian Journal of Fisheries and Aquatic Sciences 64 (6): 928–939.

Matthews, B., and Mazumder, A. 2004. A critical evaluation of intrapopulation variation of delta13C and isotopic evidence of individual specialization. Oecologia 140 (2): 361–371.

McCutchan, J.H. Jr., Lewis, W.M., Kendall, C. and McGrath, C.C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378– 390.

McKinney, R.A., Oczkowski, A.J., Prezioso, J., and Hyde, K.J.W. 2010. Spatial variability of nitrogen isotope ratios of particulate material from Northwest Atlantic continental shelf waters. Estuarine, Coastal and Shelf Science 89 (4): 287-293.

McLeod, K.L. and Leslie, H. eds. Ecosystem-based management for the oceans. Washington, DC, USA: Island Press, 2009.

McLeod, K.L., Lubchenko, J., Palumbi, S.R. and Rosenberg, A.A. 2005. Scientific consensus statement on marine ecosystem-based management. Communication Partnership for Science and the Sea. Available at: http://www.compassonline.org/.

Metcalf, S.J., Dambacher, J.M., Hobday, A.J., and Lyle, J.M. 2008. Importance of trophic information, simplification and aggregation error in ecosystem models. Marine Ecology Progress Series 360: 25-36.

Miller, T. W. 2006. Tissue-specific response of δ15N in adult Pacific herring (*Clupea pallasi*) following an isotopic shift in diet. Environmental Biology of Fishes 76 (2-4): 177-189.

Munroe, S.E.M., Simpfendorfer, C.A., and Heupel, M.R. 2014. Defining shark ecological specialisation: concepts, context, and examples. Reviews in Fish Biology and Fisheries 24 (1): 317-331.

Moore, S., and Sowles, J. 2010. Local-Scale Ecosystem-Based Fisheries in a Gulf of Maine Estuary: Managing for Complexity, Adapting to Uncertainty. Marine and Coastal Fisheries 2 (1): 146–158.

Naidu, K.S. 1991. Sea scallop, *Placopecten magellanicus*. Pages 861–897 in S. E. Shumway, editor. Scallops: biology, ecology and aquaculture. Elsevier, Amsterdam.

NEFSC. 2008. Assessment of 19 Northeast groundfish stocks through 2007. Report of the 3rd Groundfish Assessment Review Meeting (GARM III), Northeast Fisheries Science Center, Woods Hole, Massachusetts. August 4-8, 2008. NEFSC Ref Doc. 08-15. 884 p.

Novakowski, G.C., Hahn, N.S., and Fugi, R. 2008. Diet seasonality and food overlap of the fish assemblage in a pantanal pond. Neotropical Ichthyology 6 (4): 567-576.

Nye, J.A., Link, J.S., Hare, J.A. and Overholtz, W.J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United Sates continental shelf. Marine Ecology Progress Series 393: 111-129.

Ostrom, N.E., Macko, S.A., Deibel, D., and Thompson, R.J. 1997. Seasonal variation in the stable carbon and nitrogen isotope biogeochemistry of a coastal cold ocean environment. Geochimica et Cosmochimica Acta 61 (14): 2929-2942.

Pauly, D., and Chuenpagdee, R. 2007. Fisheries and coastal ecosystems: the need for integrated management. Pages 171-185 in P. Nemetz, editor. Sustainable resource management. Edward Elgar Publishing, Surrey, UK.

Pasquaud, S., Elie, P., Jeantet, C., Billy, I., Martinez, P., and Girardin, M. 2008. A preliminary investigation of the fish food web in the Gironde estuary, France, using dietary and stable isotope analyses. Estuarine, Coastal and Shelf Science 78: 267-279.

Peterson, B., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annual review of ecology and systematics 18: 293–320.

Pikitch, E., Santora, E.A., Babcock, A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heheman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., and Sainsbury, K. 2004. Ecosystem-based fishery management. Science 305: 346-347.

Platell, M.E., and Potter, I.C. 2001. Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. Journal of Experimental Marine Biology and Ecology 261 (1): 31-54.

Post, D.M. 2002. Using stable isotopes to estimate trophic positions: Models, methods, and assumptions. Ecology 83: 703-718.

Preston, T. and Owens, N.J.P. 1983. Interfacing an automatic elemental analyser with an isotope ratio mass spectrometer: the potential for fully automated total nitrogen and nitrogen-15 analysis. Analyst 108: 971–977.

Pruell, R.J., Taplin, B.K., Lake, J.L., and Jayaraman, S. 2006. Nitrogen isotope ratios in estuarine biota collected along a nutrient gradient in Narragansett Bay, Rhode Island, USA. Marine Pollution Bulletin 52 (6): 612–620.

Reum, J.C., and Essington, T.E. 2008. Seasonal variation in guild structure of the Puget Sound demersal fish community. Estuaries and Coasts 31 (4): 790-801.

RI SAMP (Rhode Island Ocean Special Area Management Plan). 2010. Rhode Island Coastal Resources Management Council. Draft, July 23rd 2010.

Root, R.B. 1967. The niche exploration pattern of the blue-gray gnatcatcher. Ecological Monographs 37: 317–350.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia: 352-388.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51: 408-418.

Smith, B.E. 2009. *The effects of bottom fishing on the benthic macrofauna, demersal fishes, and fish feeding habits of George's Bank* (Master's thesis). University of Rhode Island, Graduate School of Oceanography. Narragansett, RI.

Smith, A.D.M., Fulton, E.A., Hobday, A.J., Smith, D.C., and Shoulder, P. 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. ICES Journal of Marine Science 64: 633–639.

Smith, B.E., Dayton, J., McElroy, D., Towle, E., and Mcbride, R.S. 2010. The Seasonal and Spatial Variability of Flatfish Feeding Habits on the Northeast US Continental Shelf : Preliminary Insights from Cooperative Research.

Smith, B., and Link, J. 2010. The trophic dynamics of 50 finfish and 2 squid species of the Northeast US continental shelf. US Dept. of Commerce. NOAA Technical Memorandum NMFS-NE-216, 640 p.

Smythe, T., and Beutel, D. 2010. Fisheries activity maps: methods and data sources. Technical Report #15 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Taylor, D.L., Kutil, N.J., Malek, A.J., and Collie, J.S. 2014. Mercury bioaccumulation in cartilaginous fishes from Southern New England coastal waters: Contamination from a trophic ecology and human health perspective. Marine Environmental Research 99: 20-33.

Terceiro M. 2012. Stock assessment of scup (*Stenotomus chrysops*) for 2012. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 12-25; 104 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026, or online at http://www.nefsc.noaa.gov/nefsc/publications/

Trenkel, V.M., Huse, G., MacKenzie, B.R., Alvarez, P., Arrizabalaga, H., Castonguay, M., Goñie, N., Hátúng, H., Jansen, T., Jacobsen, J.A., Lehodey, P., Lutcavage, M., Mariani, P., Melvin, G.D., Neilson, J.D., Nøttestadb, L., Óskarssonk, G.J., Payned, M.R., Richardson, D.E., Seninah, I., and Speirs, D.C. 2014. Comparative ecology of widely distributed pelagic fish species in the North Atlantic: implications for modelling climate and fisheries impacts. Progress in Oceanography 129: 219-243.

Vander, M.J., and Vadeboncoeur, Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83 (8): 2152–2161.

Vander Zanden, M.J., and Rasmussen, J.B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography 46: 2061-2066.

Vinagre, C., and Costa, M.J. 2014. Estuarine-coastal gradient in food web network structure and properties. Marine Ecology Progress Series 503: 11-21.

Warwick, R.M. 1984. Species size distributions in marine benthic communities. Oecologia 61: 32-41.

Wilson, J.B. 1999. Guilds, functional types and ecological groups. Oikos 86: 507-522.

Table 2.1. Common and scientific names, size ranges, isotope and stomach sample sizes, total number of prey types, and Levins standardized niche breadth for each predator species included in dietary guild and stable isotope analyses.

Common Name	Scientific Name	Size Range (TL, cm)	Number of Isotopes Samples	Number of Stomach Samples	Number of Prey Types	Levins Standardized Nich Breadth
Alewife	*Alosa pseudoharengus*	10-20	28	29	12	0.02
American shad	*Alosa sapidissima*	15-25	17	18	12	0.14
Atlantic herring	*Clupea harengus*	10-30	54	98	13	0.26
Black sea bass	*Centropristis striata*	10-60	61	67	35	0.12
Bluefish	*Pomatomus saltatrix*	10-70	57	48	11	0.24
Butterfish	*Peprilus triacanthus*	4-20	69	177	12	0.16
Haddock	*Melanogrammus aeglefinus*	10-20	20	24	12	0.21
Little skate	*Leucoraja erinacea*	10-30	68	112	30	0.36
Monkfish	*Lophius americanus*	10-90	17	12	5	0.49
Scup	*Stenotomus chrysops*	5-50	67	383	31	0.15
Silver hake	*Merluccius bilinearis*	5-40	41	204	21	0.23
Smooth dogfish	*Mustelus canis*	41-80	21	24	14	0.07
Spiny dogfish	*Squalus acanthias*	41-80	70	63	15	0.15
Striped bass	*Morone saxatilis*	70-95	11	10	10	0.52
Summer flounder	*Paralichthys dentatus*	21-70	82	99	23	0.17
Weakfish	*Cynoscion regalis*	10-50	9	14	8	0.08
Winter flounder	*Pseudopleuronectes americanus*	10-70	91	248	29	0.23
Winter skate	*Leucoraja ocellata*	10-60	61	95	34	0.16
Yellowtail flounder	*Limanda ferruginea*	10-70	31	37	17	0.13

Table 2.2. Prey categories used in dietary guild analysis listed in taxonomic order.

Prey Taxon

- Fish
  - Butterfish (*Peprilus triacanthus*)
  - Scup (*Stenotomus chrysops*)
  - Sand Lance (*Ammodytes* spp.)
  - Herring (Clupeidae)
  - Silver hake (*Merluccius bilinearis*)
  - Other fish
  - Unidentified fish

- Crustaceans
  - Unidentified crustaceans
    - Unidentified decapod crab
      - Cancer crabs (Cancridae)
      - Hermit crabs (Paguroidea)
      - Spider crabs (Majoidea)
    - Unidentified decapod shrimp
      - American lobster (*Homarus americanus*)
      - Ghost and lobster shrimp (Thallasinidea)
      - Grass shrimp (*Hippolyte* spp.)
      - Sand shrimp (*Crangon septemspinosa*)
      - Pandalid shrimp (Pandalidae)
    - Unidentified Isopods (Isopoda)
      - *Politolana* spp. isopods
    - Unidentified Amphipods
      - Aordid amphipods (Aoridae)
      - Caprellid amphipods (Caprellidae)
      - Corophiid amphipods (Corophiidae)
      - Gammarid amphipods (Gammaridae)
    - Krill (Euphausiidae)
    - Mysids (Mysidacea)
    - Cumaceans (Cumacea)
    - Zooplankton

- Echinoderms
  - Sand dollar (*Echinarachnius parma*)
  - Other echinoderms (Echinodermata)

- Molluscs
  - Squid (Teuthida)
  - Bivalve molluscs (Bivalvia)
    - Clams (Veneridae)
  - Snails (Gastropoda)

- Worms
  - Polychaete worms (Polychaetae)
    - Sea mouse (Aphroditidae)
  - Other worms and parasites

- Anthozoans
  - Anemones (Actiniaria)

- Cnidarians
  - Hydroids (Hydrozoa)

- Sponges
  - Unidentified sponges (Porifera)

- Other invertebrates
- Unidentified gelatinous remains
- Unidentified animal remains
- Animal tubes
- Algae
- Sediment

Table 2.3. Stomach contents of dietary guilds and subgroups as derived from multivariate cluster analysis. Guild species are listed in italics. Values represent proportional contribution of each prey category to species-specific diet as derived from wet weight measurements.

	Planktivores	**Planktonic Omnivore**	**Benthic Omnivores**	**Benthivores**	**Crustacean Eaters**	**Crustacean & Fish Eater**	**Piscivores**	**Small Fish Eater**
	Alewife, American shad, Butterfish	*Atlantic Herring*	*Little skate, Scup, Winter flounder, Winter skate*	*Haddock & Yellowtail Flounder*	*Black Sea Bass & Smooth Dogfish*	*Silver Hake*	*Bluefish, Monkfish, Striped Bass, Spiny Dogfish, Summer Flounder*	*Weakfish*
Butterfish			0.025		0.102		0.369	
Scup			0.004		0.005		0.089	0.010
Sand lance			0.057		0.024	0.013	0.035	
Herring							0.011	
Silver hake					0.010		0.040	
Other fish			<0.001		0.061		0.065	
Unidentified fish	0.002	0.003	0.002		0.086	0.118	0.168	0.777
Unidentified crustaceans	0.017	0.003	0.034		0.017	0.043	0.001	0.152
Decapod Crabs	0.001		0.013	0.007	0.012	0.007	0.008	
Cancer crabs			0.017	0.003	0.538		0.004	
Hermit crabs			<0.001		0.002			
Spider crabs					0.021			
Decapod Shrimp	<0.001		0.008	0.002	0.004	0.226	0.001	
American lobster			<0.001		0.003			
Ghost /lobster Shrimp			0.015		0.005			
Grass shrimp			0.020		0.050	<0.001		
Sand shrimp	0.003		0.028	0.016	0.191	0.160	<0.001	
Pandalid shrimp			0.020		0.003	0.278	0.014	
Isopods		0.002	0.010	0.007	0.018			
Politolana spp isopods			0.018		<0.001			
Amphipods	0.167	0.012	0.096	0.190	0.004	0.065	0.050	
Aoridid amphipods		<0.001	0.035		0.006		<0.001	
Caprellid amphipods		0.012	0.072	<0.001				
Corophiid amphipods	0.003		0.022	0.136	0.001	0.002		
Gammarid amphipods	0.036	0.335	0.145	0.512	0.002	0.045	<0.001	
Krill		0.001	<0.001			0.001		
Mysids	0.012		0.001	0.004	0.006	0.010		
Cumaceans	<0.001	0.193	0.002	0.005		0.001		
Zooplankton	0.002	0.239						
Sand dollar			0.009	0.051	<0.001		0.005	
Other echinoderms			0.002		0.006			
Squid			0.010		0.014	0.005	0.208	0.020
Bivalves	<0.001		0.009	0.004	<0.001	<0.001	<0.001	
Clams	<0.001		0.003	0.008				
Snails	0.001		0.001	0.017	0.045	<0.001	<0.001	
Polychaete worms	0.030	0.001	0.168	0.068	0.007	0.003	0.013	0.014
Sea mouse			0.032		0.001			
Other worms	<0.001		0.001		<0.001			
Anemones			0.019		0.001			
Hydroids			0.002		<0.001	<0.001		0.007
Sponges			0.001				<0.001	
Other invertebrates	0.004	<0.001	<0.001		0.106			
Gelatinous remains	0.131							
Animal remains	0.635	0.197	0.184	0.033	0.013	0.009	0.017	0.014
Animal tubes	<0.001		0.002	0.014	<0.001		<0.001	
Algae			0.002		0.001		0.009	
Sediment	0.065		0.028	0.061	0.004	0.012	0.005	0.007

Table 2.4. Stomach contents of alewife, American shad, Atlantic herring, black sea bass, bluefish, butterfish, haddock, little skate, monkfish, and scup. Values represent proportional contribution of each prey category to species-specific diet as derived from wet weight measurements.

	Alewife	American Shad	Atlantic Herring	Black Sea Bass	Bluefish	Butterfish	Haddock	Little Skate	Monkfish	Scup
Butterfish				0.102	0.443			0.032	0.513	
Scup				0.004	0.023				0.150	
Sand lance				0.024	0.052					
Herring									0.015	
Silver hake				0.010						
Other fish					0.011					<0.001
Unidentified fish	0.002		0.003		0.259	0.001		0.001	0.180	0.003
Unidentified crustaceans	0.009	0.016	0.003	<0.001		0.026		0.051		0.035
Decapod Crabs				0.011		0.001		0.039		<0.001
Cancer crabs				0.368				0.039		0.007
Hermit crabs								<0.001		
Spider crabs				0.009						
Decapod Shrimp	<0.001	<0.001		0.004			0.003	0.025		0.002
American lobster				0.002				<0.001		
Ghost/lobster shrimp								0.019		
Grass shrimp				0.050				0.038		
Sand shrimp		0.003		0.191			0.012	0.078		0.004
Pandalid shrimp				0.003				0.045		0.008
Isopods			0.002	0.018				0.001		0.011
Politolana sp isopods				<0.001				0.001		
Amphipods	0.091	0.397	0.012	0.004		0.013	0.190	0.167		0.113
Aoridid amphipods			<0.001	0.006				0.036		0.045
Caprellid amphipods			0.012					0.001		0.232
Corophiid amphipods				0.001		0.003	0.129	0.013		<0.001
Gammarid amphipods	0.002	<0.001	0.335	0.002	<0.001	0.106	0.489	0.111		0.042
Krill			0.001							
Mysids	0.003	0.021		0.006			0.005	0.001		0.001
Cumaceans	<0.001		0.193				0.007	<0.001		<0.001
Zooplankton	<0.001	0.006	0.239			<0.001				
Sand dollar				<0.001			0.012			0.008
Other echinoderms				0.006						<0.001
Squid				0.009	0.171			0.019	0.142	0.004
Bivalves				<0.001		<0.001	0.001	0.002		0.021
Clams		<0.001								<0.001
Snails		0.001		0.045						0.001
Polychaete worms	<0.001		0.001	0.003	0.039	0.059	0.075	0.096		0.173
Sea mouse				0.001				0.047		<0.001
Other worms	<0.001			<0.001						<0.001
Anemones				0.001						
Hydroids				<0.001						<0.001
Sponges					<0.001			<0.001		
Other invertebrates			<0.001	0.106		0.004				<0.001
Gelatinous remains	<0.001					0.262				
Animal remains	0.891	0.489	0.197	0.006	0.001	0.525	0.033	0.133		0.281
Animal tubes		<0.001		<0.001				<0.001		<0.001
Algae				0.002				0.002		0.001
Sediment		0.065		0.004	<0.001		0.043	0.002		0.006

Table 2.5. Stomach contents of silver hake, smooth dogfish, spiny dogfish, striped bass, summer flounder, weakfish, winter flounder, winter skate, and yellowtail flounder. Values represent proportional contribution of each prey category to species-specific diet as derived from wet weight measurements.

	Silver Hake	Smooth Dogfish	Spiny Dogfish	Striped Bass	Summer Flounder	Weakfish	Winter Flounder	Winter Skate	Yellowtail Flounder
Butterfish			0.431	0.229	0.227			0.019	
Scup		0.006	0.002	0.185	0.085	0.010		0.004	
Sand lance	0.013		0.052		0.002			0.057	
Herring			<0.001		0.018				
Silver hake			0.027		0.053				
Other fish		0.061	0.021	0.224	0.005			0.001	
Unidentified fish	0.118	0.086	0.053	0.057	0.292	0.777	0.003	0.001	
Unidentified crustaceans	0.043	0.034	<0.001		0.001	0.152	0.017	0.032	
Decapod Crabs	0.007	0.013	<0.001		0.016		0.008	0.007	0.007
Cancer crabs		0.707			0.004			0.005	0.003
Hermit crabs		0.002							
Spider crabs		0.033							
Decapod Shrimp	0.226				0.001		0.001	0.002	0.001
American lobster		0.005							
Ghost/lobster shrimp		0.005						0.011	
Grass shrimp	<0.001							0.003	
Sand shrimp	0.160				<0.001		0.001	0.030	0.020
Pandalid shrimp	0.278		<0.001		0.029			0.006	
Isopods							0.012	0.016	0.007
Politolana sp isopods								0.034	
Amphipods	0.065		<0.001	0.149	0.001		0.050	0.053	
Aoridid amphipods					<0.001		0.009	0.050	
Caprellid amphipods							0.051	0.002	<0.001
Corophiid amphipods	0.002						0.070	0.004	0.143
Gammarid amphipods	0.045				0.001		0.114	0.314	0.535
Krill	0.001							<0.001	
Mysids	0.010						<0.001	0.001	0.003
Cumaceans	0.001						0.007	0.001	0.003
Zooplankton									
Sand dollar					0.005		0.010		0.091
Other echinoderms							0.003		
Squid	0.005	0.019	0.360	0.113	0.253	0.020	0.001	0.017	
Bivalves	<0.001				<0.001		0.008	0.004	0.007
Clams							0.008	<0.001	0.008
Snails	<0.001			<0.001			0.001		0.017
Polychaete worms	0.003	0.010	<0.001	0.001		0.014	0.194	0.210	0.062
Sea mouse							0.073	0.007	
Other worms							0.001	0.002	
Anemones							0.019		
Hydroids	<0.001					0.007	0.006	<0.001	
Sponges							0.002		
Other invertebrates									
Gelatinous remains									
Animal remains	0.009	0.020	0.037	0.025	0.005	0.014	0.247	0.074	
Animal tubes					<0.001		0.007	0.001	0.014
Algae		<0.001		0.018	<0.001		0.005	<0.001	
Sediment	0.012		0.014		<0.001	0.007	0.072	0.032	0.079

Figure 2.1. Stomach and tissue sampling locations (via otter trawl) within Rhode Island Sound and Block Island Sound from 2009-2011.

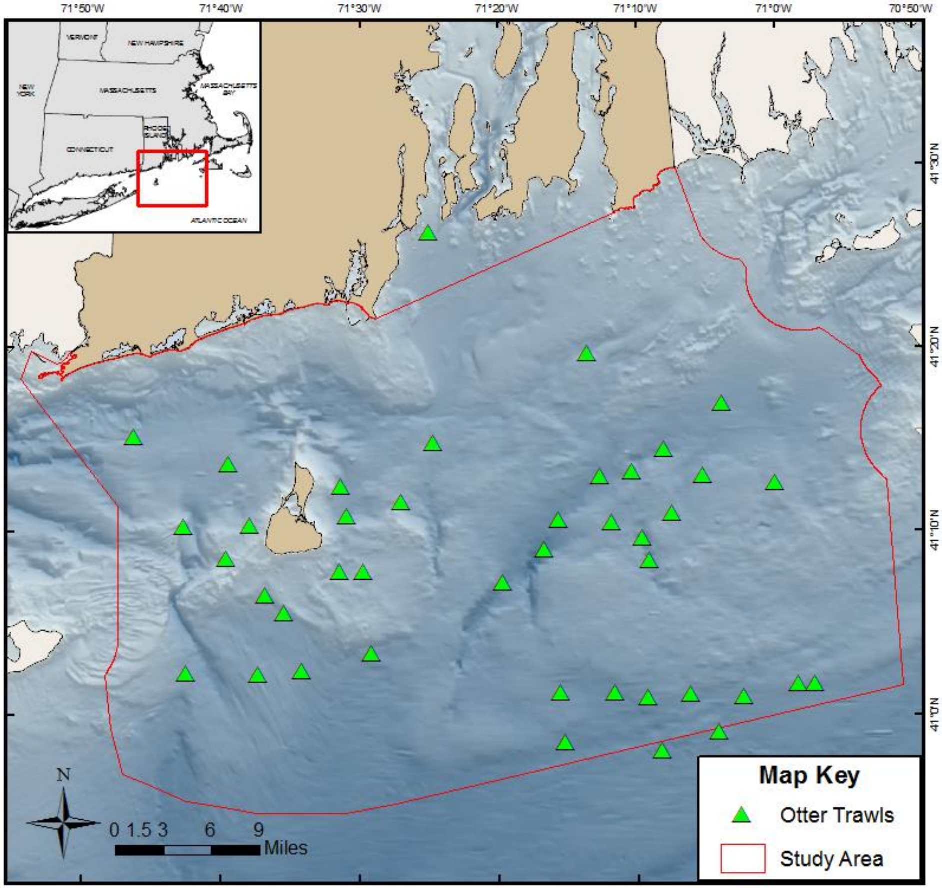


Figure 2.2. Dendrogram of dietary guild structure of the fish community in Rhode Island Sound and Block Island Sound. Symbols represent dietary guilds and subgroups as identified by (*primary prey*): Light green diamonds = planktivores (*pelagic zooplankton*), Dark purple triangles = benthic omnivores (*small crustaceans and worms*), Dark green diamond = planktivore (*benthopelagic zooplankton*), Light purple triangles = benthivores (*gammarid amphipods*), Grey square = piscivore (*small fish and crustaceans*), Blue squares = piscivores (*fish*), Orange circles = benthopelagic omnivore *(shrimp and fish)*, and Red circles = crustacean eaters (*decapod crabs and shrimp*).

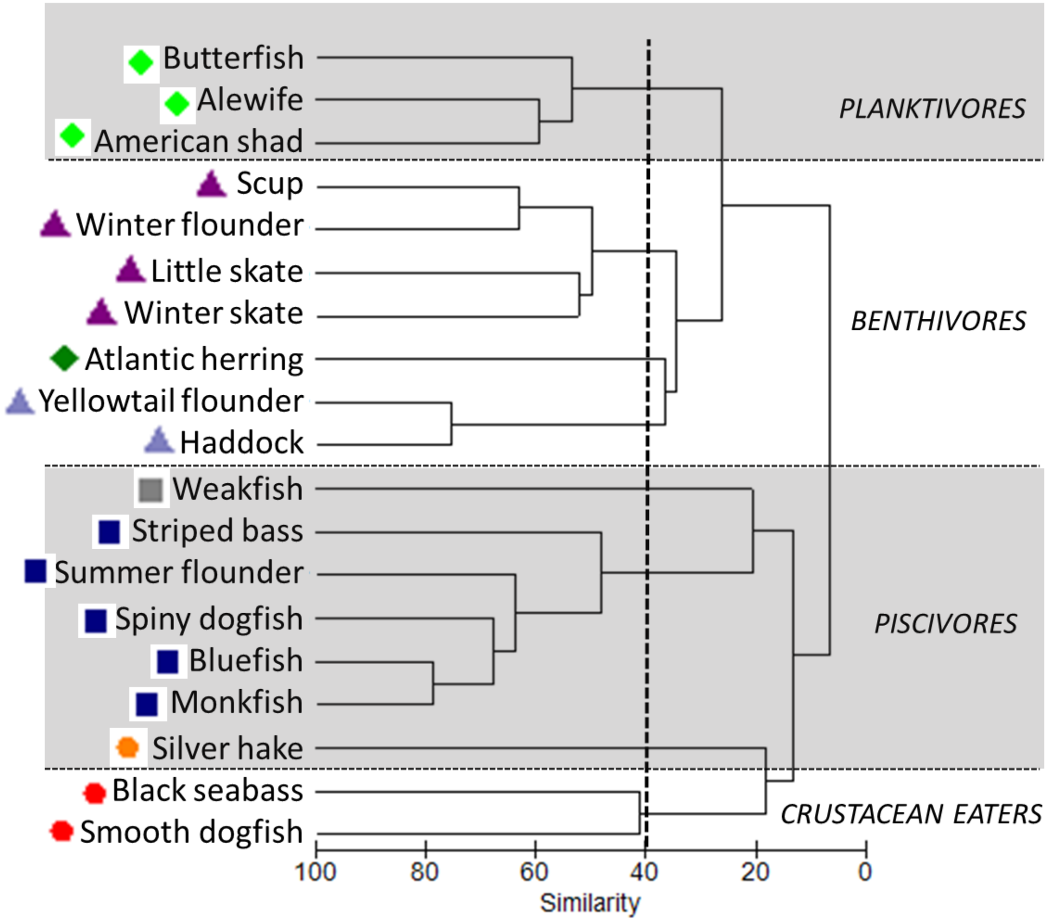


Figure 2.3. Ordination of dietary composition of fish species in Rhode Island Sound and Block Island Sound. This non-metric multidimensional scaling plot (MDS) depicts the pattern in dietary composition, with similar dietary compositions close together. Each point represents one predator species. Symbols represent dietary guilds, which are defined by dominant prey types.

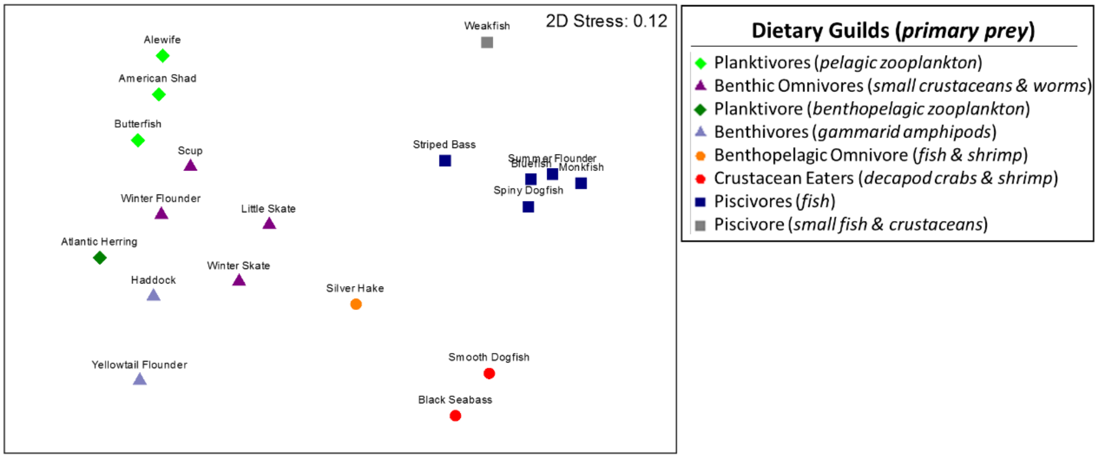


Figure 2.4. Mean proportional composition (by wet weight) of major prey items for: a) planktivores and Atlantic herring; b) benthivores and benthic omnivores; c) crustacean eaters and silver hake; and d) piscivores and weakfish. The planktivore guild includes butterfish, American shad, and alewife. The benthic omnivore group includes scup, winter flounder, little skate, and winter skate. The benthivore group includes yellowtail flounder and haddock. The crustacean eater guild includes smooth dogfish and black sea bass. The piscivore guild includes bluefish, striped bass, monkfish, summer flounder, and spiny dogfish.

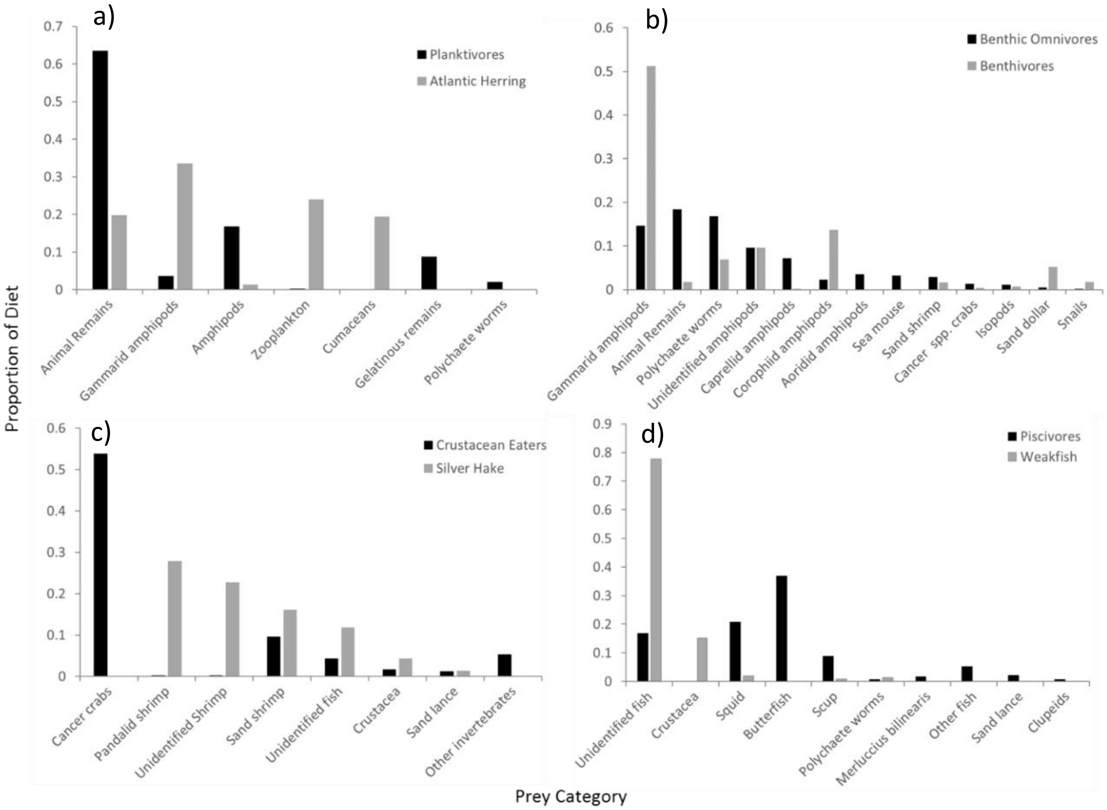


Figure 2.5. Bivariate plot of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotope signatures for each species. Symbols represent dietary guild membership (see Figure 2.3).

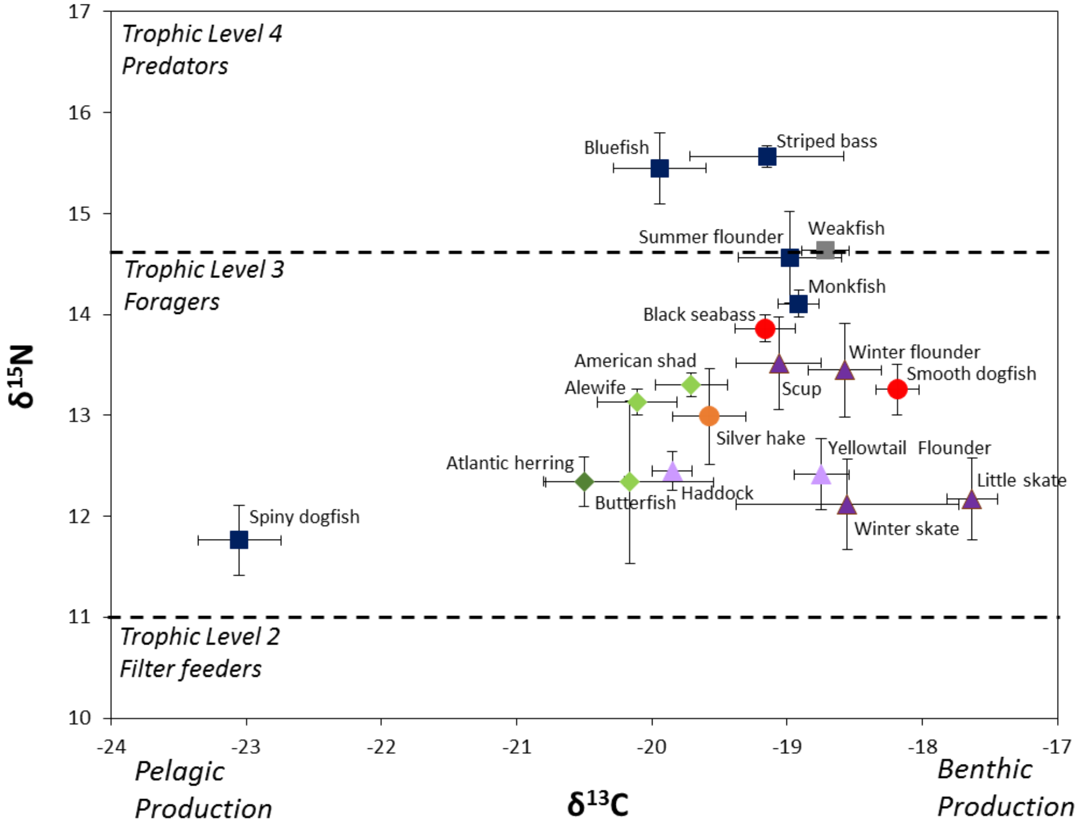


Figure 2.6. Site-specific silver hake (*Merluccius bilinearis*) diet composition in Rhode Island Sound and Block Island Sound. Each pie chart represents the diet composition of silver hake at one study site, with proportions derived from prey wet weight.

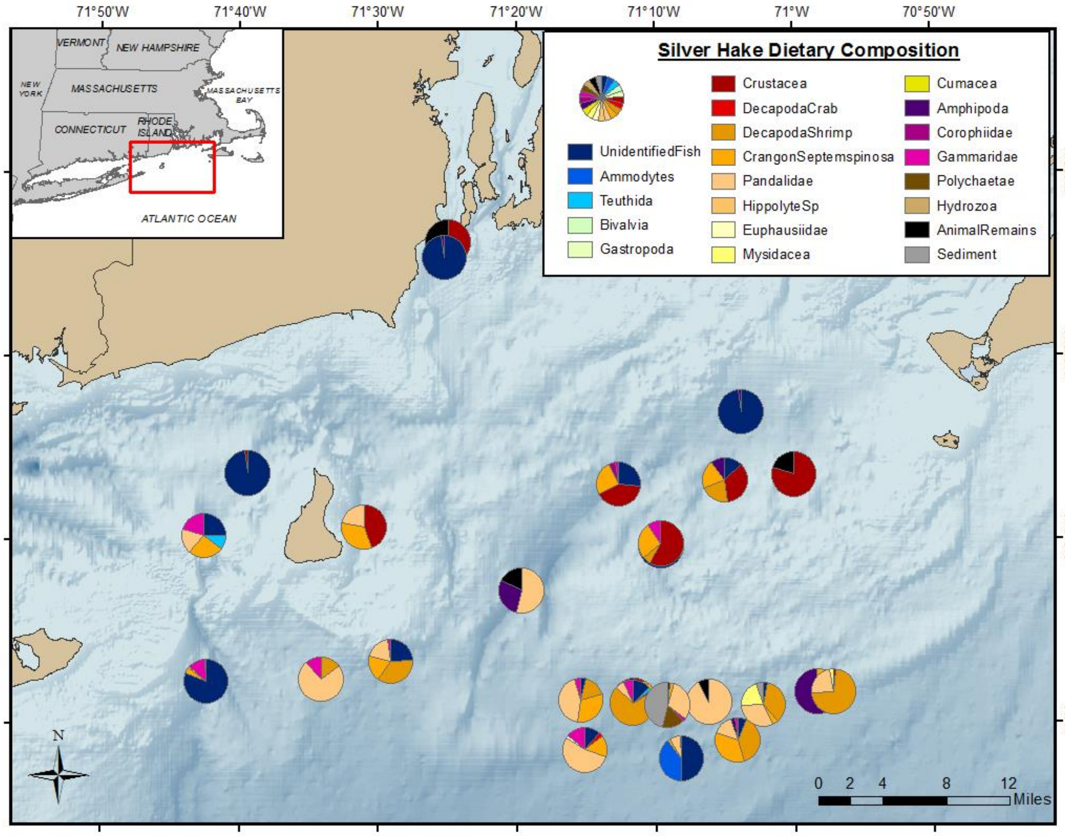


Figure 2.7. Site-specific winter flounder (*Pseudopleuronectes americanus*) diet composition in Rhode Island Sound and Block Island Sound. Each pie chart represents the diet composition of winter flounder at one study site, with proportions derived from prey wet weight.

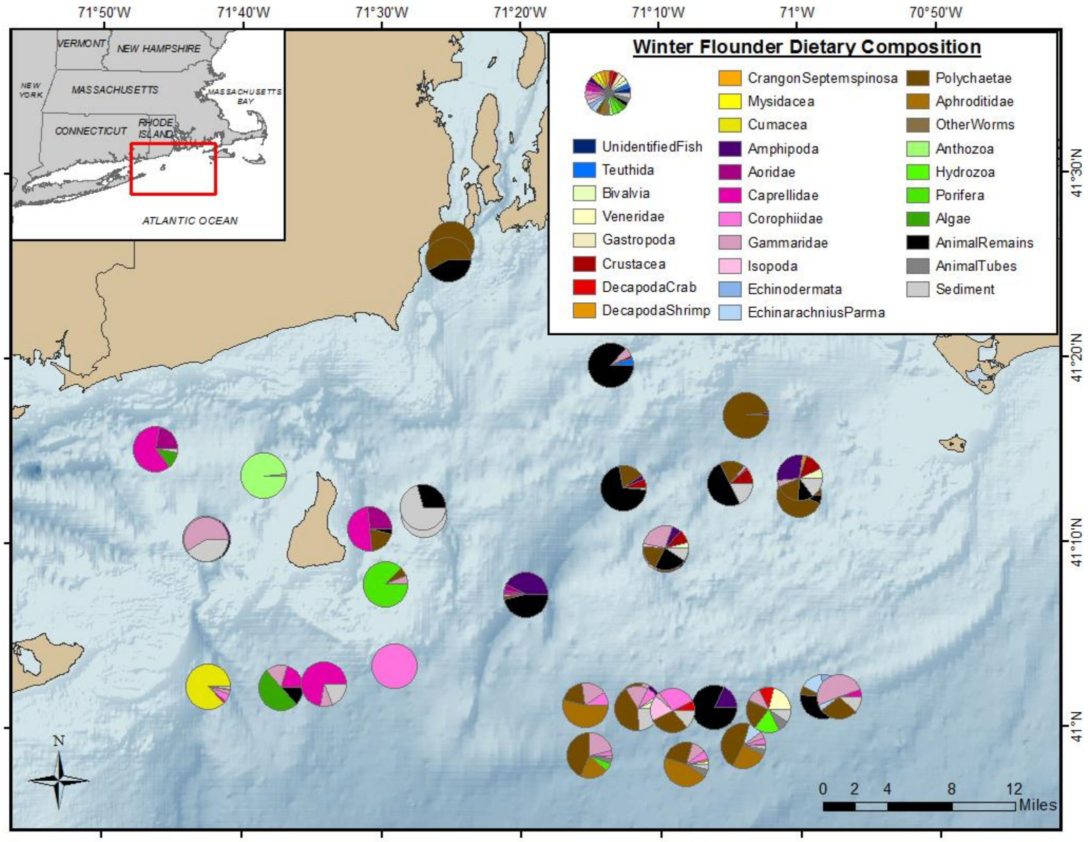


Figure 2.8. Site-specific scup (*Stenotomus chrysops*) diet composition in Rhode Island Sound and Block Island Sound. Each pie chart represents the diet composition of scup at one study site, with proportions derived from prey wet weight.

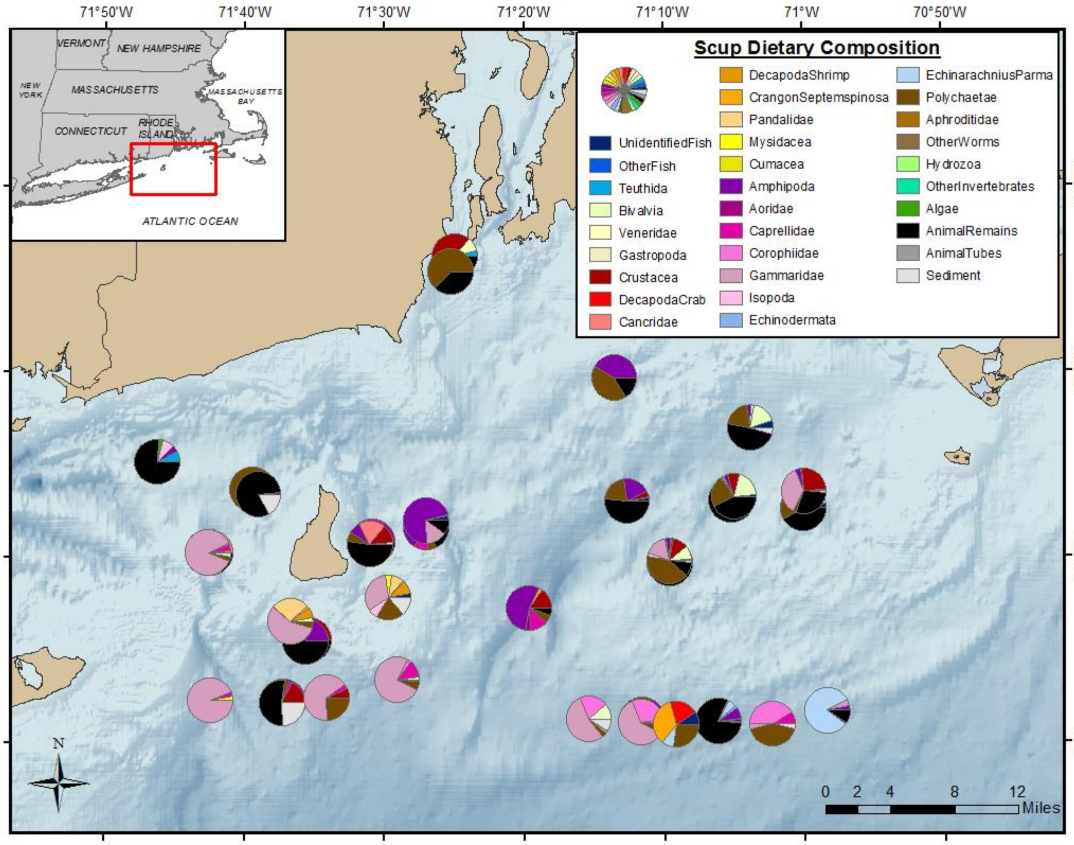


Figure 2.9. Bivariate plot of silver hake (*Merluccius bilinearis*) nitrogen and carbon stable isotope signatures. Symbols represent geographical region (Inshore RIS = Inshore Rhode Island Sound, Offshore RIS = Offshore Rhode Island Sound, Inshore BIS = Inshore Block Island Sound, and Offshore BIS = Offshore Block Island Sound).

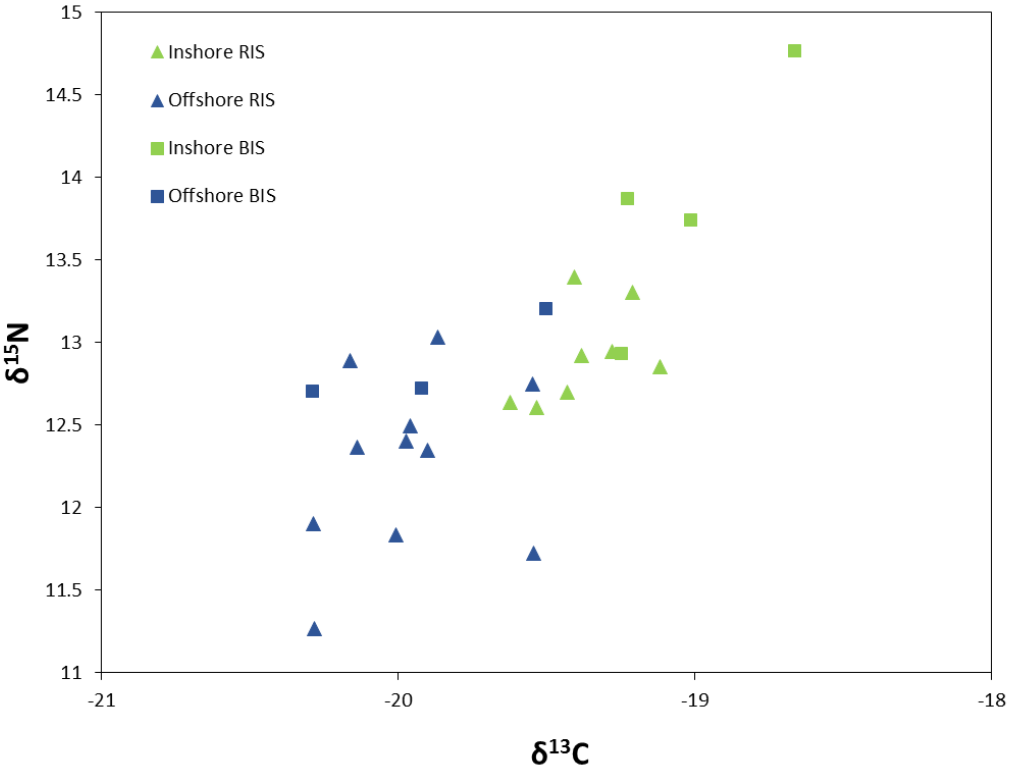


Figure 2.10. Bivariate plot of winter flounder (*Pseudopleuronectes americanus*) nitrogen and carbon stable isotope signatures. Symbols represent geographical region (Inshore RIS = Inshore Rhode Island Sound, Offshore RIS = Offshore Rhode Island Sound, Inshore BIS = Inshore Block Island Sound, and Offshore BIS = Offshore Block Island Sound).

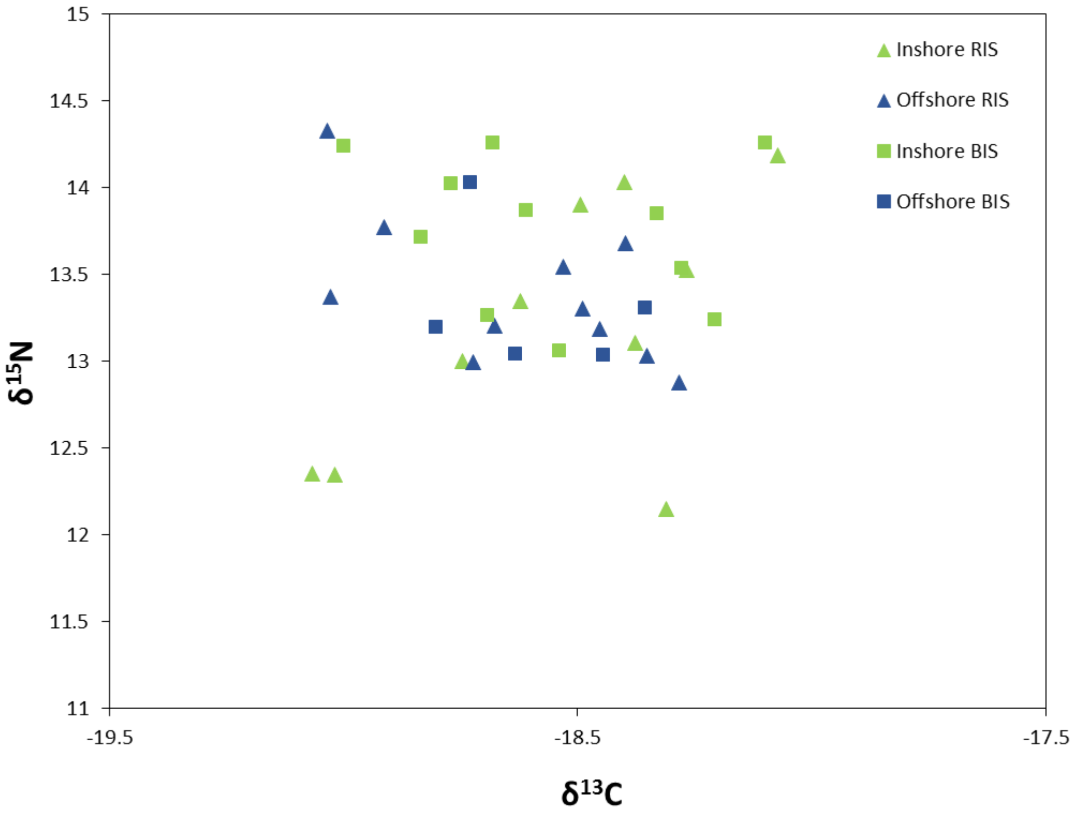
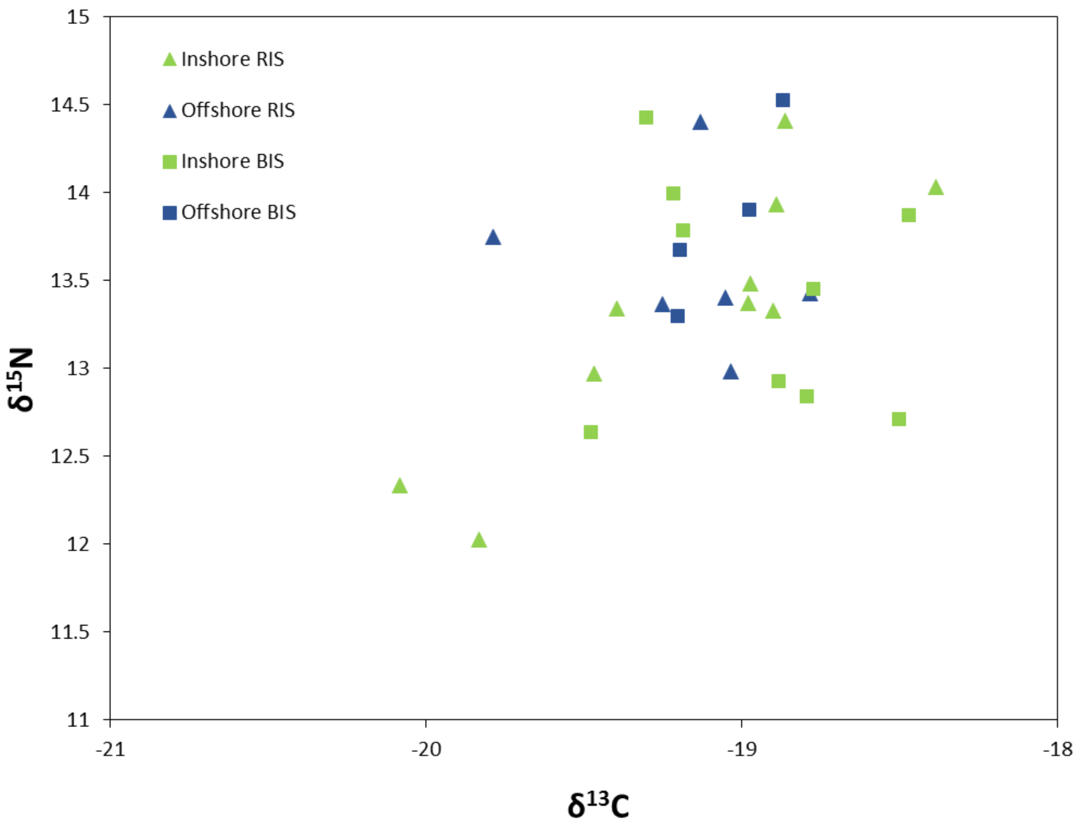


Figure 2.11. Bivariate plot of scup (*Stenotomus chrysops*) nitrogen and carbon stable isotope signatures. Symbols represent geographical region (Inshore RIS = Inshore Rhode Island Sound, Offshore RIS = Offshore Rhode Island Sound, Inshore BIS = Inshore Block Island Sound, and Offshore BIS = Offshore Block Island Sound).



CHAPTER 4

A manuscript prepared for submission to Marine Ecology Progress Series

Habitat Associations of the Demersal Fish and Invertebrate Community in a Nearshore Northwest Atlantic Ecosystem

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Abstract:

Recent interest in offshore energy development has focused attention on ecosystem-based spatial management planning in Rhode Island's nearshore waters, which requires a thorough understanding of the relationship between fish community structure and benthic habitat. To address this need, we conducted otter trawl and beam trawl surveys, multibeam sonar surveys, underwater video surveys, and water column profiles to assess site-specific species assemblages and habitat characteristics in Rhode Island and Block Island Sounds. A suite of benthic habitat parameters was derived from the bathymetry, backscatter, videographic, and oceanographic datasets and used to evaluate the relationship between the environment and fish community structure. Linear regression analysis revealed significant relationships between water depth and species abundance and diversity, such that deeper habitats support the most abundant and diverse fish communities. Nonparametric multivariate linking analysis identified seven habitat parameters that significantly influence otter and beam trawl species assemblages, suggesting that both physical features of the seafloor (i.e. benthic surface roughness, slope, minor grain size) as well as water column properties (i.e. temperature, salinity, depth) play an important role in structuring the fish community. Quantifying these relationships will allow us to predict how the demersal fish community may respond to alteration of benthic habitat resulting from offshore wind energy development as well as water temperature increase associated with global climate change. By understanding the role that habitat plays in fish community dynamics in Rhode Island and Block Island

Sounds, we hope to guide the location of future ocean uses so as to preserve the ecological and economic value of the area.

Introduction:

The physical and oceanographic characteristics of benthic habitat affect fish community structure in a variety of marine ecosystems (Luckhurst & Luckhurst 1978, Gratewick & Spite 2005, Anderson et al. 2009). For example, Hawaiian coral reef fish communities exhibit distinct relationships with the rugosity and depth of benthic habitat, while groundfish on George's Bank in the northwest Atlantic exhibit seasonally distinct relationships to bottom water temperature and depth (Friedlander & Parrish 1998, Methratta & Link 2006). Little is known, however, about fish habitat use in the temperate, transitional waters of Rhode Island Sound and Block Island Sound, USA. While many of the fishing activities in this area target specific areas having benthic habitat characteristics thought to yield the best harvest, the exact relationship between the demersal fish community and benthic habitat has yet to be defined (Costa-Pierce 2010, RI SAMP 2010, Smythe & Beutel 2010, LaFrance et al. 2014, Malek et al. 2014). With plans for offshore wind energy development in this area underway, it is essential to understand the basis of fish-habitat relationships and the functional role of different habitat types in supporting fish production to ensure sustainable development practices.

Historically, the distribution, scale, and structure of fish habitat in marine ecosystems have been difficult to assess due to limited seafloor survey techniques

(Elefteriou & McIntyre 2005). Recent technological developments, such as interferometric sonar systems and autonomous underwater vehicles, however, have begun to address this challenge (ICES 2007, Todd & Greene 2007, Brown et al. 2011). In comparison to traditional techniques, habitat assessments that utilize interferometric data, in addition to seafloor imagery and oceanographic conditions, typically produce a more holistic, and more biologically-meaningful, characterization of the seafloor (Mayer 2006, Brown et al. 2012). Despite advances in seafloor survey techniques, however, it still remains difficult to assess the link between benthic habitat and fish community structure (Johnson et al. 2012). One factor contributing to this difficulty is the range of spatial scales at which organisms may be associated with their environment (Wiens 1989, Anderson et al. 2009, Freitas et al. 2011). As such, the most effective method for combining biological and habitat data are still under debate (Brown 2011). Here we will apply a non-parametric, multivariate approach to linking fish community structure to benthic habitat at a scale relevant for local spatial management efforts.

Marine spatial planning is typically considered an “ecosystem- based” approach to management (Douvere 2008). By definition, ecosystem-based approaches consider not only species interactions and climate, but also benthic habitat. Thus, marine spatial planning, ecosystem-based fisheries management, and fish habitat characterization go hand in hand (Cogan et al. 2009). More specifically, integrated spatial management planning requires activities to be sited in appropriate habitats that will minimize, to the extent possible, the cumulative impacts on resident species and the ecological and economic services derived from this nearshore region (Beck et al. 2009). To achieve this, however, a thorough understanding of the spatial distribution of benthic habitats and their linkages to fish distribution and production is required (Foley et al. 2010). Understanding habitat requirements and distributions is especially important for vulnerable or overfished species, whose rebuilding programs could include large area closures if other management tools are unsuccessful (Gleason et al. 2010).

This project addresses the general challenge of developing an ecosystem-based approach to marine spatial planning in Rhode Island's nearshore waters, including Rhode Island Sound and Block Island Sound (Ehler & Douvere 2009, RI SAMP 2010). These bodies of water are transitional between the estuaries of Narragansett Bay and Long Island Sound and the outer continental shelf, and as such, act as important linkages between nearshore and offshore processes, including nutrient fluxes, larval transport, and the migration of the adult stages of resource species, such as American lobster, *Homarus americanus*, and winter flounder, *Pseudopleuronectes americanus* (Figure 3.1, Costa-Pierce 2010). A general understanding of the ecology of Rhode Island Sound and Block Island Sound exists, but there is a lack of site-specific data to guide spatial management planning (Hale 2010, Malek et al. 2014). Compounding the challenge, the spatial planning process is being conducted against a background of changing coastal climate. As a result, historical baseline data may no longer represent current conditions. Studies to support the management of Rhode Island's nearshore waters have become a priority since 2000, when new uses, such as offshore wind energy, aquaculture, and sand extraction were proposed in this region.

Understanding the spatial distribution of benthic habitats and the relationship to the fish community is essential in developing effective spatial management practices. As such, the primary objective of this project was to obtain site-specific data about the benthic habitats and the fish communities in Rhode Island's nearshore waters. To do this, we mapped and classified benthic habitats using interferometric sonar, seafloor video, and oceanographic sampling, and assessed fish community structure using otter trawls and beam trawls. In the end, this project sought to develop a better understanding of the fish-habitat relationships in the nearshore Northwest Atlantic ecosystem of Rhode Island and Block Island Sounds so as to guide spatial management plans and advance the field of fish-habitat research.

Methods:

Fish Community Assessment

Otter trawls and beam trawls were used to obtain habitat-specific fish and invertebrate species compositions at 82 sites in Rhode Island Sound and Block Island Sound (44 bottom trawls, 38 beam trawls, Figure 3.1). Stations were chosen to include representative ranges of depths and habitat types in the study area, and in areas targeted for offshore renewable energy development. Otter trawls were conducted in September 2009- 2011, while beam trawls were conducted in July and August 2011- 2012.

Otter trawls were carried out in collaboration with the ongoing Northeast Monitoring and Assessment Program (NEAMAP), aboard the 90’ *F/V Darana R* (http://www.neamap.net/). Each tow was conducted with a 400 cm x 12-cm, three-bridle, four-seam bottom trawl, paired with a set of Thyboron, Type IV 66” trawl doors. The cod-end was made of 12 cm stretch mesh with a 2.4-cm knotless nylon liner. All tows were 20 minutes in duration with a target tow speed of 3.0 knots, resulting in tow distances of approximately one nautical mile. The catch was processed at sea by a team of scientists from the University of Rhode Island Graduate School of Oceanography and Virginia Institute of Marine Science. Once on board, the catch from each station was sorted by species and size class. Aggregate weights (kg), counts and individual length measurements (mm) were recorded for all species collected.

Beam trawling was conducted on the 50’ *F/V Mister G* in order to sample harder bottom habitats that were inaccessible to otter trawling. Each tow was conducted with a three meter beam trawl with cod-end mesh equivalent to that of the NEAMAP otter trawl. All tows were 20 minutes in duration with a target tow speed of 4.0 knots. The catch was sorted by species, enumerated, and weighed to the nearest 0.001 kg. Individual length measurements (mm) were also recorded for all species collected (Fish: Fork length, Squid: Mantle length, Lobster: Carapace length, Crab: Carapace width).

Habitat Characterization

Acoustic Surveys

An interferometric sonar system was used to collect high-resolution side-scan sonar with 2 meter resolution at 31 otter trawl stations and 15 beam trawl stations (Figure 3.1, Table 3.1). Raw data were continuously recorded with Ocean Imaging Consultants – Geophysical Data Acquisition System (OIC-GeoDas) software and monitored in real time with a top-side monitor. A Hemisphere GPS was used to correct for vessel heading, pitch and roll, and survey lines were logged using Hypack navigation software. The data were processed into side-scan backscatter mosaics at 2 meter pixel resolution using OIC Cleansweep software (LaFrance et al. 2010). While final backscatter values are to some degree dependent on post processing techniques, exploratory analysis indicated that processing consistency was sufficient for quantitative analysis. Backscatter intensity indicates the density of the seafloor, where higher reflectance denotes harder habitat (shell, sand, cobble) and lower reflectance denotes softer habitat (mud, silt, clay) (Brown & Blondel 2008). The final side-scan backscatter mosaics were exported as geo-referenced tiff files for analysis in ArcMap.

The United States Coastal Relief Model (CRM) for the Northeast Atlantic created by the National Oceanic and Atmospheric Administration's National Geophysical Data Center (NGDC) was used to create a full coverage bathymetric map of the study area. The CRM incorporates data from NGDC's hydrographic surveys, multibeam bathymetry, and trackline bathymetry, the United States Geological Survey (USGS), and other federal government agencies and academic institutions. The resolution of the Northeast Atlantic CRM is 90 meters. The full Northeast Atlantic CRM was clipped to the extent of the study area and converted to GRID format for application in this study (Figure 3.1).

A suite of benthic habitat parameters was derived from the backscatter and bathymetry data for each of the acoustically mapped trawl stations (Table 3.1). The minimum, maximum, mean, and standard deviation of depth and slope were calculated from the bathymetry grid for each trawl site using the Spatial Analyst and Raster Processing toolboxes in ArcInfo 10.3 (Lafrance et al. 2010, Malek et al. 2010). These metrics were calculated at 90 meter resolution within a 5 meter wide buffer around each otter trawl track and a 3 meter buffer around each beam trawl track. The minimum, maximum, mean and standard deviation of backscatter were also derived from the side-scan mosaics in ArcInfo 10.3. These metrics were calculated at 2 meter resolution within a 5 meter wide buffer around each otter trawl track and a 3 meter buffer around each beam trawl track.

In addition, a map of benthic surface roughness was used to characterize the habitat complexity at each trawl site (RI SAMP 2010, Figure 3.2). The benthic surface roughness layer represents the standard deviation of the slope within a 1000 meter radius calculated at 100 meter pixel resolution. The mean, minimum, maximum, and standard deviation of the surface roughness was calculated for each of the trawls using the Raster Processing toolbox in ArcInfo 10.3 (Table 3.1). These metrics were calculated at 100 meter resolution within a 5 meter wide buffer around each otter trawl track and a 3 meter buffer around each beam trawl track.

Seafloor Video Surveys

The benthic habitat types present at each trawl site were investigated using seafloor video surveys. The video survey system is comprised of a Microvideo AM301 underwater video camera, mounted on a stainless steel video sled with two Pro-V8 LED lights for illumination. Two lasers, fixed 8 inches apart, provide scale for habitat features and enable measurement of epifaunal species. At each trawl station, the video sled drifted for 10 minutes, with the camera collecting continuous video footage. The target camera altitude was 1 meter, giving a field of view of approximately 1 m^2. The objective was to obtain at least 20 clear and useable photos for quantitative analysis from each station.

Bottom photos were analyzed with a point-count program written in Matlab that was revised for this work (Lengyel et al. 2009). Data extracted from each photo include the major and minor sediment types, the percent cover of colonial epifauna, and the frequencies of free-living animals. Epifaunal coverage and megafaunal occurrence data were excluded from these analyses due to their rarity in seafloor videos. Major and minor sediment types were recorded on a scale consistent with Wentworth grain size and were converted to numerical values for quantitative analysis (Table 3.2, Figure 3.3). Major and minor sediment types were defined as the sediment types covering ≥75% and ≤25% of the seafloor, respectively. The major grain size at each trawl station was calculated by taking the mean of the numerical major sediment type from the 20 seafloor photos at each station. The same routine was followed for classification of site-specific minor grain size. The total number of habitat types observed at each trawl site was used for categorical analysis and interpreted as a measure of habitat heterogeneity.

Oceanographic Sampling

Oceanographic data were collected at each otter trawl station using a Yellow Springs Instruments (YSI) multiparameter probe that recorded surface and bottom temperature (°C), salinity (ppt), and dissolved oxygen (mg/L). Due to intermittent equipment malfunctions, full oceanographic data were available for only 36 of the 44 otter trawl stations (Table 3.1). Surface temperature (°C), salinity (ppt), and dissolved oxygen (mg/L) were also recorded at each beam trawl station using a YSI multiparameter probe. A Sonotronics Depth and Temperature Logger (DTL) was used to record bottom water temperature (°C) at each beam trawl station. Again, due equipment malfunctions full oceanographic data were available for only 35 of the 38 beam trawl stations (Table 3.1).

Assessing Benthic Habitat and Fish Community Relationships

A suite of 24 continuous and four categorical site-specific habitat parameters, derived from bathymetry, slope, benthic surface roughness, backscatter, videographic, and oceanographic data, were combined with fish community metrics derived from trawl surveys to test for relationships between habitat characteristics and fish and invertebrate abundance, biomass, diversity, and species assemblage structure (Table 3.1). Beam trawl and otter trawl data were analyzed separately due to differences in gear selectivity (Malek et al. 2014).

Univariate Analyses

For univariate fish-habitat analyses, aggregate fish community abundance and biomass were standardized by the area swept (otter trawl area swept = 0.022 – 0.031 km^2; beam trawl area swept = 0.0066 - 0.0076 km^2) and log transformed to achieve a normal distribution. Shannon-Wiener's H was used as a diversity index because it is sensitive to changes in rare species (Hill, 1973).

Analysis of variance (ANOVA) models were used to test for the effects of categorical habitat variables, including depth strata, major habitat type, minor habitat type, and number of habitat types, on aggregate fish community abundance, biomass, and species diversity. Depth strata were defined as follows: Stratum 1: 20-40 feet (6-12m), Stratum 2: 40-60 feet (12-18m), Stratum 3: 60- 90 feet (18-27m), Stratum 4: 90-120 feet (27-37m), Stratum 5: >120 feet (>37m). Tukey Honest Significant Difference tests (Tukey HSD) were used to make pairwise comparisons between depth strata, major habitat type, minor habitat type, and number of habitat types.

Relationships between continuous habitat parameters and univariate fish community metrics were assessed with linear regression analysis in R. It was hypothesized that fish abundance, biomass, and diversity would be positively correlated with measures of bottom complexity (i.e. benthic surface roughness, slope, standard deviation of backscatter, major sediment type) (Salomon et al. 2010). It was also hypothesized that fish diversity would be positively correlated with depth (Malek et al. 2014).

Stepwise multiple linear regression models were used to assess the cumulative effects of 24 habitat parameters on aggregate fish community abundance, biomass, and species diversity (Table 3.1). Akaike's Information Criterion corrected for small sample bias (AIC_c) was used to evaluate and select the optimal regression model (Burnham & Anderson 2002).

Multivariate Analyses

For multivariate fish community response variables (e.g. species composition in trawls), associations with habitat parameters were tested using nonparametric techniques in the software package PRIMER-E (Clarke and Warwick 2001). These analyses aimed to assess which habitat parameters are most important in structuring the fish assemblages in Rhode Island Sound and Block Island Sound.

Prior to fish-habitat analysis, species-specific fish abundance data from each trawl site were fourth-root transformed to reduce the influence of highly abundant species (Clark & Green 1988). A Bray-Curtis similarity index was used to assess the similarity in fish community composition between sites and a hierarchical clustering analysis with a group-average linking algorithm was used to divide trawl sites into species assemblage groups based on the similarity of fish community composition (Clark & Gorley 2006). The cluster analysis was carried out with the SIMPROF routine, which determines statistically significant station clusters within an *a priori* ungrouped set of stations (Clarke 1993).

To test of the effect of categorical habitat parameters on fish community composition, analysis of similarity (ANOSIM) was performed on the fish community Bray-Curtis similarity matrix using depth strata, major habitat type, minor habitat type, and number of habitat types as factors. ANOSIM tests the null hypothesis that there are no differences in fish species assemblage between groups of samples when examined in the context of an *a priori* factor (depth strata, major and minor habitat type, number of habitats) (Clarke & Gorley 2006). An R value of 0 indicates there are no differences in species assemblages between factor groups, while an R value greater than 0 reflects the degree of the differences. The test is permuted 999 times to generate a significance level.

Prior to multivariate analysis of continuous habitat variables, a Draftsman plot, consisting of pairwise scatterplots, was created to assess the correlation between habitat variables. Variables that were highly correlated ($r > 0.85$), and therefore redundant, were eliminated from further analysis (see Table 3.1; variables marked with an asterisk or cross were retained). Habitat variables were then normalized to correct for differences in units, and a Euclidean distance resemblance matrix was created to assess the multivariate habitat similarity between sites. A multi-dimensional scaling plot (MDS plot) was derived from the habitat resemblance matrix to ordinate the sites in two dimensions. The MDS plot was used to visualize between-site similarity in habitat and to compare the environmental patterns to that of the fish community.

The relationship between the non-correlated habitat parameters and fish community composition was examined using the BIOENV procedure, which identifies a subset of habitat parameters that best explain fish community composition (Clarke & Gorley 2006). More specifically, the BIOENV approach analyzes the extent to which a suite of habitat variables match the species assemblage data by searching for high rank correlations between variables in the two matrices (the habitat Euclidean distance matrix and the fish community Bray-Curtis similarity matrix). Thus, the BIOENV procedure identifies combinations of benthic habitat parameters that result in the highest Spearman rank correlation with the fish community similarity matrix. A maximum of five variables was permitted in the output. Single parameter runs were also conducted to assess the significance of individual habitat parameters to fish community structure. The BIOENV procedure was permuted 999 times in order to evaluate the level of significance of the results.

The group of five benthic habitat parameters found to best explain fish community structure were then subjected to the LINKTREE procedure to classify the stations according to patterns in the selected habitat parameters. The LINKTREE routine groups the fish community samples (stations) by successive binary division using the habitat parameters as drivers and maximizing the ANOSIM R value at each division (Clarke & Gorley 2006). The ANOSIM R was constrained to be greater than 0.300 and the minimum group size was set at three. Each resulting class contains a group of fish community samples (stations), classified by quantitative thresholds of habitat parameters. An ANOSIM was performed on the habitat groups defined by the LINKTREE analysis to test whether there are significant ($p > 0.05$) differences in fish assemblages among habitat groups. ANOSIM was also used to test for differences in habitat characteristics between species assemblage groups.

Results:

Benthic Habitat and Fish Community Integration

Otter Trawls - Univariate Analyses

ANOVA models testing for the effect of categorical habitat variables (depth stratum, major habitat type, minor habitat type, and number of habitat types) on aggregate fish community metrics (abundance, biomass, and diversity) were largely insignificant, with the exception of the effect of depth strata on species diversity (Table 3.3). Tukey HSD tests revealed a significantly higher species diversity in depth strata 5 than in depth stratum 3 and 4 ($p=0.007$). Thus otter trawl sites in deeper water were characterized by higher species diversity than otter trawl sites in shallower water.

Regressions between continuous habitat parameters and otter trawl fish community metrics also revealed a relationship between depth and species diversity, such that species diversity increased with deeper minimum, maximum, and mean water depth (Table 3.4, Figures 3.4, 3.5, & 3.6). In addition, species diversity exhibited significant proportional relationships with backscatter (minimum and mean) and bottom salinity (Table 3.4, Figure 3.6). Bottom dissolved oxygen and bottom temperature, on the other hand, were negatively related to fish community diversity. In term of fish community abundance, surface and bottom salinity were significant predictor variables, such that fish abundance decreased in more saline water (Adj. R^2=0.209, p=0.003) (Table 3.4, Figure 3.4). Finally, fish community biomass was negatively related to bottom water temperature (Adj. R^2=0.100, p=0.043) (Table 3.4, Figure 3.5). The remaining regressions were not significant (Adj. $R < 0.1$, $p > 0.05$). None of the individual benthic habitat parameters displayed a significant relationship with all of the otter trawl fish community metrics, suggesting that a combination of habitat features collectively defines the relationship between the environment and the fish community.

Multiple regression analysis integrating AIC_c selection criteria suggests that a collection of six habitat variables (mean slope, bottom salinity, bottom temperature, surface salinity, surface temperature, minor grain size) best explains otter trawl abundance in Rhode Island and Block Island Sounds (Table 3.5). Otter trawl biomass, on the other hand, was best explained by a suite of 11 habitat variables: standard deviation of slope, mean depth, mean roughness, mean backscatter, standard deviation of backscatter, bottom dissolved oxygen, bottom salinity, surface dissolved oxygen, surface temperature, major grain size, and minor grain size (Table 3.5). Finally, considered together, bottom dissolved oxygen, bottom salinity, surface dissolved oxygen, and surface salinity, best explained otter trawl species diversity

(Table 3.5). Notably, salinity was a significant explanatory variable in all of these models.

Otter Trawls - Multivariate Analyses

Cluster analysis of otter trawl catch data identified three major species assemblage groups in Rhode Island and Block Island Sounds. These species assemblage groups are characterized by their dominant species as follows: 1) “Scup (*Stenotomus chrysops*) and Summer Flounder (*Paralichthys dentatus*)”, 2) “Spiny Dogfish (*Squalus acanthius*) and Sea Scallop (*Placopecten magellanicus*)”, and 3) “Silver Hake (*Merluccius bilinearis*) and Lobster (*Homarus americanus*)”. One site was determined to be unique, due to its low abundance and diversity of species.

ANOSIM analyses and MDS visualization indicate that depth stratum significantly influences the species assemblage of demersal fish communities within Rhode Island and Block Island Sounds, as sampled by otter trawls (R=0.424, p=0.001, Figure 3.7). More specifically, the fish community composition at otter trawl sites in depth stratum 3 was significantly different than the fish community composition at otter trawl sites in depth strata 4 and 5 (Stratum 3 v. Stratum 4: R=0.437, p=0.001; Stratum 3 v. Stratum 5: R=0.559, p=0.001). Fish community composition, however, was not significantly influenced by major habitat type, minor habitat type, or number of habitat types (Major Habitat Type: R=0.061, p=0.166; Minor Habitat Type: R=-0.007, p=0.540; Number of Habitat Types: R=0.007, p=0.419).

The BIOENV procedure identified five benthic habitat parameters as being most influential to fish community composition, as sampled by otter trawls (Rho=0.609, p=0.001). These parameters were mean depth, bottom temperature, standard deviation of roughness, mean slope, and bottom salinity. Considered individually, mean depth and bottom temperature both exhibited significant relationships with otter trawl fish community composition in Rhode Island and Block Island Sounds (R=0.414, p=0.001).

The LINKTREE analysis divided the otter trawl sites into three habitat groups based on thresholds of mean water depth and standard deviation of roughness: 1) Shallow, 2) Deep & Rough, and 3) Deep & Smooth (Figure 3.8). The "Shallow" habitat group was characterized by water depths of less than 39 meters. The "Deep and Rough" habitat group was characterized by water depths greater than 41 meters and more heterogeneous habitat (standard deviation of roughness greater than 0.1). The "Deep and Smooth" habitat group was characterized by water depths greater than 41 meters and less heterogeneous habitat (standard deviation of roughness less than 0.002).

The otter trawl habitat groups are remarkably similar to the species assemblage groups defined by cluster analysis, suggesting a strong link between the physical features of the benthos and the demersal fish community as sampled by otter trawls (Figure 3.8). Evidence of this relationship is apparent in the projection of the otter trawl species assemblage groups on the habitat characteristics MDS plot (Figure 3.8). Furthermore, ANOSIM analyses of the otter trawl fish community data with respect to habitat groups indicate that there are significant differences in species assemblages between habitat groups (R=0.429, p=0.001). More specifically, the “Shallow” habitat group was primarily occupied by fish communities with high abundances of scup and summer flounder, whereas the “Deep and Smooth” habitat group was inhabited by fish communities with high abundances of sea scallops and spiny dogfish, and the “Deep and Rough” habitat group was characterized by fish communities with a high diversity of species, including little *Leucoraja* spp. skates, scup, and spiny dogfish. There are also significant differences in the habitat characteristics that define each species assemblage group (ANOSIM: R=0.475, p=0.002).

In a spatial context, the “Shallow” habitat group is primarily located around Block Island, where it exhibits significant overlap with the “Scup and Summer Flounder” species assemblage group (Figure 3.9). The “Deep and Smooth” habitat group, on the other hand is located in the offshore extent of Rhode Island Sound, where the “Spiny Dogfish and Sea Scallop” species assemblage group dominates. Finally, the “Deep and Rough” habitat group is located in the deep waters surrounding Cox’s Ledge, which are primarily occupied by the “Silver Hake and Lobster” species assemblage (Figure 3.9).

Beam Trawls – Univariate Analyses

ANOVA models testing for the effect of categorical habitat variables (depth stratum, major habitat type, minor habitat type, and number of habitat types) on aggregate fish community metrics (abundance, biomass, and diversity) were largely insignificant, with the exception of the effect of depth strata on species abundance (Table 3.3). The result of the depth strata ANOVA, however, is unreliable, due to the disparity in beam trawl sample size between strata (two beam trawls in stratum 3, nine beam trawls in stratum 4, and 27 beam trawls in stratum 5).

Regressions between benthic habitat parameters and fish community metrics revealed a proportional relationship between depth and fish community abundance, such that fish abundance increased with deeper minimum, maximum, and mean water depth (Table 3.6, Figure 3.10). Beam trawl species diversity, on the other hand, was negatively related to water depth, with lower species diversity in deeper waters (Table 3.6, Figure 3.12). Fish community diversity also exhibited a significant proportional relationship with bottom water temperature, whereas fish community abundance and biomass exhibited inverse relationships with bottom water temperature (Table 3.6, Figures 3.10, 3.11 & 3.12). In addition, fish community abundance and biomass were significantly influenced by surface salinity, such that fish abundance and biomass were higher in more saline water (Table 3.6, Figures 3.10 & 3.11). Finally, fish community biomass exhibited a significant proportional relationship with minimum slope and an inverse relationship with mean backscatter (Table 3.6, Figure 3.11). When interpreting these results, it is important to consider that the aggregate abundance and biomass of beam trawls were often driven by the prevalence of sand dollars and sea stars, and thus, univariate relationships with habitat parameters likely reflect the associations of these species. Also, conversely to otter trawl catch species diversity, beam trawl species diversity reflects the number and variety of small, epifaunal species in addition to the number and variety of macrofaunal fish and invertebrate species. This detail is important to consider when interpreting and comparing the results of beam trawl and otter trawl species diversity regressions.

Multiple regression analysis suggests that a collection of five habitat variables (standard deviation of depth, bottom temperature, surface salinity, major grain size, minor grain size) best explains beam trawl abundance in Rhode Island and Block Island Sounds (Table 3.5). Beam trawl biomass, on the other hand, was best explained by a suite of three habitat variables: mean depth, surface temperature, and minor grain size (Table 3.5). Finally, considered together, bottom temperature and minor grain size best explain beam trawl species diversity (Table 3.5). Notably, temperature and grain size were significant explanatory variables in all of these models.

Beam Trawls – Multivariate Analysis

Cluster analysis of beam trawl catch data identified four major species assemblage groups in Rhode Island and Block Island Sounds. These species assemblage groups are characterized by their dominant species as follows: 1) “Skates (*Leucoraja* spp.) and *Cancer* spp. Crabs”, 2) “Sea Scallop (*Placopecten magellanicus*) and Sand Dollar (*Echinarachnius parma*)”, 3) “Silver Hake (*Merluccius bilinearis*) and Lobster (*Homarus americanus*)”, and 4) “Sea Scallop (*Placopecten magellanicus*) and Sea Star (*Asterias* spp.)”. One site was determined to be unique, due to its high abundance of yellowtail flounder, *Pleuronectes ferruginea* ("Yellowtail flounder and Sea Scallop" group).

ANOSIM analyses and MDS visualization indicate that major habitat type and number of habitat types significantly influence the species assemblage of demersal fish and invertebrate communities within Rhode Island and Block Island Sounds, as sampled by beam trawls (Major Habitat Type: R=0.229, p=0.023; Number of Habitat Types: R=0.223, p=0.015, Figures 3.13 and 3.14). In terms of major habitat type, the fish community composition at beam trawl sites characterized by mud habitat was significantly different than the fish community composition at beam trawl sites characterized by medium sand or coarse sand (Mud v. Medium Sand: R=0.308, p=0.026; Mud v. Coarse Sand: R=0.709, p=0.048). With respect to number of habitat types, the fish community composition at beam trawl sites spanning only two habitat types was significantly different than the fish community composition at beam trawl sites spanning three or more habitat types (2 Habitat Types v. 3 Habitat Types: R=0.261, p=0.002). Fish community composition, however, was not significantly influenced by depth strata or minor habitat type (Depth Strata: R=0.054, p=0.239; Minor Habitat Type: R=-0.125, p=0.111).

The BIOENV procedure identified five benthic habitat parameters as being most influential to the fish and invertebrate community composition, as sampled by beam trawls (rho=0.506, p=0.001). These parameters were mean depth, bottom temperature, minor grain size, surface salinity, and surface temperature. Considered individually, bottom temperature was the only habitat variable to exhibit a significant relationship with fish community composition (R=0.318, p=0.04).

The LINKTREE analysis divided the beam trawl sites into three groups based on thresholds of mean water depth and minor grain size: 1) Shallow, 2) Deep and Coarse Grained, 3) Deep and Fine Grained (Figure 3.15). The "Deep" habitat group was characterized by water depths greater than 39 meters. The "Shallow and Coarse" habitat group was characterized by water depths less than 35 meters and minor grain size between 3.9 and 5.8 (shell debris or pebble). The "Shallow and Fine" habitat group was characterized by water depths less than 38 meters and minor grain size between 8.45 and 9 (fine sand or mud).

These habitat groups exhibit similar patterns as the species assemblage groups defined by cluster analysis, but they do not fully explain the fish community structure observed via beam trawl sampling (Figure 3.15). Thus, there are likely additional habitat characteristics that were not incorporated in this analysis that influence the structure of beam trawl species assemblages. There are, however, significant differences in species assemblages between habitat groups (R=0.582, p=0.001). More specifically, the "Deep" habitat group was primarily occupied by fish communities with high abundances of sea scallops, sand dollars, and sea stars, where as the "Shallow and Coarse" habitat group was dominated by fish communities with high abundances of skates and cancer crabs, and the "Shallow and Fine" habitat group was characterized by fish communities with higher abundances of silver hake and American lobster. There are also significant differences in the habitat characteristics that are associated with each beam trawl species assemblage group, although between-assemblage habitat differences are not as consistent or pronounced as with otter trawl assemblages (ANOSIM: R=0.275, p=0.021).

In a spatial context, the “Deep” habitat group is primarily located along the southeastern flank of Cox’s Ledge, where the “Sea Scallop and Sand Dollar” and “Sea Scallop and Sea Star” species assemblages dominate (Figure 3.16). The “Shallow and Fine” habitat group, on the other hand, is located in the inshore extent of Rhode Island Sound, where it exhibits significant overlap with the “Silver Hake and Lobster” species assemblage group. Finally, the “Shallow and Coarse” habitat group is located around the southern end of Block Island, an area primarily occupied by the “Skates and Cancer Crabs” species assemblage.

Discussion:

The fisheries ecosystem of Rhode Island and Block Island Sounds is composed of many environmental factors, including water depth, water temperature, and benthic habitat heterogeneity. Understanding the relationship between these factors and the fish and invertebrate community is central to the protection of important habitats and the maintenance of ecosystem stability in the face of new ocean uses. Thus, the work presented here represents fundamental progress towards ecologically sound spatial management decisions and the general advancement of ecosystem based fisheries management in Rhode Island’s nearshore waters (RISAMP 2010, Fogarty 2013). Furthermore, the quantitative fish-habitat relationships established by this work could be used to predict local-scale changes in fish community structure that may result from the increasing water temperatures associated with global climate change, a key to developing adaptive fishery management plans (Attrill & Power 2002).

From a univariate perspective, water depth is a key driver of fish community diversity in Rhode Island and Block Island Sounds, with deeper habitats supporting the most abundant and diverse fish communities sampled by otter trawls and the most abundant and least diverse epifaunal communities sampled by beam trawls. While the preference of fish and invertebrate communities for specific depth ranges has been observed in a variety of ecosystems, such strong, system-wide patterns were previously undocumented in Rhode Island's nearshore waters (Persohn et al. 2009, Sonntag et al. 2009). In terms of otter trawl species diversity, depth related trends may be driven by the tendency of inshore waters to intensify the interactions between bentho-pelagic species, as the water column is truncated and benthic-pelagic coupling is enhanced. Thus, inshore fish communities are more likely to be dominated by a few abundant species (scup, skates, silver hake), therefore reducing the diversity of the fish community (Scharf et al. 2000). In terms of beam trawl species diversity, reduced species diversity in deeper waters may reflect the dominance of abundant epifaunal species, such as sea scallops, sand dollars, and sea stars, as is evident in the species assemblage analyses presented here. Overall, the results of this work suggest that when aiming to protect aggregate fish community diversity in Rhode Island and Block Island Sounds, focus should be on deeper habitats, particularly those surrounding abrupt bathymetric features, such as Cox's Ledge and Southwest Ledge, whereas when aiming to protect epifaunal diversity, priority should be given to the shallow waters surrounding Block Island.

A general paradigm about marine benthic communities is that as bottom roughness increases from smooth mud and sand to cobble and boulder ecological complexity and species diversity increase (Salomon et al. 2010). The presumed relationship is that the more heterogeneous the habitat, the more species it can support because more niches are available (Guegan & Oberdorff 2000, Levin et al. 2001, Eriksson et al. 2006). This pattern appears to hold true in Rhode Island's nearshore waters, such that areas with higher backscatter intensities and, thus, coarser sediments, support more diverse fish and invertebrate communities (Collier & Brown 2005). From a multivariate perspective, three measures of habitat roughness were found to be influential in structuring fish and invertebrate species assemblages in Rhode Island and Block Island Sounds, with the standard deviation of surface roughness and mean slope important in shaping otter trawl assemblages and minor grain size important in shaping beam trawl assemblages. Such measures of seafloor roughness, however, did not wholly explain the patterns observed in fish and invertebrate assemblages, and thus, must be considered in combination with other habitat parameters, such as oceanographic conditions and water depth.

By nature, the benthos is an intricate system, characterized by a collection of distinct environmental parameters. Relationships between such habitat parameters and fish communities has been well documented in coral reefs and seagrass beds, but the work presented here is novel to the temperate, nearshore environment of Rhode Island and Block Island Sounds (Ault & Johnson 1998, Christensen et al. 2003, Eriksson et al. 2006). Thus, the suite of habitat parameters found to collectively drive the composition of demersal fish and invertebrate communities in Rhode Island and Block Island Sounds (mean depth, bottom temperature, surface salinity, standard deviation of surface roughness, mean slope, minor grain size, and surface water temperature) provide unique insight into fish-habitat relationships on the Northwest Atlantic continental shelf. Three of these habitat parameters (mean depth, bottom water temperature, and surface salinity) were identified as influential for both otter trawl and beam trawl species assemblages, suggesting that a wide variety of fish and invertebrate communities are driven, at least in part, by these features. Furthermore, out of the seven habitat parameters highlighted in our analyses, three are indicators of seafloor structure (standard deviation of surface roughness, mean slope, and minor grain size), supporting the hypothesis that the physical features of the benthos play an important role in shaping the demersal fish and invertebrate community in temperate marine ecosystems. Oceanographic conditions also appear to play a key role in structuring the fish community in Rhode Island and Block Island Sounds, as water temperature, salinity, and depth were consistently identified as highly influential parameters in BIOENV analyses. Thus, the results of this work suggest that the relationship between the demersal fish and invertebrate community and habitat is not defined by one distinctive parameter, but rather a combination of seafloor and oceanographic features.

Consistencies between the habitat groups and demersal fish assemblages identified in this study further suggest that the fish community in Rhode Island and Block Island Sound is shaped by the physical environment. Since most habitat features are relatively static and most fish and invertebrates are mobile, the fish community is likely shaped by the environment and not vice versa. One ecological mechanism that may account for this fish-habitat association is the interaction of predators and prey (Stein 1977). If trophic interactions within the fish community are strong, then prey likely act as the link to the environment as they seek out the most hospitable environment, and the predators follow the prey (Powers et al. 1985). If most predators in an ecosystem are generalist feeders, however, then the fish community is likely directly linked to the physical features of the habitat, as predators consume whichever prey are available.

It is important to interpret the results of any multivariate fish-habitat analysis with care, as the suite of habitat parameters included in the analysis likely do not include all features that influence fish community structure (Mellin et al. 2009). Environmental parameters not measured in this study that may be important to consider include: bottom current velocity and direction, turbidity, and primary productivity. Furthermore, the acoustic surveys and fish trawls employed in this study mainly surveyed sandy bottom areas in order to avoid gear damage. To develop a full understanding of the functional relationship between benthic habitat and the demersal fish community, a greater variety of bottom types should be sampled, as differences in fish assemblage are most pronounced between areas with vastly different bottom types (i.e. mud v. boulder) (Kendall et al. 2004, Gomelyuk 2009). Thus, while this work provides a strong foundation of knowledge, further research is needed to develop a mechanistic understanding of the functional relationship between the fish and invertebrate community and their habitat in Rhode Island's nearshore waters.

The spatial scale of this research is relevant to local marine spatial planning efforts and will provide guidance for siting future offshore development projects in habitats that will minimize the effect on essential fish habitats and their associated macrofauna (RI SAMP 2010, Collie et al. 2013). While all habitat types play a role in structuring and supporting the fish and invertebrate community in Rhode Island and Block Island Sound, conservation priority should be given to habitats that support ecologically vulnerable or economically valuable species, such as lobster, sea scallops, and yellowtail flounder. Thus, this work suggests that the areas on and surrounding Cox's Ledge should be protected from high-disturbance offshore development projects, as these areas play a critical role in the life histories of a number of conservation-targeted and fishery-supporting species. With a small-scale offshore wind energy facility planned for implementation in Block Island Sound in 2016, this work is particularly timely as it provides a baseline for measuring the effects of such projects on benthic habitat and fish community structure, an essential step if larger offshore wind energy ventures are to proceed sustainably across the US northeast continental shelf.

Literature Cited:

Anderson, T.J., Syms, C., Roberts, D.A., and Howard, D.F. 2009. Multi-scale fish–habitat associations and the use of habitat surrogates to predict the organisation and abundance of deep-water fish assemblages. Journal of Experimental Marine Biology and Ecology 379 (1-2): 34–42.

Ault, T.R. and Johnson, C.R. 1998. Spatially and temporally predictable fish communities on coral reefs. Ecological Monographs 68: 25-50.

Auster, P.J., Malatesta, R.J., and Donaldson, C.L.S. 1997. Distributional responses to small-scale habitat variability by early juvenile silver hake, Merluccius bilinearis. Environmental Biology of Fishes 50: 195–200.

Beck, M.W., Ferdaña, Z., Kachmar, J., Morrison, K.K., Taylor P. 2009. Best Practices for Marine Spatial Planning. The Nature Conservancy, Arlington, VA.

Bigelow, H.B and Schroeder, W.C. 2002. Fishes of the Gulf of Maine.

Brown, C.J., and Blondel, P. 2009. Developments in the application of multibeam sonar backscatter for seafloor habitat mapping. Applied Acoustics 70 (10): 1242-1247.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach, Second Ed. Springer-Verlag, New York. New York.

Carpenter, S.R., Kitchell, J.F. and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. Bioscience 35: 634-639.

Christensen, JD, Jeffrey, C.F.G. and Caldow, C. 2003. Cross-shelf habitat utilization patterns of reef fishes in south western Puerto Rico. Gulf and Caribbean Research 14: 9-27.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd., Plymouth, UK, 190 pp.

Clarke K.R., and Green R.H. 1988. Statistical design and analysis for a “biological effects” study. Marine Ecology Progress Series 46: 213-226.

Clarke, K.R., and Warwick, R.M. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth, 172pp.

Cogan, C.B., Todd, B.J., Lawton, P., and Noji, T.T. 2009. The role of marine habitat mapping in ecosystem-based management. ICES Journal of Marine Science 66: 2033-2042.

Collie, J.S., Beck, M.W., Craig, B., Essington, T.E., Fluharty, D., Rice, J., and Sanchirico, J.N. 2013. Marine spatial planning in practice. Estuarine, Coastal and Shelf Science 117: 1-11.

Collier, J.S., and Brown, C.J. 2005. Correlation of sidescan backscatter with grain size distribution of surficial seabed sediments. Marine Geology 214 (4): 431-449.

Douvere, F. 2008. The importance of marine spatial planning in advancing ecosystem-based sea use management. Marine Policy 32: 762-771.

Driscoll, N.W. 1992. Side-scan sonar investigation of shallow-water depositional processes in and around Block Island Sound: before and after the Nor'easter of 1992. Storming Media Pentagon Reports, retrieved online from http://www.stormingmedia.us/48/4888/A488813.html.

Ehler, C., and Douvere, F. 2009. Marine Spatial Planning: A Step-by-step Approach toward Ecosytem-based Management. UNESCO Intergovernmental Oceanographic Commission, Paris, France.

Elefteriou, A., and McIntyre, A. 2005. Methods for the Study of Marine Benthos. Wily-Blackwell.

Eriksson, B.K., Ruback, A. and Hillebrand, H. 2006. Biotic habitat complexity controls species diversity and nutrient effects on net biomass production. Ecology 87 (1):246-254.

Foley, M.M., Halpern, B., Micheli, F., Armsby, M., Caldwell, M., Crain, C., Prahler, E., Sivas, D., Rohr, N., Beck, M.W., Carr, M., Crowder, L., Duffy, J.E., Hacker, S., McLeod, K., Peterson, C., Regan, H., Ruckelshaus, M., Sandifer, P., and Steneck, R. 2010. Guiding ecological principles for marine spatial planning. Marine Policy 34: 955-966.

Freitas, R., Ricardo, F., Pereira, F., Sampaio, L., Carvalho, S., Gaspar, M., Quintino, V., and Rodrigues, A.M. 2011. Benthic habitat mapping: concerns using a combined approach (acoustic, sediment, and biological data). Estuarine, Coastal and Shelf Science 92 (4): 598-606.

Friedlander, A.M. and Parrish, J.D. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224 (1): 1-30.

Garrison, L.P. and Link, J.S. 2000. Dietary guild structure of the fish community in the northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202: 231-240.

Gerry, S.P. 2008. Feeding mechanics of a trophic generalist and a specialist shark species: A comparison of diet, behavior and function. Dissertation Abstracts International 69 (5): 184.

Gleason, M., McCreary, S., Miller-Henson, M., Ugoretz, J., Fox, E., Merrifiend, M., McClintock, W., Serpa, P., and Hoffman, K. 2010. Science-based and stakeholder-driven protected area network planning: as successful case study from north central California. Ocean and Coastal Management 53: 52-68.

Gratewick, B. and Speight, M.R. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66: 650-667.

Gomelyuk, V.E. 2009. Fish assemblages composition and structure in three shallow habitats in north Australian tropical bay, Garig Ganuk Barlu National Park, Northern Territory, Australia. Journal of Marine Biological Association of the United Kingdom 89 (3): 449-460.

Guegan, J.F., Lek, S. and Oberdorff, T. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. Nature. 391 (6665): 382-384.

Hill, M.O. 1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54 (2): 327-432.

Hobson, R.D. 1972. Chapter 8 – Surface roughness in topography: quantitative approach. *in* R.J. Chorley, editor. Spatial analysis in geomorphology. Harper & Row, New York, New York. USA.

Hunter, M.D. and Price, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology. 73 (3): 724-732.

International Council for the Exploration of the Sea (ICES). 2007. Acoustic seabed classification of marine physical and biological landscapes. Cooperative Research Report No. 286, 183 pp.

Johnson, A., Jenkins, S., Hiddink, J.G., and Hinz, H. 2012. Linking temperate demersal fish species to habitat: scales, patterns, and future directions. Fish and Fisheries 14 (3): 256-280.

Kendall, M.S., Christensen, J.D., Caldow, C., Coyne, M., Jeffrey, C., Monaco, M.E., Morrison, W. and Hillis-Starr, Z. 2004. The influence of bottom type and shelf position on biodiversity of tropical fish inside a recently enlarged marine reserve. Aquatic Conservation: Marine and Freshwater Ecosystems 14 (2): 113-132.

LaFrance, M., King, J.W., Oakley, B.A., and Pratt, S. 2014. A comparison of top-down and bottom-up approaches to benthic habitat mapping to inform offshore wind energy development. Continental Shelf Research 83: 24-44.

LaFrance, M., Shumchenia, E., King, J., Pockalny, R., Oakley, B., Pratt, S., Boothroyd, J., 2010. Benthic habitat distribution and subsurface geology at selected sites from the Rhode Island Ocean Special Area Management Study Area. Technical Report #4 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R. and Pawson, D. 2001. Environmental influences on regional deep-sea species diversity. Ecology, Evolution and Systematics 32: 51-93.

Luckhurst B.E. & Luckhurst K. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Marine Biology 49: 317-323.

Malek, A.J., Collie, J.S., and Gartland, J. 2014. Fine-Scale Spatial Patterns in the Demersal Fish and Invertebrate Community in a Northwest Atlantic Ecosystem. Estuarine, Coastal and Shelf Science 147: 1-10.

Malek, A.J., LaFrance, M., Collie, J., and King, J. 2010 Fisheries Ecology in Rhode Island and Block Island Sounds for the Rhode Island Ocean Special Areas Management

Plan. Technical Report #19 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Mayer, L.A. 2006. Frontiers in seafloor mapping and visualization. Marine Geophysical Research 27: 7-17.

McLeod, K.L., Lubchenko, J., Palumbi, S.R. and Rosenberg, A.A. 2005. Scientific consensus statement on marine ecosystem-based management. Communication Partnership for Science and the Sea. Available: http://www.compassonline.org/ .

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J. and Lean, D.R.S. 1989. Bottom-Up and Top-Down Impacts on Freshwater Pelagic Community Structure. Ecological Monographs 59: 289–309.

Methratta, E., and Link, J. 2006. Seasonal variation in groundfish habitat associations in the Gulf of Maine-Georges Bank region. Marine Ecology Progress Series 326: 245–256.

Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United Sates continental shelf. Marine Ecology Progress Series 393: 111-129.

Pauly, D., and Chuenpagdee, R. 2007. Fisheries and coastal ecosystems: the need for integrated management. Pages 171-185 *in* P. Nemetz, editor. Sustainable resource management. Edward Elgar Publishing, Surrey, UK.

Persohn, C., Lorance, P. and Trenkel, V.M. 2009. Habitat preferences of selected demersal fish species in the Bay of Biscay and Celtic Sea, North-East Atlantic. Fisheries Oceanography 18 (4): 268-285.

Power, M.E., Matthews, W.J. and Stewart, A.J. 1985. Grazing Minnows, Piscivorous Bass, and Stream Algae: Dynamics of a Strong Interaction. Ecology 66: 1448–1456.

Rhode Island Special Area Management Plan (RI SAMP). 2010. Coastal Resources Management Council, Wakefield, Rhode Island.

Salomon, A.K., Gaichas, S.K., Shears, N.T., Smith, J.E., Madin, E.M.P. and Gaines, S.D. 2010. Key features and context-dependence of fishery-induced trophic cascades. Conservation Biology 24 (2): 382-394.

Scharff, F.S., Juanes, F. and Rountree, R.A. 2000. Predator size-prey size relationships of marine fish predators: Interspecific variation and effects ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series 208: 229-248.

Sonntag, N., Garthe, S. and Adler, S. 2009. A freshwater species wintering in a brackish environment: Habitat selection and diet of Slavonian grebes in the southern Baltic Sea. Estuarine, Coastal and Shelf Science 84 (2): 186-194.

Stein, R.A.1977. Selective predation, optimal foraging and the predator-prey interaction between fish and crayfish. Ecology 58: 1237-1253.

Todd, B.J., and Greene, H.G. 2007. Mapping the seafloor for habitat characterization. Geological Association of Canada, Special Paper 47, 519 pp.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397

Zamon, J.E. 2003. Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. Marine Ecology Progress Series 261: 243-255.

Table 3.1. Sources, resolutions, and coverage of all habitat parameters for otter trawls and beam trawls. Habitat variables marked with an asterisk (*) were retained in the otter trawl BIOENV analysis. Habitat variables marked with a cross (†) were retained in the beam trawl BIOENV analysis. Habitat variables marked with a superscript c (^{c}) are categorical and were used in ANOVA and ANOSIM analyses.

Source	Resolution	Habitat Variable	Data Coverage (%)	
			Otter Trawls	Beam Trawls
Bathymetry	90m	Minimum depth	100	100
		Maximum depth	100	100
		Mean depth*†	100	100
		Standard deviation of depth†	100	100
		Depth Strata^c	100	100
Slope	90m	Minimum slope	100	100
		Maximum slope	100	100
		Mean slope*	100	100
		Standard deviation of slope	100	100
Side-scan	2m	Minimum backscatter*	71	45
		Maximum backscatter*	71	45
		Mean backscatter*†	71	45
		Standard deviation of backscatter*	71	45
Roughness	100m	Minimum roughness	100	100
		Maximum roughness	100	100
		Mean roughness*†	100	100
		Standard deviation of roughness*†	100	100
Oceanographic Sampling	N/A	Surface temperature (°C)*†	75	97
		Surface salinity (ppt)*†	82	97
		Surface Dissolved Oxygen (mg/L)*†	82	97
		Bottom Temperature (°C)*†	75	97
		Bottom Salinity (ppt)*	82	0
		Bottom Dissolved Oxygen (mg/L)*	82	0
Video Surveys	1m	Major Grain Size *†	100	58
		Minor Grain Size *†	100	58
		Major Habtiat Type^c	100	58
		Minor Habitat Type^c	100	58
		Number of Habitat Types^c	100	58

Table 3.2. Categorical and numerical habitat types and corresponding grain sizes. Photos of each habitat type are provided in Figure 3.3.

Categorical Habitat Type	Numerical Habitat Type	Grain Size (mm)
Rock ridge	1	256+
Boulder	2	128-257
Cobble	3	64-127
Pebble	4	2-63
Shell debris	5	N/A
Coarse sand	6	0.5-2
Medium sand	7	0.25-0.5
Fine sand	8	0.062-0.24
Mud	9	0.001-0.061

Table 3.3. P-values from Analysis of Variance (ANOVA) models testing for the effects of categorical habitat variables (depth strata, major habitat type, minor habitat type, and number of habitat types) on otter trawl and beam trawl fish community abundance, biomass, and species diversity. Bold text signifies a significant result (p<0.05).

	OTTER TRAWLS			**BEAM TRAWLS**		
	Abundance	*Biomass*	*Diversity*	*Abundance*	*Biomass*	*Diversity*
Depth Strata	0.947	0.167	**0.007**	**0.011**	0.914	0.337
Major Habitat Type	0.607	0.226	0.420	0.256	0.385	0.089
Minor Habitat Type	0.756	0.362	0.200	0.247	0.395	0.386
Number of Habitat Types	0.357	0.355	0.698	0.488	0.940	0.359

Table 3.4. Adjusted R-squared and p values of linear regressions between continuous habitat variables and log transformed otter trawl fish community abundance (number per km^2), biomass (kg per km^2), and diversity (Shannon Weiner's H).

	Abundance		**Biomass**		**Diversity**	
	Adj R-squared	*p-value*	*Adj R-squared*	*p-value*	*Adj R-squared*	*p-value*
Minimum Depth	-0.0159	0.4911	0.0295	0.1665	**0.252**	**0.0015**
Maximum Depth	0.0033	0.2998	0.0831	0.0543	**0.3037**	**0.0004**
Mean Depth	-0.0105	0.4236	0.0669	0.0759	**0.2801**	**0.0008**
StDev Depth	-0.0042	0.3602	0.0144	0.2323	-0.0289	0.7879
Minimum Slope	-0.235	0.6258	-0.019	0.5395	-0.0166	0.5017
Maximum Slope	-0.0296	0.8246	0.0417	0.1285	-0.0198	0.5536
Mean Slope	-0.0287	0.7811	0.0299	0.1653	-0.0235	0.6252
StDev Slope	-0.0198	0.5537	0.0137	0.2359	-0.0184	0.5302
Minimum Roughness	-0.0052	0.3689	0.0752	0.0639	-0.0187	0.535
Maximum Roughness	0.0193	0.2083	0.0789	0.0593	0.0789	0.0593
Mean Roughness	0.0019	0.3103	0.0843	0.053	-0.0095	0.413
StDev Roughness	0.0744	0.0649	0.0339	0.1516	0.0549	0.0972
Minimum Backscatter	0.0721	0.07838	-0.0337	0.8798	**0.2704**	**0.0016**
Maximum Backscatter	-0.0041	0.3563	-0.0041	0.3563	0.0029	0.3058
Mean Backscatter	0.0478	0.1243	-0.0302	0.7293	**0.1769**	**0.0109**
StDev Backscatter	-0.0140	0.4507	-0.0289	0.6938	-0.0312	0.7632
Bottom Dissolved Oxygen	0.0937	0.04117	0.0254	0.1791	**0.3309**	**0.00018**
Bottom Salinity	**0.2050**	**0.00369**	-0.0245	0.667	**0.1209**	**0.0231**
Bottom Temperature	0.0137	0.241	**0.1006**	**0.04297**	**0.2832**	**0.001**
Surface Dissolved Oxygen	-0.0298	0.9018	-0.0117	0.4418	0.0332	0.1504
Surface Salinity	**0.2086**	**0.0034**	0.073	0.0638	0.0751	0.061
Surface Temperature	0.0171	0.2244	-0.0313	0.8105	0.0539	0.1068
Major Grain Size	0.0826	0.0363	-0.0226	0.7624	0.0219	0.1739
Minor Grain Size	0.0653	0.0563	-0.0047	0.3738	-0.02352	0.8111

Table 3.5. Summary statistics of stepwise multiple linear regression models that were used to assess the cumulative impact of 24 habitat parameters on otter trawl and beam trawl abundance, biomass, and species diversity. Optimal regression models were selected using Akaike's Information Criterion corrected for small sample bias (AIC_c).

Response Variable	Optimal Model	F(df)	p-value	R^2	Adjusted R^2	AICc
Otter Trawl						
Abundance	Mean Slope + Bottom Salinity + Bottom Temperature + Surface Salinity + Surface Temperature + Minor Grain Size	3.88 (6,18)	0.0116	0.5638	0.4185	79.28
Biomass	StDev Slope + Mean Depth + Mean Roughness + Mean Backscatter + StDev Backscatter + Bottom Dissolved Oxygen + Bottom Salinity + Surface Dissolved Oxygen + Surface Temperature + Major Grain Size + Minor Grain Size	6.13 (11,11)	0.0028	0.8596	0.7193	84.45
Species Diversity	Bottom Dissolved Oxygen + Bottom Salinity + Surface Dissolved Oxygen + Surface Salinity	8.54 (4,30)	0.0001	0.5325	0.4701	48.58
Beam Trawl						
Abundance	StDev Depth + Bottom Temperature + Surface Salinity + Major Grain Size + Minor Grain Size	4.95 (5,13)	0.0093	0.6558	0.5235	60.53
Biomass	Mean Depth + Surface Temperature + Minor Grain Size	5.34 (3,16)	0.0096	0.5005	0.4069	36.07
Species Diversity	Bottom Temperature + Minor Grain Size	4.10 (2,18)	0.0340	0.3132	0.2369	26.43

Table 3.6. Adjusted R-squared and p values of linear regressions between continuous habitat variables and log transformed beam trawl fish community abundance (number per km^2), biomass (kg per km^2), and diversity (Shannon Weiner's H).

	Abundance		Biomass		Diversity	
	Adj R-squared	*p-value*	*Adj R-squared*	*p-value*	*Adj R-squared*	*p-value*
Minimum Depth	**0.1745**	**0.0053**	0.0772	0.0505	**0.1367**	**0.0128**
Maximum Depth	**0.15**	**0.0094**	0.06425	0.068	**0.1086**	**0.0246**
Mean Depth	**0.1597**	**0.00749**	0.0757	0.05221	**0.1206**	**0.0186**
StDev Depth	-0.0141	0.4904	-0.0268	0.8567	-0.0125	0.4662
Minimum Slope	-0.05704	0.8673	**0.2266**	**0.0227**	-0.0201	0.4327
Maximum Slope	-0.0263	0.4731	-0.0521	0.7449	0.0693	0.1444
Mean Slope	-0.0123	0.3892	-0.0579	0.903	0.0776	0.1313
StDev Slope	0.0102	0.2915	-0.0269	0.4772	0.1114	0.0889
Minimum Roughness	-0.0069	0.3894	-0.0267	0.7677	0.0315	0.153
Maximum Roughness	-0.0247	0.6958	-0.0283	0.8478	-0.0283	0.8478
Mean Roughness	-0.0164	0.5135	-0.0244	0.6851	0.0164	0.217
StDev Roughness	-0.0298	0.8972	-0.0302	0.9562	-0.024	0.6563
Minimum Backscatter	-0.08531	0.8161	-0.0504	0.5284	-0.0765	0.7089
Maximum Backscatter	0.0293	0.2677	0.0293	0.2677	-0.0128	0.3768
Mean Backscatter	0.08593	0.1726	**0.34**	**0.0214**	-0.0098	0.3673
StDev Backscatter	-0.0563	0.5605	-0.0639	0.6076	-0.0652	0.6168
Bottom Temperature	**0.4147**	**0.00001**	**0.1878**	**0.0043**	**0.3413**	**0.00009**
Surface Dissolved Oxygen	0.009	0.2589	0.0087	0.2608	0.01901	0.2039
Surface Salinity	**0.1453**	**0.0125**	**0.1102**	**0.0271**	0.09895	0.03464
Surface Temperature	-0.0052	0.3716	0.0391	0.1288	0.0108	0.2479
Major Grain Size	-0.0197	0.4494	-0.0225	0.4717	-0.04812	0.8516
Minor Grain Size	0.01497	0.2643	0.0048	0.3065	-0.02258	0.4725

Figure 3.1. Map of study area and sampling locations. The background bathymetry is derived from the National Oceanic and Atmospheric Administration (NOAA) National Geophysical Data Center (NGDC) Coastal Relief Model for the Northeast Atlantic region. Black shading indicates areas surveyed with sidescan sonar. Yellow triangles indicate otter trawl stations and green squares indicate beam trawl stations.

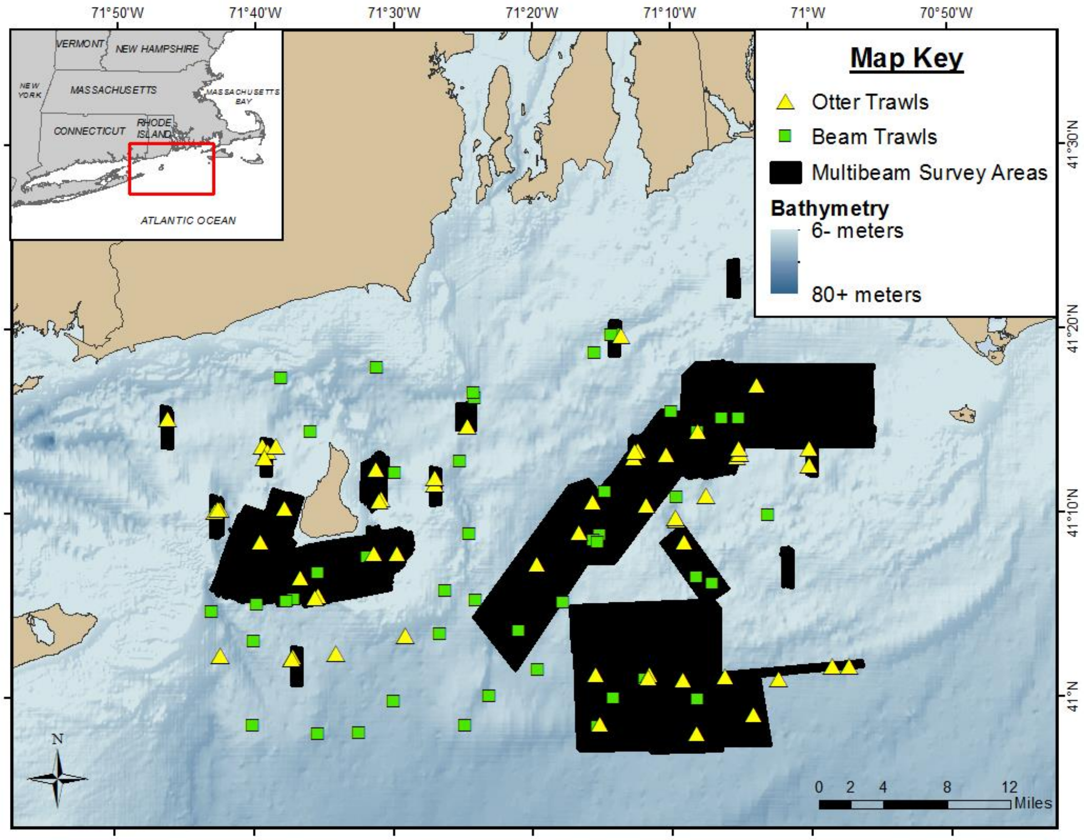


Figure 3.2. Map of benthic surface roughness in Rhode Island Sound and Block Island Sound at 100 meter resolution (RISAMP 2010). Otter trawl locations are indicated with yellow triangles and beam trawl locations are indicated by green squares.

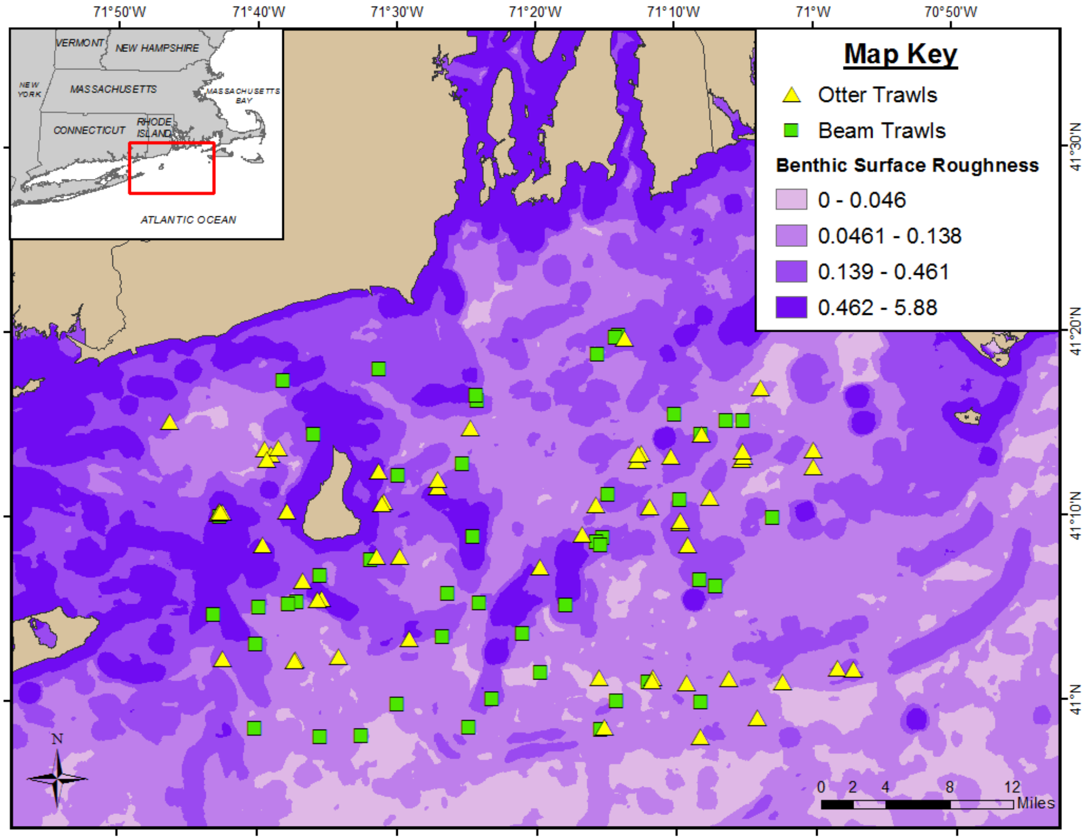


Figure 3.3. Photos of habitat types encountered during video surveys, in order of decreasing grain size. For numerical classification, see Table 3.2.

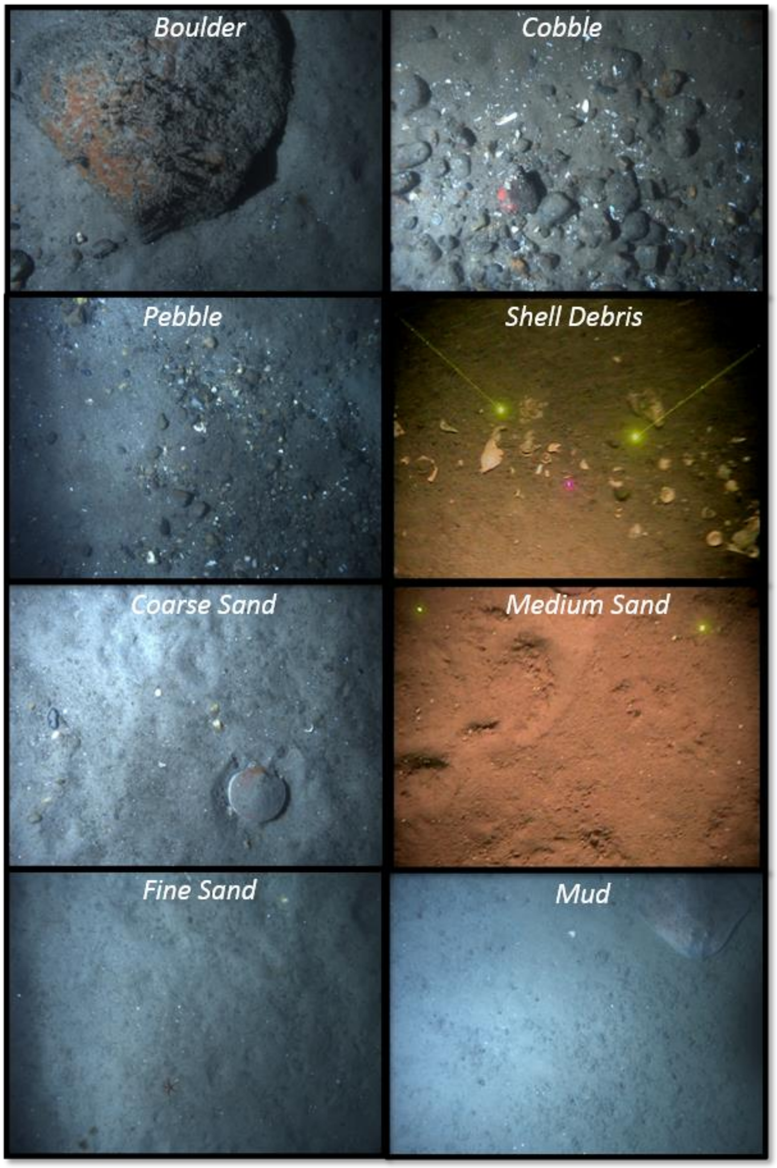


Figure 3.4. Regressions of continuous habitat variables against log transformed otter trawl abundance (number per km^2). Adjusted R-squared and p values are given in Table 3.4.

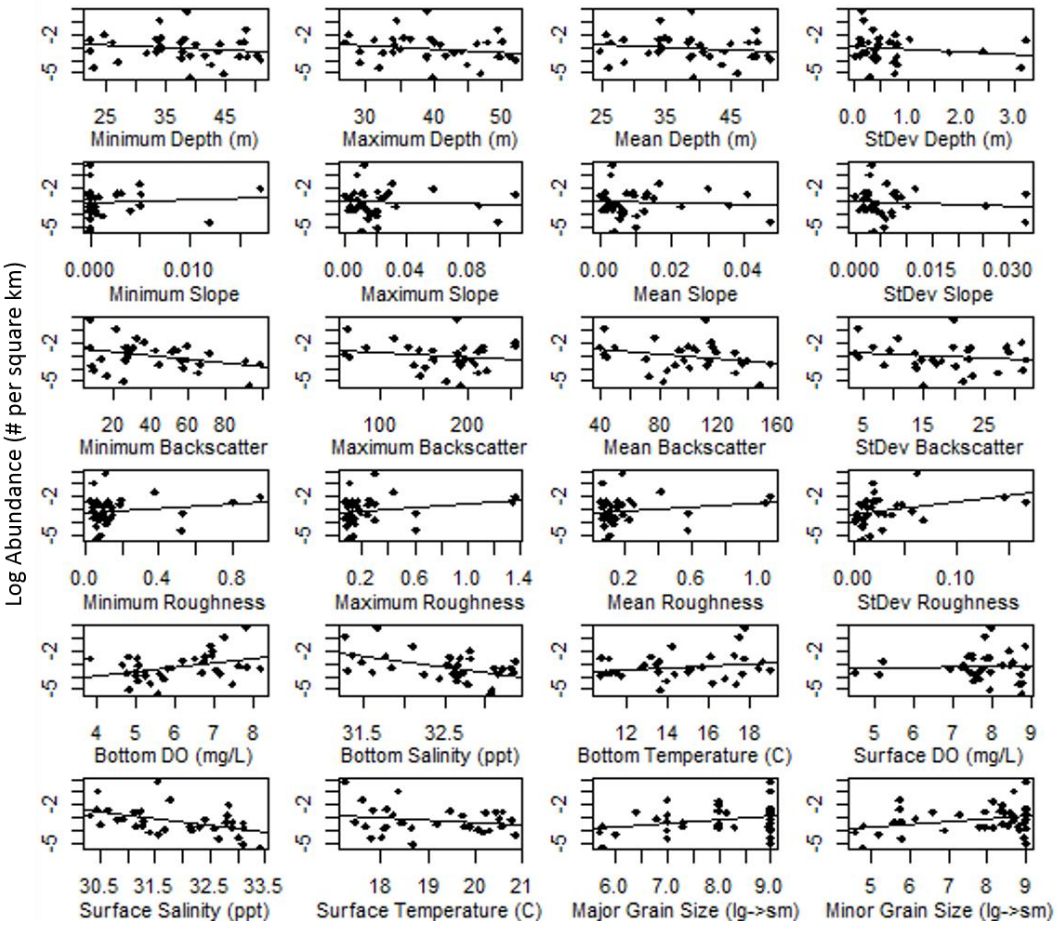


Figure 3.5. Regressions of continuous habitat variables against log transformed otter trawl biomass (kg per km^2). Adjusted R-squared and p values are given in Table 3.4.

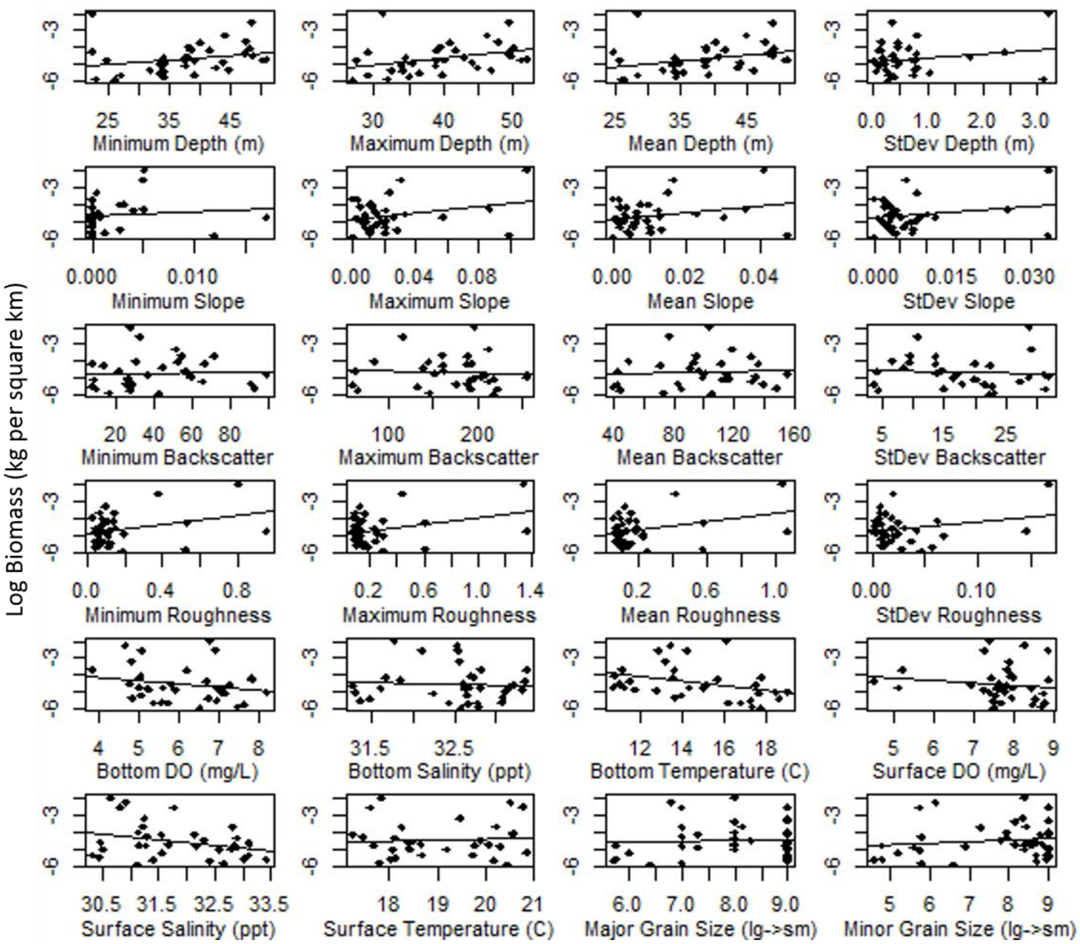


Figure 3.6. Regressions of continuous habitat variables against log transformed otter trawl species diversity (Shannon Weiner's H). Adjusted R-squared and p values are given in Table 3.4.

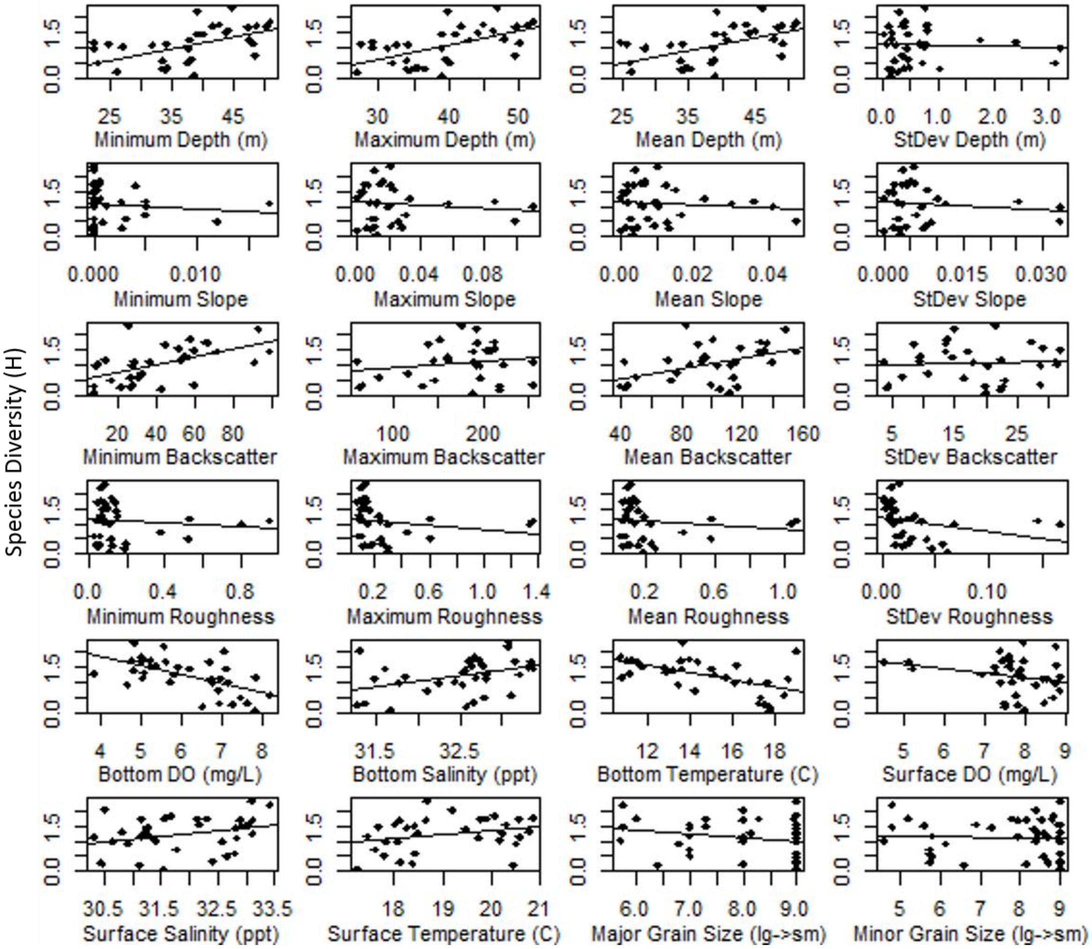


Figure 3.7. Multidimensional scaling plot depicting the pattern in otter trawl fish and invertebrate species composition in Rhode Island and Block Island Sounds, with similar species compositions close together. Each point represents the species composition of one otter trawl. Symbols represent depth strata (Stratum 3 = 60-90ft, Stratum 4 = 90-120ft, Stratum 5 >120ft). Analysis of similarity indicates that otter trawl fish community composition is significantly between depth strata (R=0.424, p=0.001).

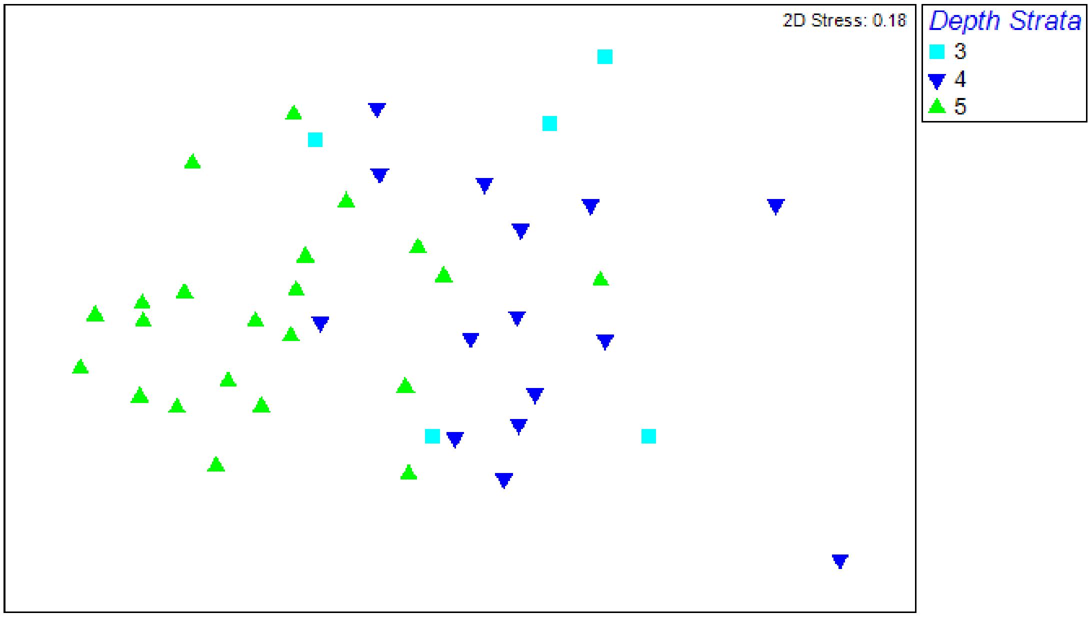


Figure 3.8. Multidimensional scaling plot depicting the pattern in habitat characteristics at otter trawl sites in Rhode Island and Block Island Sounds, with similar habitats appearing close together. Each point represents the habitat features at one otter trawl station. Symbols represent habitat group, as defined by BIOENV analysis. Dashed contours represent species assemblage groups as defined by CLUSTER analysis. Analysis of similarity indicates that there are significant differences in habitat characteristics between otter trawl species assemblage groups (R=0.475, p=0.001).

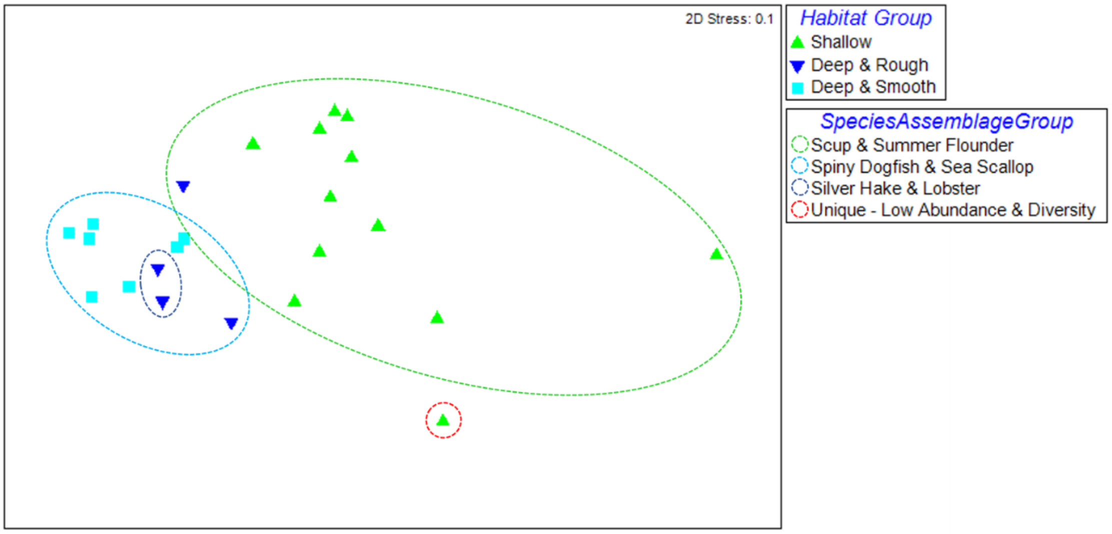


Figure 3.9. Map of depicting the spatial patterns in otter trawl habitat and species assemblage groups in Rhode Island and Block Island Sounds. Color coded symbols represent habitat group, as defined by BIOENV and LINKTREE analysis. Dashed contours represent species assemblage groups, as defined by CLUSTER analysis.

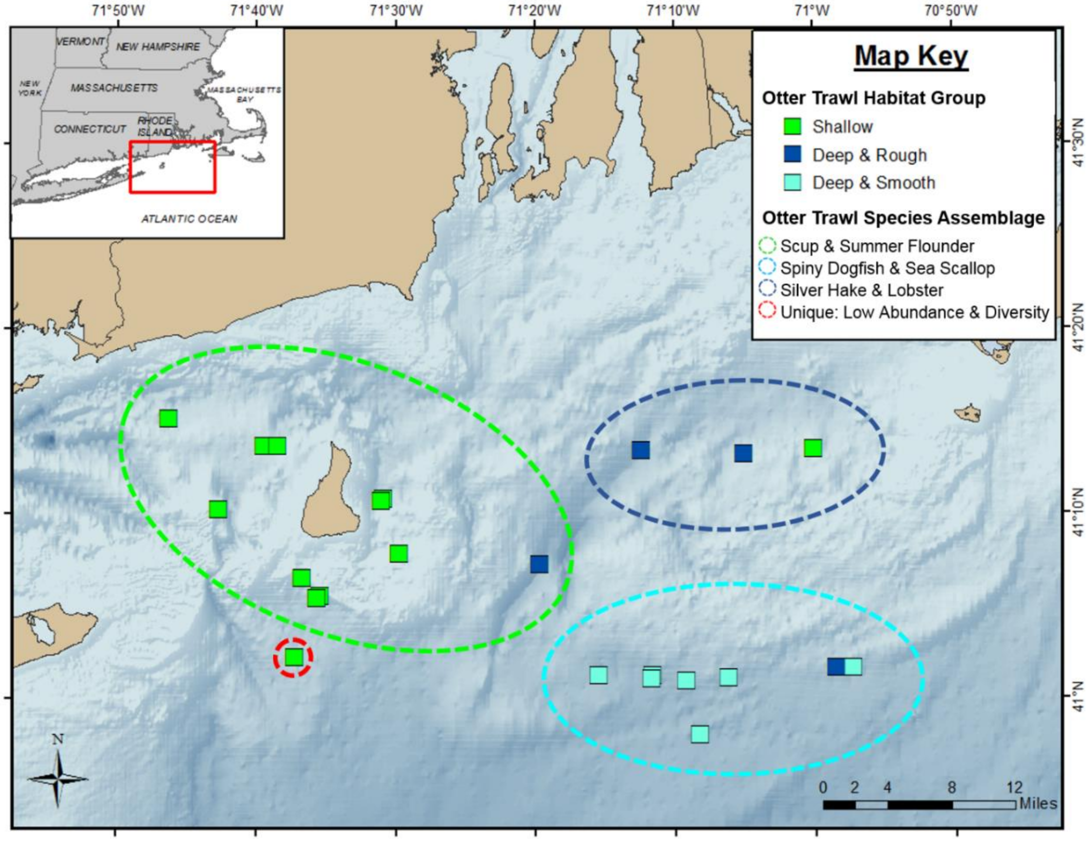


Figure 3.10. Regressions of continuous habitat variables against log transformed beam trawl abundance (number per km^2). Adjusted R-squared and p values are given in Table 3.6.

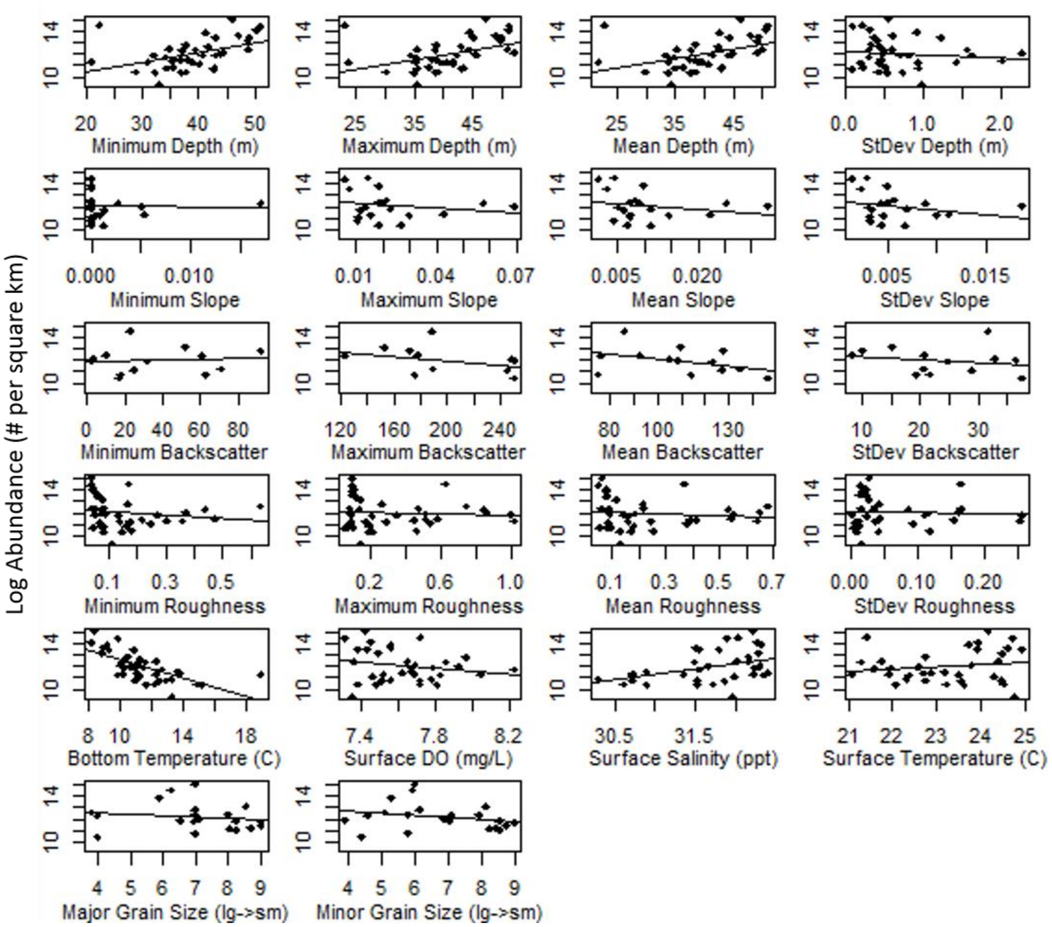


Figure 3.11. Regressions of continuous habitat variables against log transformed beam trawl biomass (kg per km^2). Adjusted R-squared and p values are given in Table 3.6.

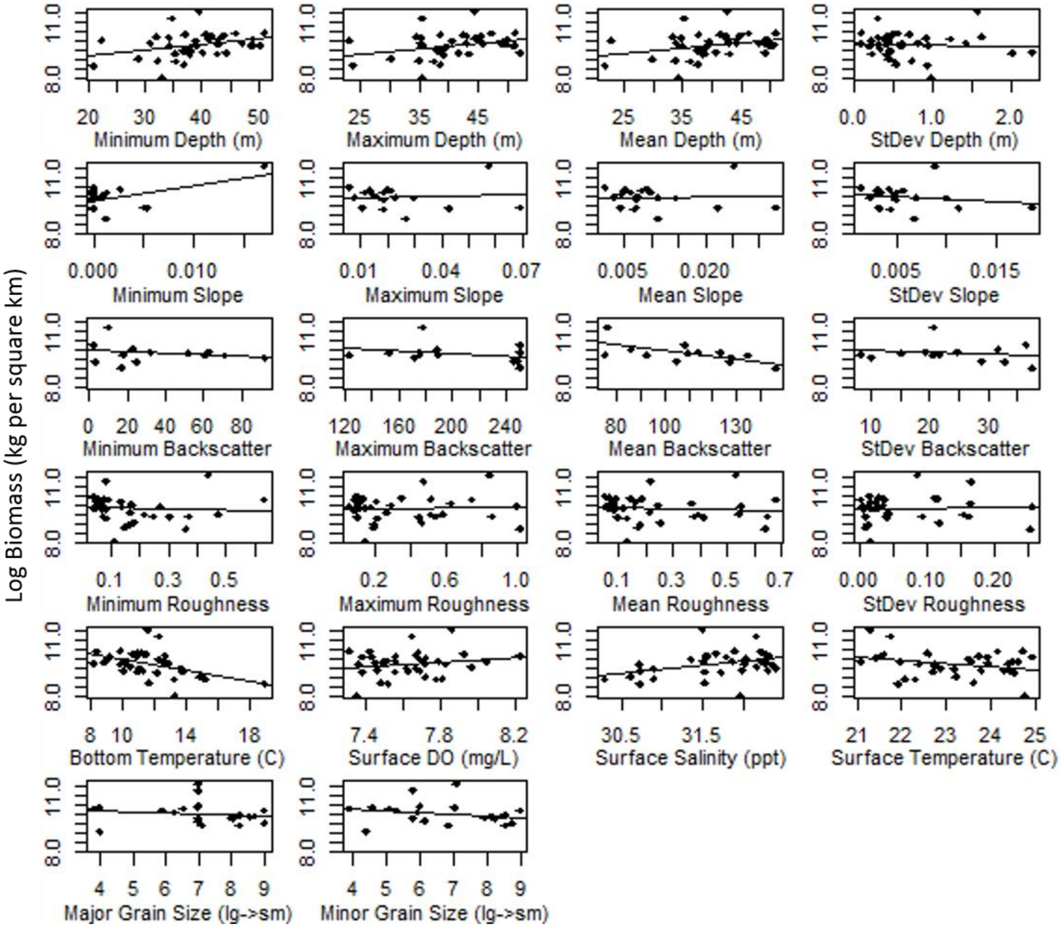


Figure 3.12. Regressions of continuous habitat variables against beam trawl species diversity (Shannon Weiner's H). Adjusted R-squared and p values are given in Table 3.6.

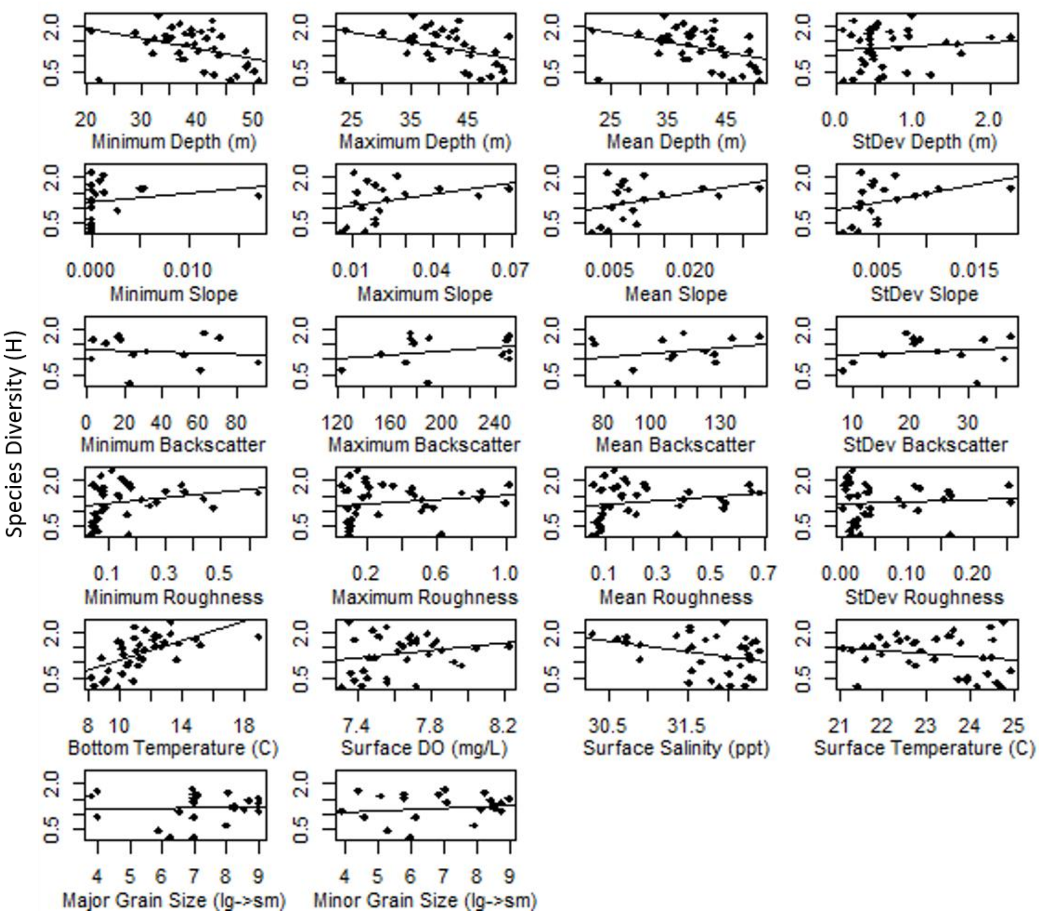


Figure 3.13. Multidimensional scaling plot depicting the pattern in beam trawl fish and invertebrate species composition in Rhode Island and Block Island Sounds, with similar species compositions close together. Each point represents the species composition of one beam trawl. Symbols represent major habitat type (pink circles = pebble, dark blue inverted triangles = coarse sand, green triangles = medium sand, red diamonds = fine sand, and light blue squares = mud). Analysis of similarity indicates that beam trawl fish community composition is significantly different between major habitat types (R=0.229, p=0.023).

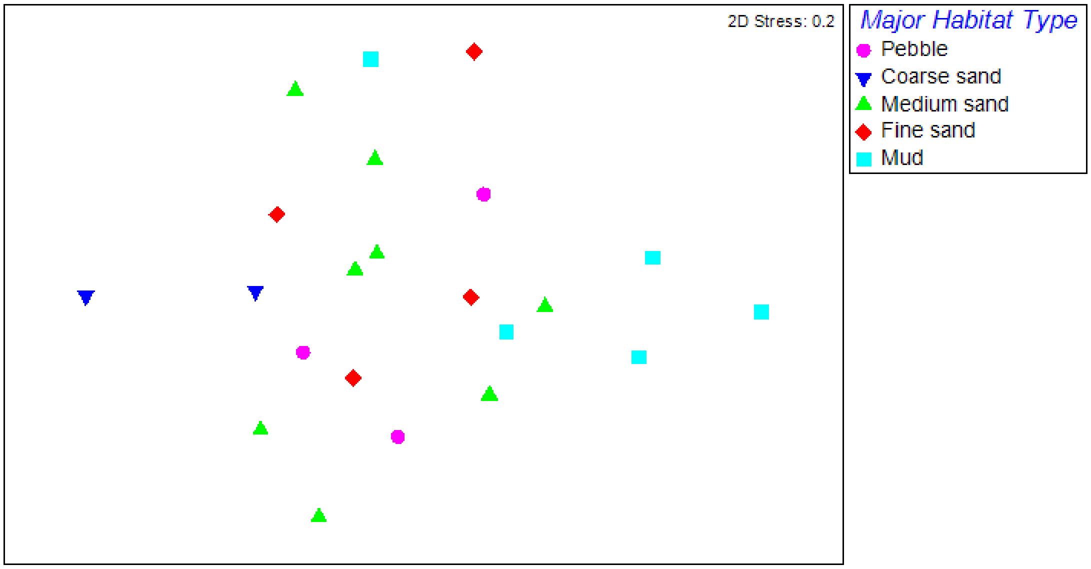


Figure 3.14. Multidimensional scaling plot depicting the pattern in beam trawl fish and invertebrate species composition in Rhode Island and Block Island Sounds, with similar species compositions close together. Each point represents the species composition of one beam trawl. Symbols represent number of habitat types (pink circles = 1, green triangles = 2, light blue squares = 3, dark blue inverted triangles = 4, red diamonds = 5). Analysis of similarity indicates that beam trawl fish community composition is significantly different at sites with different numbers of habitat types (R=0.223, p=0.015).

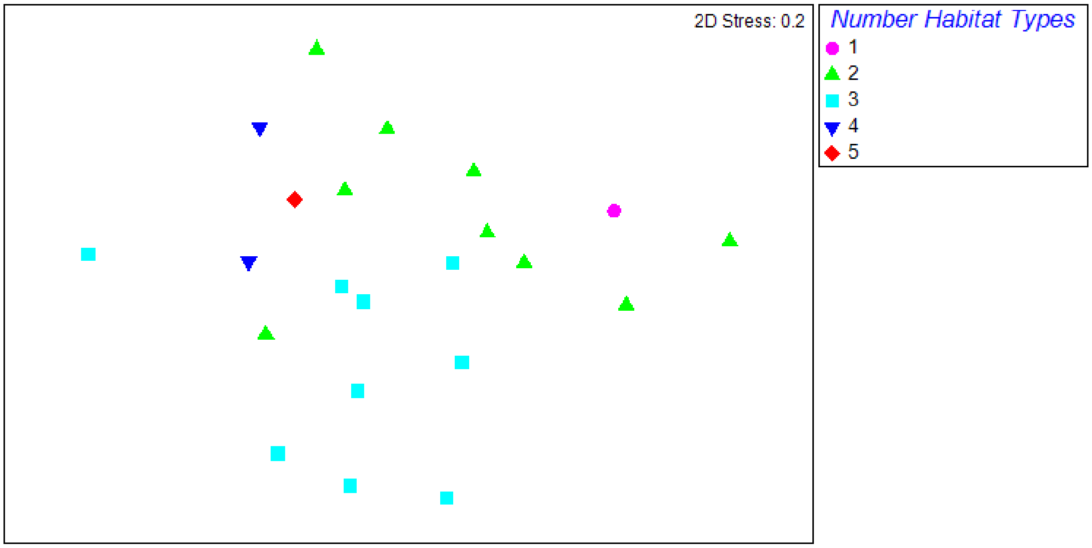


Figure 3.15. Multidimensional scaling plot depicting the pattern in habitat characteristics at beam trawl sites in Rhode Island and Block Island Sounds, with habitats appearing close together. Each point represents the habitat features at one otter trawl station. Symbols represent habitat group, as defined by BIOENV and LINKTREE analysis. Dashed contours represent species assemblage groups as defined by CLUSTER analysis. Analysis of similarity indicates that there are significant differences in habitat characteristics between beam trawl species assemblage groups (R=0.506, p=0.001).

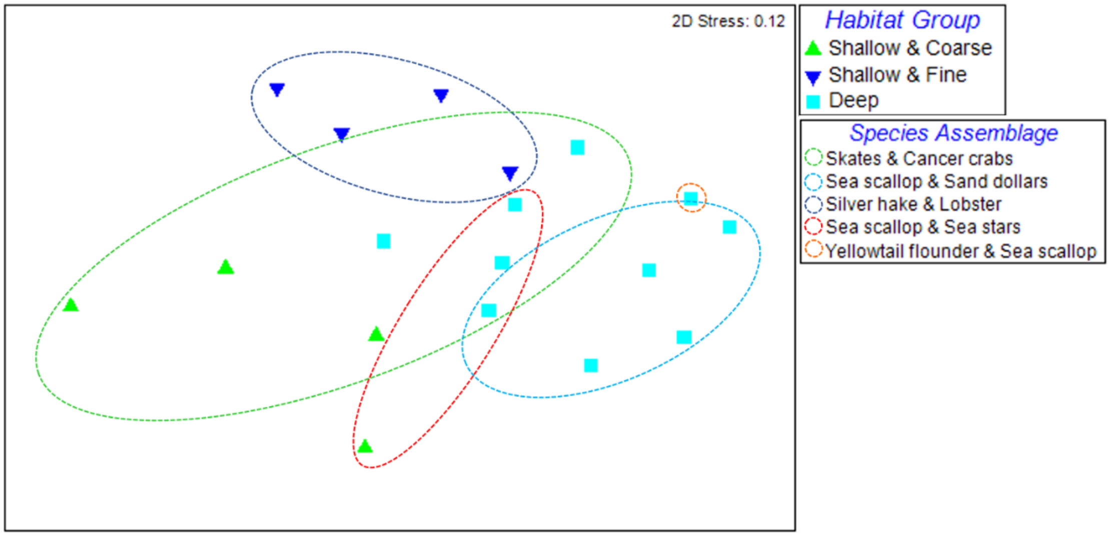
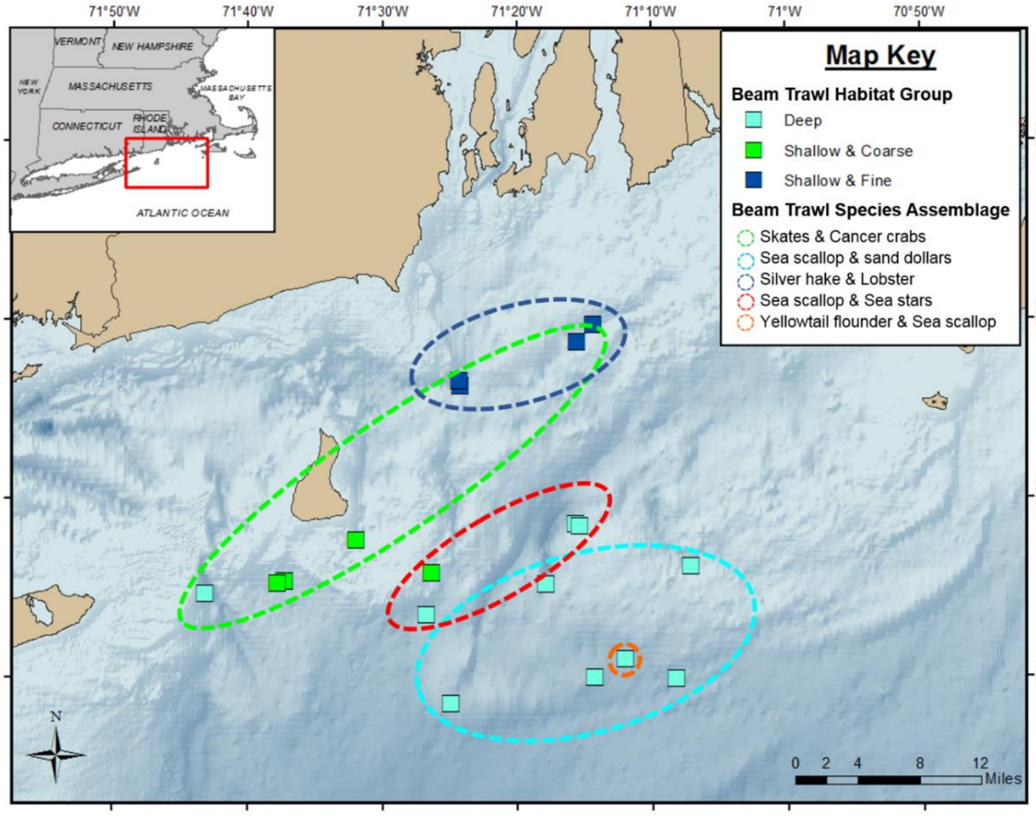


Figure 3.16. Map depicting the spatial patterns in beam trawl habitat and species assemblage groups in Rhode Island and Block Island Sounds. Color coded symbols represent habitat group, as defined by BIOENV and LINKTREE analysis. Dashed contours represent species assemblage groups, as defined by CLUSTER analysis.



CHAPTER 5

Speculative Discussion and Concluding Statements

By

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Discussion:

As is outlined in the manuscripts of this dissertation, there are many factors, both biotic and abiotic, that influence the structure and function of the demersal fish and invertebrate community in Rhode Island and Block Island Sounds. It is logistically infeasible, however, to assess each and every one of these factors in a short term research project such as this. Thus, I hope to use this concluding section to consider additional ecological and environmental factors that may influence the fisheries ecosystem dynamics in Rhode Island's nearshore waters, as well as to discuss the theoretical and practical implications of this work.

In terms of spatial structure of the fish and invertebrate community, there are many factors that could play a role that were not addressed explicitly by this work. For example, the schooling behavior of certain fish species may influence the structure and spatial distribution of the fish community. Previous work has shown that large aggregations of prey attract schools of predators, which, in turn, shape the fish community through top-down control (McQueen et al. 1989, Zamon 2003). Evidence of this phenomenon in Rhode Island and Block Island Sounds is apparent in the diet analysis and spatial distribution of the spiny dogfish, *Squalus acanthias,* and longfin inshore squid, *Doryteuthis pealei* (chapter 3, Gerry 2008). Spiny dogfish are opportunistic feeders and are known to exhibit schooling behavior, therefore, dominating the assemblage and size of the fish community when they are present (chapter 2). In Rhode Island and Block Island Sounds, spiny dogfish, along with summer flounder and winter skate are key predators of longfin squid, a common schooling species (chapter 3). This suggests that squid inhabit both the benthic and pelagic realm in Rhode Island and Block Island sounds and, therefore, attract bottom feeders (e.g. summer flounder, winter skates) as well as semi-pelagic feeders (e.g. spiny dogfish, striped bass). Thus, the predator-prey interactions and schooling behaviors of dogfish and squid appear to play an important role in the fisheries ecosystem dynamics of Rhode Island's nearshore waters. Techniques, such as mid-water trawls or acoustic surveys, would be best suited for testing this hypothesis (Wisner 1962, Misund & Aglen 1992, Simmonds & MacLennan 2008).

Scup, *Stenotomus chrysops*, are similar to dogfish in their schooling behaviors (Bigelow & Schroeder 2002). Scup, however, are smaller and more benthivorous in their feeding regime and, therefore, tend to school in areas with aggregations of small benthic prey, such as amphipod tube mats (Steimle 1999). In this study, the diet of scup and other benthivorous species, such a winter flounder, were dominated by gammarid and caprellid amphipods around the southern extent of Block Island (chapter 3). Conversely, polychaete worms were more prevalent in the diets of benthivorous species, including scup, in Rhode Island Sound, particularly on and around Cox's Ledge (chapter 3). Previous studies have found that the areas surrounding Block Island Sound exhibit unique geologic environments that are favorable for infaunal and epifaunal amphipods, whereas Cox's Ledge exhibits geologic environments that are favorable to polychaete worms (LaFrance et al. 2014). Thus, feeding on benthic prey appears to be an important link between demersal fish species and their habitats in Rhode Island and Block Island Sounds.

Furthermore, the habitats south of Block Island and around Cox's Ledge may serve as important foraging grounds for demersal fish, as amphipods and polychaete worms are key prey items for many species (chapter 3, Smith & Link 2010). As the development of new ocean uses proceeds, it will be important to protect such unique benthic habitats and the food resources they provide so as to sustain vulnerable groundfish species and maintain overall ecosystem balance.

With respect to the interplay between species assemblages and trophic structure, the results of this work suggest that both bottom-up and top-down trophic cascades play a role, as otter trawl and beam trawl species assemblages were characterized by a wide array of species, including predators (spiny dogfish, summer flounder, silver hake), planktivores (sea scallop), detritivores (American lobster, Cancer crabs), and omnivores (scup, skates, winter flounder) (Hunter & Price 1992). In the context of bottom-up trophic mechanics, planktivore species would be the first fishes to respond to changes in primary productivity, with predator populations changing in response to availability of their food source (planktivore species) (McQueen et al. 1989). Conversely, top-down trophic cascades are based on the theory that predators structure the ecological community via predation, such that an increase in predator populations (dogfish, bluefish, striped bass) leads to a decrease in prey species abundance (squid, herring, butterfish) (Carpenter et al. 1985). Top predators usually take many years to reach maturity and may commit substantial parental investment to each offspring (ovovivipary or vivipary). Thus, even small changes in the number of spawning adults in predator populations can have long-term impacts on fish community structure, including prey resources. This process is exemplified by the initial decline of the northern cod, *Gadus morhua*, population and the subsequent increase in its primary prey species, crabs and lobster (Frank et al. 2005). Thus, when attempting to predict the effects of development and exploitation on the fish and invertebrates community in Rhode Island's nearshore waters, it is essential to consider such trophic cascades, as impacts to specific species will likely propagate throughout the food web.

The mobility of most fish and invertebrate species is a factor that must be considered when discussing spatial patterns in species assemblages, trophic structure, and habitat use in temperate marine environments such as Rhode Island and Block Island Sounds, particularly at the fine spatial scale of this research. The mobility of fishes allows them to move between ecosystems and habitats at will, thus obscuring spatial patterns in diet and isotopic signatures and reducing the measurability of habitat associations (Hobson 1999, Woolnough et al. 2009). However, some fish exhibit strong site fidelity or habitat preferences, which can improve our ability to detect fine scale trophic structure and habitat use (Meyer et al. 2000). In Rhode Island and Block Island Sounds, such a phenomenon is evident in the persistent isotopic spatial patterns of winter flounder and black sea bass, species known for site fidelity, versus the absence of spatial structure in the isotopic signatures of highly mobile herring and scup (chapter 3, Sisson 1974, Howell et al. 1999). Similarly, the amenability of sessile or slow-moving species (which are more strongly associated with specific locations) to fish-habitat research is also evident in

Rhode Island and Block Island Sounds, where species assemblages characterized by sea scallops, skates, crabs, and lobster (less mobile species) exhibit persistent habitat associations (chapter 4).

Another factor that potentially impacts the structure and function of demersal fish communities is ontogenetic shifts in diet. Although we did not achieve large enough sample sizes to statistically assess ontogenetic patterns of the fish species in Rhode Island and Block Island Sounds, exploratory analyses suggest that a number of species exhibited size-based shifts in diet and isotopic signatures. Spiny dogfish presents one of the best examples of this phenomena, as young spiny dogfish exhibit planktivorous feeding behavior, where as adults exhibit more piscivorous foraging strategies (Smith & Link 2010). These tendencies were evident in the elevated $\delta^{15}N$ and trophic positions of larger spiny dogfish in Rhode Island and Block Island Sounds. Bluefish also exhibited enriched $\delta^{15}N$ at larger sizes, again reflecting a shift towards piscivory around age 1 (Szczebak & Taylor 2011). For most species, however, our otter trawl surveys did not effectively capture a wide variety of size classes, which limited our ability to fully assess ontogenetic shifts in diet and isotopic signatures.

Size-based patterns in habitat use may also influence the structure of the demersal fish community in Rhode Island's nearshore waters. Red hake provides a good example of this, as it exhibits a symbiotic relationship with scallops during early juvenile stages and a preference for sandy habitat as adults (Steiner et al. 1982). The methodologies employed for this research, however, are insufficient to assess red hake’s size-based habitat use in Rhode Island’s nearshore waters. The American lobster is also known to exhibit ontogenetic patterns in habitat use, but given the low catch efficiency of lobster in otter and beam trawls, additional trap-based sampling programs would be needed to fully assess this relationship in Rhode Island and Block Island Sound.

The fish-habitat relationships established by this work provide a useful step towards the delineation of Essential Fish Habitat (EFH) in Rhode Island and Block Island Sounds (Peterson et al. 2000). Essential Fish Habitat is defined as the environment(s) required for the successful spawning, feeding, recruitment, and growth to maturity of fished species and their prey (Benaka 1999). EFH refers to both abiotic and biotic habitat features, and is inclusive of both water-column and seafloor environments. Thus, essential fish habitat may include: spawning grounds, migration corridors, nursery grounds, foraging grounds, and theoretically, larval conduits. A common approach to determining EFH for a given species is to identify the distribution patterns of each life stage throughout the year, and to classify the habitat in areas where high densities of individuals are found. While my dissertation research deviated from this classical design, its identification of spatial patterns in species assemblages and habitat use are certainly applicable to EFH delineation in Rhode Island and Block Island Sounds. More specifically, the results of this work suggest that the deep waters surrounding Cox’s Ledge are important in supporting economically valuable species, such as sea scallops and lobsters. Furthermore, the area immediately south and east of Block Island exhibits marked habitat heterogeneity, and thus, is likely an important environment for the early life stages of many fish and invertebrate species. The fish-habitat relationships established by this work are particularly timely as a series of closed areas have been proposed in Rhode Island Sound with the purpose of protecting essential fish habitat. In order to substantiate the classification of EFH in Rhode Island and Block Island Sounds, however, further research is needed to establish the functional relationships between individual fish species and location-specific habitat features and verify their persistence over time. In addition to application in marine reserve and closed area planning, the delineation of EFH is also key to the general advancement of ecosystem-based fisheries management (Rosenberg et al. 2000).

Interestingly, the same areas in Rhode Island Sound that have been proposed as EFH closed areas have also been leased for development of a large-scale (200+ turbine) offshore wind energy facility. Considered theoretically, offshore wind energy development could have a number of impacts on the fisheries ecosystem in Rhode Island and Block Island Sounds, including but not limited to: habitat alteration via scouring, sedimentation, and construction of turbine support structures, shifts in surface and subsurface currents around and within turbine fields, changes in pelagic and benthic productivity and the associated trophic cascades, and modification of foraging behaviors and migration patterns due to electromagnetic fields. With respect to direct impacts on fish and invertebrate communities, sedimentation could smother sessile species (i.e. sea scallops), scouring could create inhospitable environments surrounding turbines, alteration of surface and subsurface currents could advect larvae to unsuitable habitats, reduced productivity could limit food availability (or vice versa), and EMF around cables could obstruct inshore-offshore migrations (i.e. lobster) or attract elasmobranch predators to false food sources within the windfarm field and along the cable route to shore. Furthermore, turbine construction would introduce large structures into the relatively low relief seafloor of Rhode Island Sound, providing high relief habitat for some species and eliminating essential low relief habitat for other species. From an ocean-use context, windfarms are often closed to fishing and can act as de-facto marine reserves, reducing fishing mortality and potentially increasing fish biomass. Thus, with the true ecological repercussions of offshore wind energy development yet to be seen, research such as this is essential to begin to understand, predict and mitigate impacts to fisheries ecosystem dynamics in areas slated for wind energy development. Overall, as the designation of essential fish habitat and/or the development of offshore wind energy facilities proceeds in Rhode Island and Block Island Sounds, this research will play a critical role in the development of new ocean use policies and the advance of ecosystem-based fisheries management.

Literature Cited:

Benaka, L.R. 1999. *Fish habitat: essential fish habitat and rehabilitation*. American Fisheries Society Publishing. Bethesda, Maryland.

Bigelow, H.B and Schroeder, W.C. 2002. Fishes of the Gulf of Maine, Third Edition. B.B.Collette and G. Klein-Macphee (Eds.). Smithsonian Books. Washington, DC.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. Bioscience 35: 634-639.

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

Gerry, S.P. 2008. Feeding mechanics of a trophic generalist and a specialist shark species: A comparison of diet, behavior and function. Dissertation Abstracts International 69(5): 184.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120 (3): 314–326.

Howell, P.T., Molnar, D.R., and Harris, R.B. 1999. Juvenile winter flounder distribution by habitat type. Estuaries 22 (4): 1090-1095.

Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724-732.

LaFrance, M., King, J.W., Oakley, B.A., and Pratt, S. 2014. A comparison of top-down and bottom-up approaches to benthic habitat mapping to inform offshore wind energy development. Continental Shelf Research 83: 24-44.

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J., Lean, D.R.S., 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59: 289–309.

Meyer, C.G., Holland, K.N., Wetherbee, B.M., and Lowe, C.G. 2000. Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. Environmental Biology of Fishes 59 (3): 235-242.

Misund, O.A., and Aglen, A. 1992. Swimming behaviour of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling. ICES Journal of Marine Science 49 (3): 325-334.

Peterson, C.H., Summerson, H.C., Thomson, E., Lenihan, H.S., Grabowski, J., Manning, L., Micheli, F., and Johnson, G. 2000. Synthesis of linkages between benthic and fish communities as a key to protecting essential fish habitat. Bulletin of Marine Science 66 (3): 759-774.

Rosenberg, A., Bigford, T.E., Leathery, S., Hill, R.L., and Bickers, K. 2000. Ecosystem approaches to fishery management through essential fish habitat. Bulletin of Marine Science 66 (3): 535-542.

Simmonds, J., and MacLennan, D.N. 2008. *Fisheries Acoustics: Theory and Practice*. John Wiley & Sons.

Sisson, R.T. 1974. The growth and movement of scup (*Stenotomus chrysops*) in Narragansett Bay, RI and along the Atlantic coast. RI Division of Fish and Wildlife Completion Report.

Smith, B., and Link, J. 2010. The trophic dynamics of 50 finfish and 2 squid species of the Northeast US continental shelf. US Dept. of Commerce. NOAA Technical Memorandum NMFS-NE-216, 640 p.

Steimle, F. W. (1999). *Essential fish habitat source document: Scup,* Stenotomus chrysops*, life history and habitat characteristics*. DIANE Publishing.

Steiner, W.W., Luczkovich, J.J., and Olla, B.L. 1982. Activity, Shelter Usage, Growth and Recruitment of Juvenile Red Hake *Urophycis chuss*. Marine Ecology Progress Series 7 (2): 125-135.

Szczebak, J.T., and Taylor, D.L. 2011. Ontogenetic patterns in bluefish (*Pomatomus saltatrix*) feeding ecology and the effect on mercury biomagnification. Environmental Toxicology and Chemistry 30 (6): 1447-1458.

Wisner, R. L. 1962. Midwater trawl surveys. Limnology and Oceanography 7 (suppl): xxxix-xli.

Woolnough, D.A., Downing, J.A., and Newton, T.J. 2009. Fish movement and habitat use depends on water body size and shape. Ecology of Freshwater Fish 18 (1): 83-91.

Zamon, J.E. 2003. Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. Marine Ecology Progress Series 261: 243-255.

APPENDIX. Supplementary Data & Maps

A. Otter Trawl Station Details. All stations presented here were sampled during the fall (September/October). RIS = Rhode Island Sound, BIS = Block Island Sound.

Station	Year	Region	Depth (ft)	Total Abundance	Total Biomass (kg)	Total Species	Species Richness (H')
A	2009	RIS	140	91676	2127.97	21	1.75
B	2009	RIS	100	13485	254.33	17	1.68
D	2009	BIS	121	99417	985.73	17	1.39
H	2009	BIS	123	7953	277.69	18	1.89
I	2009	RIS	161	48949	2435.33	26	2.32
J	2009	BIS	62	10232	3652.39	21	2.17
K	2009	BIS	98	2857	280.10	22	2.64
L	2009	BIS	104	46383	494.46	17	1.49
M	2009	RIS	147	67133	2330.54	24	2.07
N	2009	RIS	115	14078	379.56	19	1.88
O	2009	BIS	113	15536	218.99	17	1.66
P	2009	RIS	125	96436	2492.36	23	1.92
Q	2009	RIS	110	21450	351.26	20	1.91
T	2009	BIS	60	10359	341.23	17	1.73
U	2009	BIS	100	3315	394.36	17	1.97
7065	2010	RIS	144	4375	452.55	21	2.39
7067	2010	RIS	134	1664	217.73	18	2.26
7069	2010	RIS	123	1794	643.39	14	1.76
A	2010	RIS	140	3746	295.08	23	2.68
B	2010	RIS	108	2441	223.35	15	1.79
D	2010	BIS	117	2979	204.41	17	2.00
H	2010	BIS	127	1370	111.33	19	2.49
J	2010	BIS	78	7004	268.92	21	2.26
K	2010	BIS	104	1578	121.17	15	1.90
L	2010	BIS	102	5683	136.49	14	1.50
M	2010	RIS	140	1805	176.88	24	3.05
N	2010	RIS	114	6516	448.68	20	2.16
T	2010	BIS	78	1648	203.48	17	2.16
U	2010	BIS	106	589	78.76	9	1.27
7065	2011	RIS	150	8770	621.08	20	2.09
BI2	2011	BIS	77	3450	84.84	10	1.10
BI5	2011	BIS	81	2674	109.99	14	1.65
BI6	2011	BIS	118	16820	1275.44	19	1.85
BI7	2011	BIS	126	2353	2073.05	16	1.93
BI8	2011	BIS	121	14956	2878.20	15	1.46
J	2011	BIS	60	6444	223.34	23	2.51
L	2011	BIS	105	33376	447.48	26	2.40
LB5	2011	RIS	147	6300	746.92	23	2.51
LB6	2011	RIS	141	1369	158.68	18	2.35
LB7	2011	RIS	138	2831	265.74	22	2.64
LB8	2011	RIS	127	1772	420.68	20	2.54
LB9	2011	RIS	162	7205	401.32	21	2.25
LB10	2011	RIS	165	4825	335.53	23	2.59
LB11	2011	RIS	152	2374	347.58	19	2.32

B. Beam Trawl Station Details. 2010 stations were sampled during the winter (November), while 2011 and 2012 stations were sampled during the summer (July/August). RIS = Rhode Island Sound, BIS = Block Island Sound.

Station	Year	Region	Depth (ft)	Total Abundance	Total Biomass (kg)	Total Species	Species Richness (H')
6864	2010	RIS	160	1884	136.05	23	2.92
6914	2010	RIS	140	790	134.41	25	3.60
A2	2010	RIS	120	233	85.53	18	3.12
O	2010	BIS	115	3425	84.34	20	2.34
OFF1	2010	RIS	130	5365	172.64	28	3.14
OFF2	2010	RIS	170	22562	229.52	25	2.39
OFF3	2010	RIS	160	2708	159.96	28	3.42
PG1	2010	BIS	110	2954	128.85	21	2.50
Q	2010	RIS	110	840	86.36	20	2.83
T	2010	RIS	80	965	67.10	17	2.34
XX	2010	RIS	145	333	70.46	17	2.76
1	2011	BIS	135	1780	821.92	20	2.54
4	2011	RIS	140	1245	235.15	25	3.37
6	2011	RIS	102	1117	219.49	28	3.85
7	2011	RIS	143	2286	222.62	21	2.59
8	2011	RIS	128	1705	239.89	22	2.82
10	2011	RIS	145	7712	198.00	17	1.79
11	2011	RIS	165	9914	136.69	22	2.28
12	2011	RIS	150	26324	253.78	23	2.16
13	2011	RIS	160	3766	145.94	25	2.91
15	2011	RIS	125	2774	113.31	19	2.27
18	2011	RIS	130	663	128.93	22	3.23
19	2011	RIS	118	597	148.84	16	2.35
20	2011	RIS	140	1391	90.90	23	3.04
6914	2011	RIS	140	1082	151.41	23	3.15
NIX1	2011	RIS	125	691	99.37	15	2.14
PG3	2011	BIS	73	15375	179.85	14	1.35
U	2011	BIS	115	2206	567.94	16	1.95
6914	2012	RIS	130	502	90.47	20	3.06
7065	2012	RIS	160	1853	133.23	22	2.79
F1	2012	BIS	120	712	87.28	18	2.59
F2	2012	BIS	110	62	28.97	11	2.42
F3	2012	BIS	130	245	60.25	15	2.54
F4	2012	BIS	80	606	45.88	21	3.12
F6	2012	BIS	130	660	164.65	20	2.93
F7	2012	BIS	130	412	86.59	20	3.16
F8	2012	BIS	155	5907	153.35	19	2.07
F10	2012	BIS	160	5302	187.76	22	2.45
F12	2012	BIS	120	403	57.86	20	3.17
F13	2012	RIS	120	254	49.44	19	3.25
F14	2012	RIS	135	1281	225.58	23	3.07
F15	2012	RIS	150	5124	190.51	19	2.11
F16	2012	RIS	170	13845	262.26	23	2.31
F22	2012	RIS	110	110	24.48	17	3.40
F26	2012	RIS	125	297	81.86	19	3.15
F28	2012	RIS	140	358	152.31	19	3.06
NIX1	2012	RIS	125	758	101.82	18	2.56
Q	2012	BIS	115	1026	200.26	16	2.16
S5	2012	RIS	95	261	65.68	17	2.88
T	2012	BIS	70	146	18.09	19	3.61
U	2012	BIS	115	433	130.10	18	2.80

C. Common names, Latin names, and catch rates of all species sampled during otter trawl surveys.

Common Name	Latin Name	Mean Abundance (# per trawl)	Mean Biomass (kg per trawl)
Alewife	*Alosa pseudoharengus*	93.279	4.355
American eel	*Anguilla rostrata*	0.082	0.115
American lobster	*Homarus americanus*	3.311	1.045
American shad	*Alosa sapidissima*	8.623	0.892
Atlantic cod	*Gadus morhua*	0.262	0.762
Atlantic herring	*Clupea harengus*	163.672	4.580
Atlantic mackerel	*Scomber scombrus*	26.820	1.326
Atlantic moonfish	*Selene setapinnis*	0.410	0.027
Atlantic torpedo	*Torpedo nobiliana*	0.131	16.033
Barndoor skate	*Raja laevis*	0.230	1.205
Bay anchovy	*Anchoa mitchilli*	2.590	0.010
Black seabass	*Centropristis striata*	3.492	3.586
Blue crab	*Callinectes sapidus*	0.066	0.141
Blue mussel	*Mytilus edulis*	0.197	0.055
Blue runner	*Caranx crysos*	0.016	0.012
Blueback herring	*Alosa aestivalis*	5.344	0.274
Bluefish	*Pomatomus saltatrix*	1.393	4.761
Bluespotted cornetfish	*Fistularia tabacaria*	0.066	0.016
Butterfish	*Peprilus triacanthus*	8043.131	167.852
Cancer spp. crab	*Cancer* spp.	1.508	0.149
Clearnose skate	*Raja eglanteria*	0.262	3.785
Crevalle jack	*Caranx hippos*	0.033	0.018
Cunner	*Tautogolabrus adspersus*	0.475	0.432
Fourspot flounder	*Paralichthys oblongus*	9.197	1.538
Gulf Stream flounder	*Citharichthys arctifrons*	1.033	0.190
Haddock	*Melanogrammus aeglefinus*	0.574	0.043
Horseshoe crab	*Limulus polyphemus*	0.016	0.888
Leucoraja skate spp. (immature)	*Leucoraja* spp.	8.803	0.388
Little skate	*Leucoraja erinacea*	134.541	75.342
Longfin inshore squid	*Doryteuthis pealeii*	2060.656	36.642
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	1.623	0.167
Monkfish	*Lophius americanus*	0.328	6.083
Northern kingfish	*Menticirrhus saxatilis*	0.016	0.028
Northern puffer	*Sphoeroides maculatus*	0.049	0.005
Northern searobin	*Prionotus carolinus*	3.885	0.629
Ocean pout	*Macrozdarces americanus*	1.000	0.161
Ocean quahog	*Arctica islandica*	1.213	2.612
Planehead filefish	*Monocanthus hispidus*	0.016	0.003
Pollock	*Pollachius virens*	0.016	0.025
Red hake	*Urophycis chuss*	5.869	1.734
Rough scad	*Trachurus lathami*	4.738	0.714
Round herring	*Etrumeus teres*	20.246	2.542
Round scad	*Decapterus punctatus*	4.689	0.430
Sand dollar	*Echinarachnius parma*	0.033	0.008
Scup	*Stenotomus chrysops*	1093.607	60.464
Sea raven	*Hemitripterus americanus*	0.328	2.625
Sea scallop	*Placopectin magellanicus*	8.164	1.921
Sea star	*Asterias spp.*	22.049	2.553
Short bigeye	*Pristigenys alta*	0.033	0.010
Silver hake	*Merluccius bilinearis*	126.393	14.905
Smooth dogfish	*Mustelus canis*	0.820	5.069
Spider crab	*Libinia emarginata*	0.131	0.045
Spiny dogfish	*Squalus acanthias*	72.770	330.044
Spot	*Leiostomus xanthurus*	0.016	0.025
Spotted hake	*Urophycis regia*	5.033	1.162
Striped bass	*Morone saxatilis*	0.230	14.943
Striped searobin	*Prionotus evolans*	1.098	1.536
Summer flounder	*Paralichthys dentatus*	5.197	8.925
Weakfish	*Cynoscion regalis*	0.738	1.111
Windowpane	*Scophthalmus aquosus*	5.803	1.581
Winter flounder	*Pseudopleuronectes americanus*	48.918	15.521
Winter skate	*Leucoraja ocellata*	28.738	36.772
Witch flounder	*Glyptocephalus cynoglossus*	1.082	9.320
Yellowtail flounder	*Pleuronectes ferruginea*	3.213	1.123

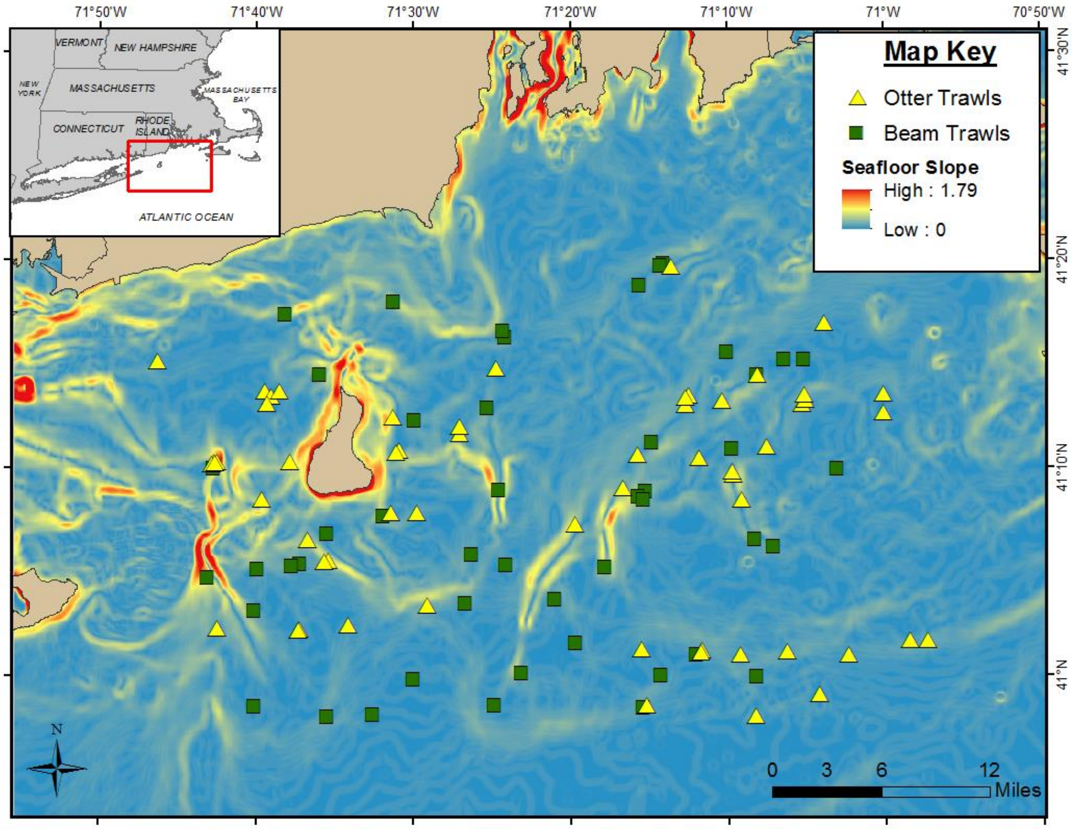
D. Common Names, Latin names, and catch rates of all species sampled during beam trawl surveys.

Common Name	Latin Name	Mean Abundance (# per trawl)	Mean Biomass (kg per trawl)
American lobster	*Homarus americanus*	1.115	0.580
Smooth astarte	*Astarte castanea*	0.115	0.015
Asterias spp. Seastars	*Asterias* spp.	344.846	25.455
Atlantic torpedo	*Torpedo nobiliana*	0.019	80.000
Barndoor skate	*Raja laevis*	0.442	1.466
Black seabass	*Centropristis striata*	0.288	0.018
Blood star	*Henricia* spp.	0.712	0.025
Blue crab	*Callinectes sapidus*	0.154	0.388
Blue mussel	*Mytilus edulis*	0.712	0.286
Butterfish	*Peprilus triacanthus*	0.173	0.073
Cancer spp. crab	*Cancer* spp.	79.173	8.643
Channeled whelk	*Busycon canaliculatus*	0.192	0.495
Clearnose skate	*Raja eglanteria*	0.038	2.680
Cockle	*Laevicardium* spp	0.327	0.028
Crumb of bread sponge	*Halichondria panicea*	0.077	0.225
Cunner	*Tautogolabrus adspersus*	0.038	0.683
Finger Sponge	*Haliclona* spp.	0.173	0.153
Fourspot flounder	*Paralichthys oblongus*	7.923	1.211
Gulf Stream flounder	*Citharichthys arctifrons*	1.788	0.151
Haddock	*Melanogrammus aeglefinus*	0.019	0.020
Hairy sea cucumber	*Sclerodactyla briareus*	0.019	0.105
Hermit crab	*Pagurus* spp.	16.827	0.641
Horse mussel	*Modiolus modiolus*	0.077	0.440
Horseshoe crab	*Limulus polyphemus*	0.019	2.805
Leucoraja spp. skates (immature)	*Leucoraja* spp.	38.462	6.677
Little skate	*Leucoraja erinacea*	88.231	49.238
Longfin inshore squid	*Doryteuthis pealeii*	7.750	0.271
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	2.538	0.230
Mantis shrimp	*Squilla empusa*	0.038	0.068
Margined sea star	*Astropecten* spp.	806.077	18.010
Monkfish	*Lophius americanus*	1.096	4.844
Moon snail	*Polinices heros*	11.538	0.847
Northern puffer	*Sphoeroides maculatus*	0.865	0.160
Northern searobin	*Prionotus carolinus*	2.115	0.627
Nudibranch	*Nudibrachia* spp.	0.385	0.021
Ocean pout	*Macrozdarces americanus*	0.346	0.475
Ocean quahog	*Arctica islandica*	2.077	1.715
Orange footed sea cucumber	*Cucumaria frondosa*	1.250	0.415
Pandalid shrimp	*Pandalus* spp.	7.577	0.099
Pipefish	*Syngnathus* spp.	0.288	0.010
Rat tailed sea cucumber	*Paracaudina chilensis*	0.058	0.025
Red hake	*Urophycis chuss*	3.942	0.616
Ribbed mussel	*Modiolus demissus*	0.038	0.030
Sand dollar	*Echinarachnius parma*	19123.788	277.252
Scup	*Stenotomus chrysops*	1.769	0.267
Sea mouse	*Aphrodita hastata*	0.885	0.072
Sea raven	*Hemitripterus americanus*	0.231	0.828
Sea scallop	*Placopectin magellanicus*	193.173	38.001
Sea urchin	*Strongylocentrotus droebachiensis*	0.192	0.057
Short-browed mud shrimp	*Callianassa atlantica*	0.077	0.015
Silver hake	*Merluccius bilinearis*	4.827	0.803
Smallmouth flounder	*Etropus microstomus*	0.231	0.080
Inquiline Snailfish	*Liparis inquilinus*	2.115	0.022
Spider crab	*Libinia emarginata*	1.192	0.240
Spiny dogfish	*Squalus acanthias*	0.058	2.720
Sponge	Spongiidae	4.077	6.119
Spotted hake	*Urophycis regia*	1.769	0.406
Striped searobin	*Prionotus evolans*	0.269	0.477
Summer flounder	*Paralichthys dentatus*	0.654	1.466
Surf clam	*Spisula solidissima*	0.442	0.081
Waved whelk	*Buccinum undatum*	0.365	0.068
White sea cucumber	*Eupentacta quinquesemita*	3.308	0.160
Windowpane	*Scophthalmus aquosus*	3.442	1.197
Winter flounder	*Pseudopleuronectes americanus*	3.135	5.492
Winter skate	*Leucoraja ocellata*	41.212	24.415
Witch flounder	*Glyptocephalus cynoglossus*	0.038	0.530
Yellowtail flounder	*Pleuronectes ferruginea*	1.923	1.475

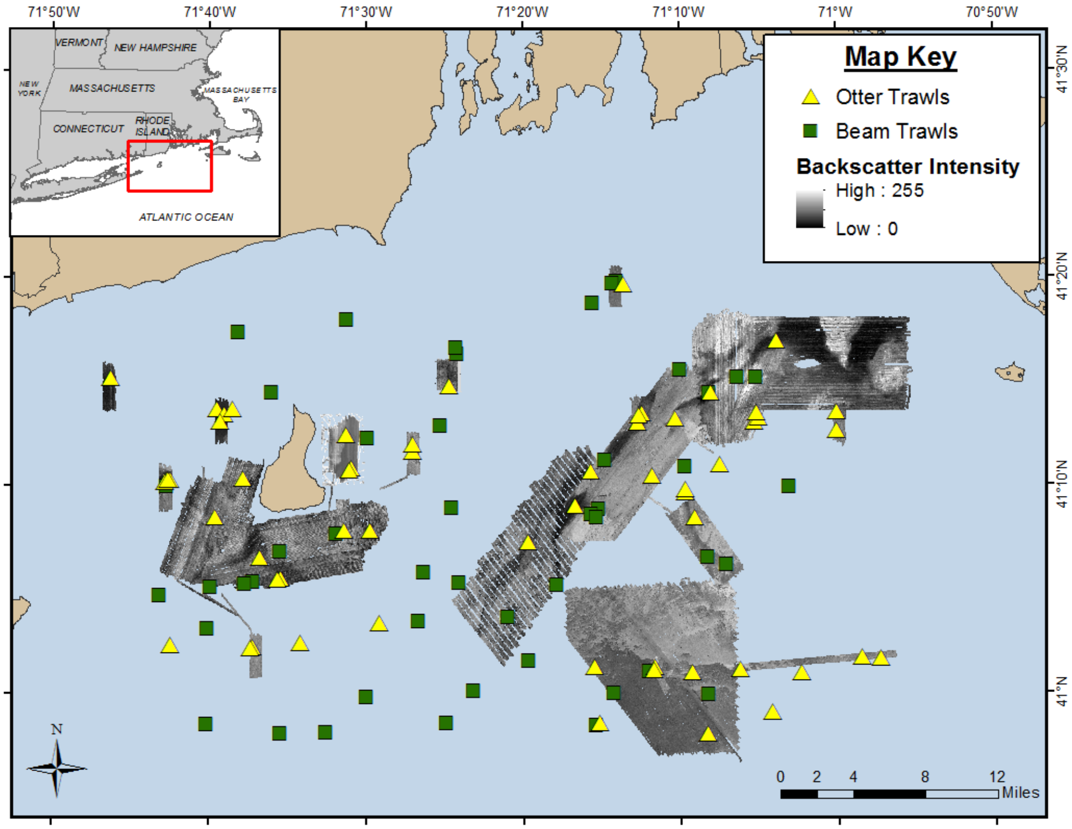
E. Common names, size classes, isotope sample sizes, and stomach sample sizes of each species included in trophic analyses.

Common Name	Size Class	Size Range (cm)	Isotopes Samples	Stomach Samples
Alewife	Small	10-20	28	29
American shad	Small	15-25	17	18
Ameican lobster	Small	5-8	6	0
Atlantic cod	Large	51-80	1	1
Atlantic herring	Small	10-20	51	93
	Medium	21-30	3	5
Barndoor skate	Medium	25-40	2	1
Black sea bass	Small	10-25	2	4
	Medium	26-60	59	63
Blueback herring	Small	10-20	7	7
Bluefish	Small	10-30	30	25
	Medium	31-70	27	0
Butterfish	Small	4-20	69	177
Clearnose skate	Large	50-60	0	1
Haddock	Small	10-20	20	24
Little skate	Small	10-30	68	112
Longfinned squid	Small	3-20	76	0
Monkfish	Small	10-25	1	0
	Medium	26-60	9	7
	Large	61-90	7	5
Pollock	Small	10-20	1	1
Scup	Small	5-25	62	340
	Medium	26-50	5	43
Sean scallop	Small	4-13	44	0
Silver hake	Small	5-20	18	97
	Medium	21-40	23	107
Smooth dogfish	Medium	41-60	1	1
	Large	60-80	20	23
Spiny dogfish	Medium	41-60	6	4
	Large	60-80	64	59
Spot	Small	17	0	1
Striped bass	Large	70-95	11	10
Summer flounder	Medium	21-40	26	24
	Large	41-70	56	75
Weakfish	Small	10-25	6	10
	Medium	26-50	3	4
Winter flounder	Small	10-20	7	16
	Medium	21-40	75	223
	Large	41-70	9	9
Winter skate	Small	10-30	23	33
	Medium	31-60	38	62
Yellowtail flounder	Small	10-20	2	2
	Medium	21-40	22	29
	Large	41-70	7	6

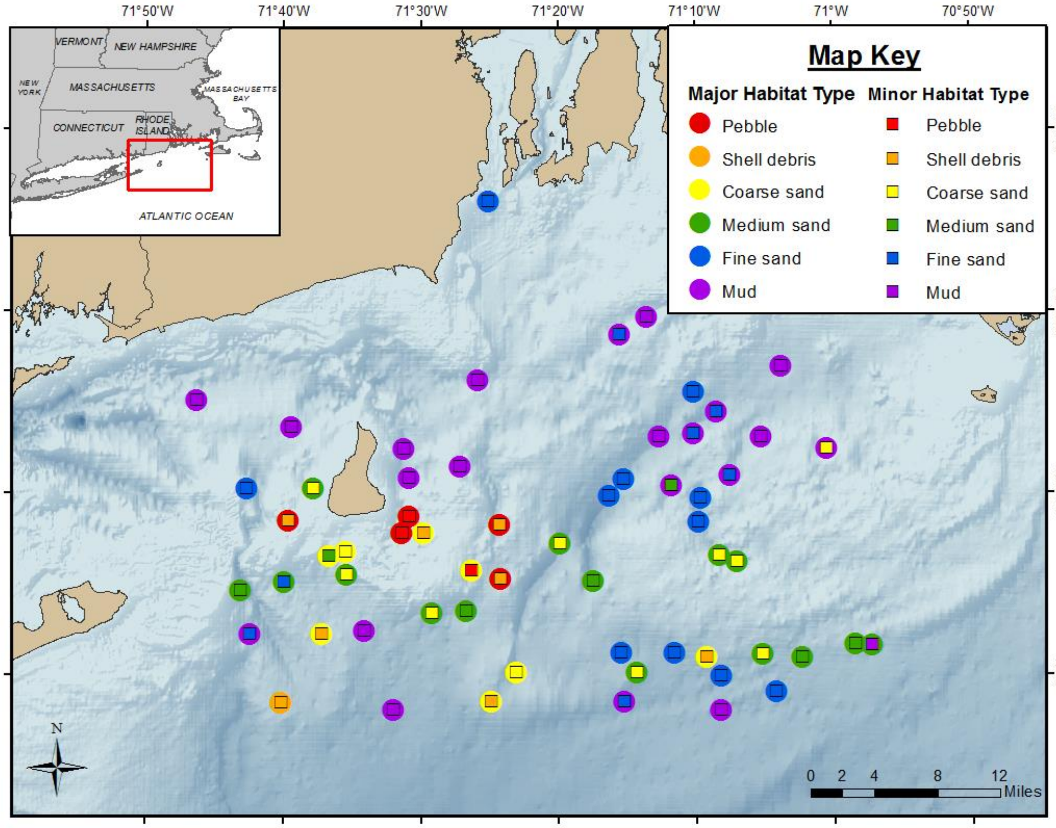
F. Map of seafloor slope in Rhode Island and Block Island Sounds. This layer was derived from the NGDC's Coastal Relief Model bathymetry grid using the Spatial Analyst toolbox in ArcInfo 10.3. Otter trawls are indicated by yellow triangles and beam trawls are indicated by green squares.



G. Map of backscatter intensity (as measured from sidescan sonar) in Rhode Island and Block Island Sounds. This layer was collected, processed, and compiled by the King Lab at URI GSO. Otter trawls are indicated by yellow triangles and beam trawls are indicated by green squares.



H. Map of major and minor habitat types as observed via underwater video surveys in Rhode Island and Block Island Sounds. Major habitat types are indicated by color coded circles and minor habitat types are indicated by color coded inlaid squares.



BIBLIOGRAPHY:

Able, K. W., Grothues, T. M., Morson, J. M., and Coleman, K. E. 2014. Temporal variation in winter flounder recruitment at the southern margin of their range: is the decline due to increasing temperatures? ICES Journal of Marine Science 71(8): 2186-2197.

Abrantes, K., and Barnett, A. 2011. Intrapopulation variations in diet and habitat use in a marine apex predator, the broadnose sevengill shark, *Notorynchus cepedianus*. Marine Ecology Progress Series 442: 133–148.

Alonso, M.K., Crespo, E.A., Garcia, N.A., Pedraza, S.N., Mariotti, P.A., and Mora, N.J. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environmental Biology of Fishes 63: 193–202.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd., Plymouth, UK, 214 pp.

Anderson, T. J., Syms, C., Roberts, D. A., Howard, D. F., 2009. Multi-scale fish–habitat associations and the use of habitat surrogates to predict the organization and abundance of deep-water fish assemblages. Journal of Experimental Marine Biology and Ecology 379: 34–42.

Anderson, T.J. McArthur, M.A., Syms, C., Nichol, S., Brooke, B., 2013. Infaunal biodiversity and ecological function on a remote oceanic island: The role of biogeography and bio-physical surrogates. Estuarine, Coastal and Shelf Science 117: 227-237.

Ault, T.R. and Johnson, C.R. 1998. Spatially and temporally predictable fish communities on coral reefs. Ecological Monographs 68: 25-50.

Auster, P.J., Joy, K., and Valentine, P.C. 2001. Fish species and community distributions as proxies for seafloor habitat distributions: the Stellwagen Bank National Marine Sanctuary example (Northwest Atlantic, Gulf of Maine). Environmental Biology of Fishes 60(4): 331-346.

Auster, P.J., and Link, J. 2009. Compensation and recovery of feeding guilds in a northwest Atlantic shelf fish community. Marine Ecology Progress Series 382: 163–172.

Auster, P.J., Malatesta, R.J., and Donaldson, C.L.S. 1997. Distributional responses to small-scale habitat variability by early juvenile silver hake, Merluccius bilinearis. Environmental Biology of Fishes 50: 195–200.

Beck, M.W., Ferdaña, Z., Kachmar, J., Morrison, K.K., Taylor P. 2009. Best Practices for Marine Spatial Planning. The Nature Conservancy, Arlington, VA.

Bell, R.J., Fogarty, M.J., Collie, J.S. 2014a. Stability in marine fish communities. Marine Ecology Progress Series 504: 221-239.

Bell, R.J., Richardson, D.E., Hare, J.A., Lynch, P.D., and Fratantoni, P. S. 2014b. Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. ICES Journal of Marine Science, fsu217.

Benaka, L.R. 1999. *Fish habitat: essential fish habitat and rehabilitation*. American Fisheries Society Publishing. Bethesda, Maryland.

Bigelow, H.B and Schroeder, W.C. 2002. Fishes of the Gulf of Maine, Third Edition. B.B.Collette and G. Klein-Macphee (Eds.). Smithsonian Books. Washington, DC.

Black, G.A.P., Mohn, R.K., Robert, G., and Tremblay, M.J. 1993. Atlas of the biology and distribution of the sea scallop, *Placopecten magellanicus,* and Iceland scallop, *Chlamys islandica*, in the Northwest Atlantic. Canadian Technical Report of Fisheries and Aquatic Sciences: 1915.

Bohaboy, E.C., Malek, A.J., Collie, J.S., 2010. Baseline characterization: data sources, methods, and results. Technical Report #13 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Bowman, R.E., Stillwell, C.E., Michaels, W.L., and Grosslein, M.D. 2000. Food of northwest Atlantic fishes and two common species of squid. NOAA Tech. Memo. NMFS-NE-155, Woods Hole, MA.

Bonzek, C.F., Garland, J., Lange, J.D. Jr., Latour, R.J., 2010. Northeast Area Monitoring and Assessment Program Final Report Fall 2007 - Fall 2010. Virginia Institute of Marine Science, 220 p. Accessed at http://www.neamap.net/publications/NEAMAP_Data%20Report_Fall07-Fall2011.pdf

Bosman, S. H., Methven, D.A., Courtenay, S. C., Hanson, J. M., 2011. Fish assemblages in a north Atlantic coastal ecosystem: Spatial patterns and environmental correlates. Estuarine, Coastal and Shelf Science 92: 232–245.

Bowman, I.R., Craig, N., & Drew, C. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography 33 (5): 1182–1190.

Brown, C.J., and Blondel, P. 2009. Developments in the application of multibeam sonar backscatter for seafloor habitat mapping. Applied Acoustics 70 (10): 1242-1247.

Buckel, J.A., Conover, D.O., Steinberg, N.D., and McKown, K.A. 1999. Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependent loss of juvenile striped bass (*Morone saxatilis*). Canadian Journal of Fisheries and Aquatic Sciences 56 (2): 275-287.

Bulman C.M., Althaus, F., He, X., Bax, N.J., and Williams, A. 2001. Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. Marine and Freshwater Research 52: 537–548.

Bundesamt für Seeschifffart unh Hydrologie (BSH). 2013. Investigation of the impacts of offshore wind turbines on the marine environment. Federal Maritime and Hydrographic Agency, Hamburg, Germany, 87 pp.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretical Approach, Second Ed. Springer-Verlag, New York. New York.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. Bioscience 35: 634-639.

Cabana, G., and Rasmussen, J.B. 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences of the United States of America, 93 (20): 10844–10847.

Carlisle, A.B., Goldman, K.J., Litvin, S.Y., Madigan, D.J., Bigman, J.S., Swithenbank, A.M., and Block, B.A. 2015. Stable isotope analysis of vertebrae reveals ontogenetic changes in habitat in an endothermic pelagic shark. Proceedings of the Royal Society of London B: Biological Sciences 282 (1799): 20141446.

Carrassón, M., & Cartes, J.E. 2002. Trophic relationships in a Mediterranean deep-sea fish community: partition of food resources, dietary overlap and connections within the benthic boundary layer. Marine Ecology Progress Series 241: 41-55.

The Centre for Environment, Fisheries, and Aquaculture Science (CEFAS). 2004. Offshore Wind Farms: Guidance Note for Environmental Impact Assessment in Respect of FEPA and CPA Requirements, Version 2. Lowestoft, United Kingdom, 44 pp.

Chassot, E., Melin, F., Le Pape, O., Gascuel, D., 2007. Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. Marine Ecology Progress Series 343: 45–55.

Christensen, JD, Jeffrey, C.F.G. and Caldow, C. 2003. Cross-shelf habitat utilization patterns of reef fishes in south western Puerto Rico. Gulf and Caribbean Research 14: 9-27.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd., Plymouth, UK, 190 pp.

Clarke, K.R., Somerfield, P.J., Chapman, M.G., 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. Journal of Experimental Marine Biology and Ecology 330: 55–80.

Clarke, K.R., and Warwick, R.M. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E, Plymouth, 172pp.

Clément, M., Chiasson, A.G., Veinott, G., and Cairns, D.K. 2014. What otolith microchemistry and stable isotope analysis reveal and conceal about anguillid eel movements across salinity boundaries. Oecologia: 1-11.

Cogan, C. B., Todd, B. J., Lawton, P., Noji, T. T., 2009. The role of marine habitat mapping in ecosystem-based management. ICES Journal of Marine Science 66: 2033–2042.

Collie, J.S., Adamowicz, W.L., Beck, M.W., Craig, B., Essington, T.E., Fluharty, D., Rice, J., Sanchirico, J.N., 2013. Marine spatial planning in practice. Estuarine, Coastal and Shelf Science 117: 1-11.

Collie, J.S., Beck, M.W., Craig, B., Essington, T.E., Fluharty, D., Rice, J., and Sanchirico, J.N. 2013. Marine spatial planning in practice. Estuarine, Coastal and Shelf Science 117: 1-11.

Collie, J.S., Wood, A.D., Jeffries, H.P., 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences 65: 1352-1365.

Collier, J.S., and Brown, C.J. 2005. Correlation of sidescan backscatter with grain size distribution of surficial seabed sediments. Marine Geology 214 (4): 431-449.

Colwell, R.K. and Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567-576.

Costa-Pierce, B., 2010. Ecology of the SAMP. Chapter #2 in Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Crowder, L., Norse, E., 2008. Essential ecological insights for marine ecosystem-based management and marine spatial planning. Marine Policy 32: 772-778.

Cury, P.M., Mullon, C., Garcia, S.M., Shannon, L.J., 2005. Viability theory for an ecosystem approach to fisheries. ICES Journal of Marine Science 62: 577–584.

Deegan, L. A., 1993. Nutrient and energy transport between estuaries and coastal marine ecosystems by fish migration. Canadian Journal of Fisheries and Aquatic Science 50: 74-79.

Douvere, F. 2008. The importance of marine spatial planning in advancing ecosystem-based sea use management. Marine Policy 32: 762-771.

Douvere, F., Ehler, C. N., 2009. New perspectives on sea use management: initial findings from European experience with marine spatial planning. Journal of Environmental Management 90: 77–88.

DeNiro, M.J., and Epstein, S. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science 197: 261–263.

Dixon, H.J., Dempson, J.B., and Power, M. 2015. Assessing the use of different marine growth zones of adult Atlantic salmon scales for studying marine trophic ecology with stable isotope analysis. Fisheries Research 164: 112-119.

Driscoll, N.W. 1992. Side-scan sonar investigation of shallow-water depositional processes in and around Block Island Sound: before and after the Nor'easter of 1992. Storming Media Pentagon Reports, retrieved online from http://www.stormingmedia.us/48/4888/A488813.html.

Ehler, C., and Douvere, F. 2009. Marine Spatial Planning: A Step-by-step Approach toward Ecosytem-based Management. UNESCO Intergovernmental Oceanographic Commission, Paris, France.

Elefteriou, A., and McIntyre, A. 2005. Methods for the Study of Marine Benthos. Wily-Blackwell.

Eriksson, B.K., Ruback, A., Hillebrand, H., 2006. Biotic habitat complexity controls species diversity and nutrient effects on net biomass production. Ecology 87: 246-254.

Estrada, J.A., Rice, A.N. Lutcavage, M.E., and Skomal, G.B. 2003. Predicting trophic position in sharks of the northwest Atlantic Ocean using stable isotope analysis. Journal of the Marine Biological Association of the UK 83: 1347-1350

Fogarty, M.J. 2013. The art of ecosystem-based fishery management. Canadian Journal of Fisheries and Aquatic Sciences 71 (3): 479-490.

Foley, M.M., Halpern, B.S., Micheli, F., Armsby, M.H., Caldwell, M.R., Crain, C.R., Prahler, E., Rohr, N., Sivas, D.,Beck, M.W., Carr, M.H., Crowder, L.B., Duffy, J.E., Hacker, S.D., McLeod, K.L., Palumbi, S.R., Peterson, C.H., Regan, H.M., Ruckelshaus, M.H., Sandifer, P.A., Steneck, R.S., 2010. Guiding ecological principles for marine spatial planning. Marine Policy 35: 955-966.

France, R.L. 1993. Carbon-13 enrichment in benthic compared to planktonic algae: food web implications. Marine Ecology Progress Series 124: 307-312.

Franco, A., Pérez-Ruzafa, A., Drouineau, H., Franzoi, P., Koutrakis, E.T., Lepage, M., Verdiell-Cubedo, D., Bouchoucha, M., López-Capel, A., Riccato, F., Sapounidis, A., Marcos, C., Oliva-Paterna, F.J., Torralva-Forero, M., Torricelli, P., 2012. Assessment of fish assemblages in coastal lagoon habitats: Effect of sampling method. Estuarine, Coastal and Shelf Science 112: 115-125.

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

Freitas, R., Ricardo, F., Pereira, F., Sampaio, L., Carvalho, S., Gaspar, M., Quintino, V., and Rodrigues, A.M. 2011. Benthic habitat mapping: concerns using a combined approach (acoustic, sediment, and biological data). Estuarine, Coastal and Shelf Science 92 (4): 598-606.

Friedland, K. D., Stock, C., Drinkwater, K. F., Link, J. S., Leaf, R. T., Shank, B. V, Rose, J. M., Pilskaln, C.H., Fogarty, M.J., 2012. Pathways between primary production and fisheries yields of large marine ecosystems. PloS ONE 7, e28945.

Friedlander, A.M., and Brown, E. 2003. Fish Habitat Utilization Patterns and Evaluation of the Efficacy of Marine Protected Areas in Hawaii: Integration and Evaluation of NOS Digital Benthic Habitats Maps and Reef Fish Monitoring Studies. Final Report to NOAA National Ocean Service Biogeography Program, 1-78.

Friedlander, A.M. and Parrish, J.D. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224 (1): 1-30.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography 33 (5): 1182-1190.

Gabriel, W.L., 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, Northwest Atlantic. Journal of Northwest Atlantic Fisheries Science 14: 29-46.

Garrison, L.P. 2000. Spatial and dietary overlap in the Georges Bank groundfish community. Canadian Journal of Fisheries and Aquatic Sciences 57 (8): 1679–1691.

Garrison, L., and Link, J. 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202: 231–240.

Gerry, S.P. 2008. Feeding mechanics of a trophic generalist and a specialist shark species: A comparison of diet, behavior and function. Dissertation Abstracts International 69(5): 184.

Gilliland, P. M., Laffoley, D., 2008. Key elements and steps in the process of developing ecosystem- based marine spatial planning. Marine Policy 32: 787–796.

Gleason, M., McCreary, S., Miller-Henson, M., Ugoretz, J., Fox, E., Merrifiend, M., McClintock, W., Serpa, P., and Hoffman, K. 2010. Science-based and stakeholder-driven protected area network planning: as successful case study from north central California. Ocean and Coastal Management 53: 52-68.

Gratewick, B., and Speight, M.R., 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66: 650-667.

Gomelyuk, V.E. 2009. Fish assemblages composition and structure in three shallow habitats in north Australian tropical bay, Garig Ganuk Barlu National Park, Northern Territory, Australia. Journal of Marine Biological Association of the United Kingdom 89(3): 449-460.

Guegan, J.F., Lek, S., Oberdorff, T., 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. Nature 391: 382-384.

Hahm, W., and Langton, R.W. 1984. Prey selection based on predator/prey weight ratios for some Northwest Atlantic fish. Marine Ecology Progress Series 19 (1-2): 1-5.

Hale, S. S., 2010. Biogeographical patterns of marine benthic macroinvertebrates along the Atlantic coast of the northeastern USA. Estuaries and Coasts 33: 1039–1053.

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

Hansson, S., Hobbie, J.E., Ragnar, E., Larsson, U., Fry, B., and Johansson, S. 1997. The stable nitrogen isotope ratio as a marker of food-web. Ecology 78 (7): 2249–2257.

Hasbrouck, E.C, Scotti, J., Stent, J., Gerbino, K., 2011. Rhode Island commercial fishing and seafood industries: The development of an industry profile. Commercial Fisheries Research Foundation, Kingston, Rhode Island, 124 pp.

Hawkins, C.P., and MacMahon, J.A. 1989. Guilds: the multiple meanings of a concept. Annual Review of Entomology 34: 423-451.

Hesslein, R.H., Hallard, K.A., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen, in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by $\delta^{34}S$, $\delta^{13}C$, and $\delta^{15}N$. Canadian Journal of Fisheries and Aquatic Sciences 50: 2071-2076.

Hill, M.O., 1973. Diversity and evenness: A unifying notation and its consequences. Ecology 54: 327- 432.

Hobson, R.D. 1972. Chapter 8 – Surface roughness in topography: quantitative approach. *in* R.J. Chorley, editor. Spatial analysis in geomorphology. Harper & Row. New York, New York.

Hobson, K.A and Welch, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{14}N$ analysis. Marine Ecology Progress Series 84: 9-18.

Hobson, K.A., Ambrose, W.G., and Renaud, P.E. 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya : insights from delta13C and delta15N analysis. Marine Ecology Progress Series 128: 1–10.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120 (3): 314–326.

Hopkins, T.L., and Baird, R.C. 1975. Net feeding in mesopelagic fishes. Fishery Bulletin 73 (4): 908-914.

Howell, P.T., Molnar, D.R., and Harris, R.B. 1999. Juvenile winter flounder distribution by habitat type. Estuaries 22 (4): 1090-1095.

Hulbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724-732.

Hyslop, E. J. 1980. Stomach contents analysis-a review of methods and their application. Journal of Fish Biology 17 (4): 411–429.

Iampietro, P.J.,Young, M.A., and Kvitek, R.G. 2008. Multivariate prediction of rockfish habitat suitability in Cordell bank national marine sanctuary and Del Monte Shalebeds, California, USA. Marine Geodesy 31 (4): 359-371.

International Council for the Exploration of the Sea (ICES). 2007. Acoustic seabed classification of marine physical and biological landscapes. Cooperative Research Report No. 286, 183 pp.

Iverson, R.L., 1990. Control of marine fish production. Limnology and Oceanography 35: 1593-1604.

Jay, S. 2010. Planners to the rescue: Spatial planning facilitating the development of offshore wind energy. Marine Pollution Bulletin 60 (4): 493-499.

Jennings, S., Kaiser, M., and Reynolds, J.D. 2009. Marine Fisheries Ecology. John Wiley & Sons.

Johnson, A., Jenkins, S., Hiddink, J.G., and Hinz, H. 2012. Linking temperate demersal fish species to habitat: scales, patterns, and future directions. Fish and Fisheries 14 (3): 256-280.

Johnson, J.E., and Welch, D.J. 2009. Marine fisheries management in a changing climate: a review of vulnerability and future options. Reviews in Fisheries Science 18 (1): 106-124.

Jordaan, A., Chen, Y., Townsend, D.W., Sherman, S., 2010. Identification of ecological structure and species relationships along an oceanographic gradient in the Gulf of Maine using multivariate analysis with bootstrapping. Canadian Journal of Fisheries and Aquatic Sciences 67: 701-719.

Kendall, M.S., Christensen, J.D., Caldow, C., Coyne, M., Jeffrey, C., Monaco, M.E., Morrison, W. and Hillis-Starr, Z. 2004. The influence of bottom type and shelf position on biodiversity of tropical fish inside a recently enlarged marine reserve. Aquatic Conservation: Marine and Freshwater Ecosystems 14 (2): 113-132.

Kruskal, J.B., Wish, M., 1978. Multidimensional Scaling. Sage Publications, Beverly Hills, California, 92 pp.

LaFrance, M., King, J.W., Oakley, B.A., and Pratt, S. 2014. A comparison of top-down and bottom-up approaches to benthic habitat mapping to inform offshore wind energy development. Continental Shelf Research 83: 24-44.

LaFrance, M., Shumchenia, E., King, J., Pockalny, R., Oakley, B., Pratt, S., Boothroyd, J., 2010. Benthic habitat distribution and subsurface geology at selected sites from the Rhode Island Ocean Special Area Management Study Area. Technical Report #4 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Langton, R.W., Auster, P.J., and Scheider, D.C. 1995. A spatial and temporal perspective on research and management of groundfish in the northwest Atlantic. Review in Fisheries Science 3 (3): 201-229

Latour, R.J, Brush, M.J., and Bonzek, C.F. 2003. Toward ecosystem-based fisheries management: strategies for multispecies modeling and associated data requirements. Fisheries 28 (9): 10-22.

Layman, C.A., Arrington, D.A., Montana, C.G., and Post, D.M. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88: 42–48.

Levins, R. 1968: Evolution in Changing Environments: Some Theoretical Explorations. Princeton, NJ: Princeton University Press.

Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Ecology, Evolution and Systematics 32: 51-93.

Lindeboom, H. J., Kouwenhoven, H. J., Bergman, M. J. N., Bouma, S., Brasseur, S., Daan, R., Fijn, R. C., de Haan, D., Dirksen, S., van Hal, R., Hille Ris Lambers, R., ter Hofstede, R., Krijgsveld, K.L., Leopold, M., Scheidat, M., 2011. Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. Environmental Research Letters 6, 035101.

Link, J.S., 2010. *Ecosystem-based Fisheries Management: Confronting Tradeoffs*. Cambridge University Press, New York, USA.

Link, J.S., and Auster, P.J. 2013. The challenges of evaluating competition among marine fishes: who cares, when does it matter, and what can one do about it? Bulletin of Marine Science 89 (1): 213-247.

Link, J.S., Bolles, K., and Milliken, C.G. 2000. The Feeding Ecology of Flatfish in the Northwest Atlantic. Journal of Northwest Atlantic Fisheries Science 30: 1-17.

Link, J.S. 2010. Ecosystem-Based Fisheries Management: Confronting Tradeoffs. Cambridge University Press, Cambridge, UK.

Logan, J., Haas, H., Deegan, L., and Gaines, E. 2006. Turnover rates of nitrogen stable isotopes in the salt marsh mummichog, *Fundulus heteroclitus*, following a laboratory diet switch. Oecologia 147 (3): 391-395.

Logan, J.M., and Lutcavage, M.E. 2010. Stable isotope dynamics in elasmobranch fishes. Hydrobiologia 644: 231-244.

Luckhurst B.E. & Luckhurst K. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Marine Biology 49: 317-323.

MacAvoy, S.E., Macko, S.A., and Garman, G.C. 2001. Isotopic turnover in aquatic predators: quantifying the exploitation of migratory prey. Canadian Journal of Fisheries and Aquatic Sciences 58 (5): 923-932.

MacKenzie, K.M., Palmer, M.R., Moore, A., Ibbotson, A.T., Beaumont, W.R., Poulter, D.J., and Trueman, C.N. 2011. Locations of marine animals revealed by carbon isotopes. Scientific reports 1: 21.

MacNeil, M.A., Drouillard, K.G., and Fisk, A.T. 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. Canadian Journal of Fisheries and Aquatic Sciences 63: 345-353.

Mahon, R., Brown, S. K., Zwanenburg, K. C., Atkinson, D. B., Buja, K. R., Claflin, L., Howell, G. D., Monaco, M.E., O'Boyle, R.N., Sinclair, M., 1998. Assemblages and biogeography of demersal fishes of the east coast of North America. Canadian Journal of Fisheries and Aquatic Sciences 55: 1704–1738.

Malek, A.J., Collie, J.S., and Gartland, J. 2014. Fine-Scale Spatial Patterns in the Demersal Fish and Invertebrate Community in a Northwest Atlantic Ecosystem. Estuarine, Coastal and Shelf Science 147: 1-10.

Malek, A.J., LaFrance, M., Collie, J., and King, J. 2010 Fisheries Ecology in Rhode Island and Block Island Sounds for the Rhode Island Ocean Special Areas Management Plan. Technical Report #19 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Marasco, R.J., Goodman, D., Grimes, C.B., Lawson, P.W., Punt, A.E., and Li, T.J.Q. 2007. Ecosystem-based fisheries management: some practical suggestions. Canadian Journal of Fisheries and Aquatic Sciences 64 (6): 928–939.

Matthews, B., and Mazumder, A. 2004. A critical evaluation of intrapopulation variation of delta13C and isotopic evidence of individual specialization. Oecologia 140 (2): 361–371.

Mayer, L.A. 2006. Frontiers in seafloor mapping and visualization. Marine Geophysical Research 27: 7-17.

McCutchan, J.H. Jr., Lewis, W.M., Kendall, C. and McGrath, C.C. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378– 390.

McKinney, R.A., Oczkowski, A.J., Prezioso, J., and Hyde, K.J.W. 2010. Spatial variability of nitrogen isotope ratios of particulate material from Northwest Atlantic continental shelf waters. Estuarine, Coastal and Shelf Science 89 (4): 287-293.

McLeod, K.L. and Leslie, H. (Eds.) 2009. *Ecosystem-based management for the oceans*. Island Press. Washington, DC, USA.

McLeod, K.L., Lubchenko, J., Palumbi, S.R.,Rosenberg, A.A., 2005. Scientific consensus statement on marine ecosystem-based management. Communication Partnership for Science and the Sea. Available: http://www.compassonline.org/.

McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J., Lean, D.R.S., 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59: 289–309.

Metcalf, S.J., Dambacher, J.M., Hobday, A.J., and Lyle, J.M. 2008. Importance of trophic information, simplification and aggregation error in ecosystem models. Marine Ecology Progress Series 360: 25-36.

Methratta, E., Link, J., 2006. Evaluation of quantitative indicators for marine fish communities. Ecological Indicators 6: 575–588.

Meyer, C.G., Holland, K.N., Wetherbee, B.M., and Lowe, C.G. 2000. Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. Environmental Biology of Fishes 59 (3): 235-242.

Miller, T. W. 2006. Tissue-specific response of δ15N in adult Pacific herring (*Clupea pallasi*) following an isotopic shift in diet. Environmental Biology of Fishes 76 (2-4): 177-189.

Misund, O.A., and Aglen, A. 1992. Swimming behaviour of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling. ICES Journal of Marine Science 49 (3): 325-334.

Munroe, S.E.M., Simpfendorfer, C.A., and Heupel, M.R. 2014. Defining shark ecological specialisation: concepts, context, and examples. Reviews in Fish Biology and Fisheries 24 (1): 317-331.

Moore, S., and Sowles, J. 2010. Local-Scale Ecosystem-Based Fisheries in a Gulf of Maine Estuary: Managing for Complexity, Adapting to Uncertainty. Marine and Coastal Fisheries 2 (1): 146–158.

Naidu, K.S. 1991. Sea scallop, *Placopecten magellanicus*. Pages 861–897 in S. E. Shumway, editor. Scallops: biology, ecology and aquaculture. Elsevier. Amsterdam.

NEFSC. 2008. Assessment of 19 Northeast groundfish stocks through 2007. Report of the 3rd Groundfish Assessment Review Meeting (GARM III), Northeast Fisheries Science Center, Woods Hole, Massachusetts. August 4-8, 2008. NEFSC Ref Doc. 08-15. 884 p.

Nixon, S. W., Fulweiler, R. W., Buckley, B. A., Granger, S. L., Nowicki, B. L., Henry, K. M., 2009. The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay. Estuarine, Coastal and Shelf Science 82: 1–18.

Nixon, S., Granger, S., Oviatt, O., Fields, L., Mercer, J., 2010. Spatial and temporal variability of surface chlorophyll, primary production, and benthic metabolism in Rhode Island and Block Island Sounds. Technical Report #9 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Novakowski, G.C., Hahn, N.S., and Fugi, R. 2008. Diet seasonality and food overlap of the fish assemblage in a pantanal pond. Neotropical Ichthyology 6 (4): 567-576.

Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series 393: 111-129.

Ostrom, N.E., Macko, S.A., Deibel, D., and Thompson, R.J. 1997. Seasonal variation in the stable carbon and nitrogen isotope biogeochemistry of a coastal cold ocean environment. Geochimica et Cosmochimica Acta 61 (14): 2929-2942.

Oviatt, C. A., 2004. The changing ecology of temperate coastal waters during a warming trend. Estuaries 27: 895–904.

Pauly, D., Chuenpagdee, R., 2007. Fisheries and coastal ecosystems: the need for integrated management in sustainable resource management. Edward Elgar Publishing, Surrey, UK, 14 pp.

Pasquaud, S., Elie, P., Jeantet, C., Billy, I., Martinez, P., and Girardin, M. 2008. A preliminary investigation of the fish food web in the Gironde estuary, France, using dietary and stable isotope analyses. Estuarine, Coastal and Shelf Science 78: 267-279.

Persohn, C., Lorance, P., Trenkel, V.M., 2009. Habitat preferences of selected demersal fish species in the Bay of Biscay and Celtic Sea, North-East Atlantic. Fisheries Oceanography 18: 268-285.

Peterson, B., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annual review of ecology and systematics 18: 293–320.

Peterson, C.H., Summerson, H.C., Thomson, E., Lenihan, H.S., Grabowski, J., Manning, L., Micheli, F., and Johnson, G. 2000. Synthesis of linkages between benthic and fish communities as a key to protecting essential fish habitat. Bulletin of Marine Science 66 (3): 759-774.

Pikitch, E., Santora, E.A., Babcock, A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heheman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., and Sainsbury, K. 2004. Ecosystem-based fishery management. Science 305: 346-347.

Planque, B., Loots, C., Petitgas, P., Lindstrøm, U., Vaz, S., 2011. Understanding what controls the spatial distribution of fish populations using a multi-model approach. Fisheries Oceanography 20: 1–17.

Platell, M.E., and Potter, I.C. 2001. Partitioning of food resources amongst 18 abundant benthic carnivorous fish species in marine waters on the lower west coast of Australia. Journal of Experimental Marine Biology and Ecology 261 (1): 31-54.

Post, D.M. 2002. Using stable isotopes to estimate trophic positions: Models, methods, and assumptions. Ecology 83: 703-718.

Power, M.E., Matthews, W.J. and Stewart, A.J. 1985. Grazing Minnows, Piscivorous Bass, and Stream Algae: Dynamics of a Strong Interaction. Ecology 66: 1448–1456.

Preston, T. and Owens, N.J.P. 1983. Interfacing an automatic elemental analyser with an isotope ratio mass spectrometer: the potential for fully automated total nitrogen and nitrogen-15 analysis. Analyst 108: 971–977.

Pruell, R.J., Taplin, B.K., Lake, J.L., and Jayaraman, S. 2006. Nitrogen isotope ratios in estuarine biota collected along a nutrient gradient in Narragansett Bay, Rhode Island, USA. Marine Pollution Bulletin 52 (6): 612–620.

Punt, M.J., Groeneveld, R. A., van Ierland, E. C., Stel, J. H., 2009. Spatial planning of offshore wind farms: A windfall to marine environmental protection? Ecological Economics 69: 93–103.

Reum, J.C., and Essington, T.E. 2008. Seasonal variation in guild structure of the Puget Sound demersal fish community. Estuaries and Coasts 31 (4): 790-801.

Rhode Island Special Area Management Plan (RI SAMP), 2010. Coastal Resources Management Council, Wakefield, Rhode Island.

Root, R.B. 1967. The niche exploration pattern of the blue-gray gnatcatcher. Ecological Monographs 37: 317–350.

Rosenberg, A., Bigford, T.E., Leathery, S., Hill, R.L., and Bickers, K. 2000. Ecosystem approaches to fishery management through essential fish habitat. Bulletin of Marine Science 66 (3): 535-542.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia: 352-388.

Salomon, A.K., Gaichas, S.K., Shears, N.T., Smith, J.E., Madin, E.M.P., Gaines, S.D., 2010. Key features and context-dependence of fishery-induced trophic cascades. Conservation Biology 24: 382-394.

Scharff, F.S., Juanes, F. and Rountree, R.A. 2000. Predator size-prey size relationships of marine fish predators: Interspecific variation and effects ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series 208: 229-248.

Schoener, T.W. 1970. Nonsynchronus spatial overlap of lizards in patchy habitats. Ecology 51: 408-418.

Scopel, D.A., Golet, W.J., Watson, W.H., 2009. Home range dynamics of the American lobster, *Homarus americanus*. Marine and Freshwater Behavior and Physiology 42: 63-80.

Simmonds, J., and MacLennan, D.N. 2008. *Fisheries Acoustics: Theory and Practice*. John Wiley & Sons.

Sisson, R.T. 1974. The growth and movement of scup (*Stenotomus chrysops*) in Narragansett Bay, RI and along the Atlantic coast. RI Division of Fish and Wildlife Completion Report.

Smith, B.E. 2009. *The effects of bottom fishing on the benthic macrofauna, demersal fishes, and fish feeding habits of George's Bank* (Master's thesis). University of Rhode Island, Graduate School of Oceanography. Narragansett, RI.

Smith, B., Collie, J.S., Lengyel, N.L., 2013. Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fish on northern Georges Bank. Marine Ecology Progress Series 472: 199-217.

Smith, B.E., Dayton, J., McElroy, D., Towle, E., and Mcbride, R.S. 2010. The Seasonal and Spatial Variability of Flatfish Feeding Habits on the Northeast US Continental Shelf: Preliminary Insights from Cooperative Research.

Smith, A.D.M., Fulton, E.A., Hobday, A.J., Smith, D.C., and Shoulder, P. 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. ICES Journal of Marine Science 64: 633–639.

Smith, B., and Link, J. 2010. The trophic dynamics of 50 finfish and 2 squid species of the Northeast US continental shelf. US Dept. of Commerce. NOAA Technical Memorandum NMFS-NE-216, 640 p.

Sonntag, N., Garthe, S., Adler, S., 2009. A freshwater species wintering in a brackish environment: Habitat selection and diet of Slavonian grebes in the southern Baltic Sea. Estuarine, Coastal and Shelf Science 84: 186-194.

Smythe, T., Beutel, D., 2010. Fisheries activity maps: methods and data sources. Technical Report #15 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, Rhode Island.

Stauffer, Gary (compiler). 2004. NOAA Protocols for Groundfish Bottom Trawl Surveys of the

Nation's Fishery Resources. U.S. Dep. Commerce, NOAA Tech. Memo. NMFS-F/SPO-65, 205 p.

Steimle, F. W. (1999). *Essential fish habitat source document: Scup,* Stenotomus chrysops*, life history and habitat characteristics*. DIANE Publishing.

Stein, R.A.1977. Selective predation, optimal foraging and the predator-prey interaction between fish and crayfish. Ecology 58: 1237-1253.

Steiner, W.W., Luczkovich, J.J., and Olla, B.L. 1982. Activity, Shelter Usage, Growth and Recruitment of Juvenile Red Hake *Urophycis chuss*. Marine Ecology Progress Series 7 (2): 125-135.

Szczebak, J.T., and Taylor, D.L. 2011. Ontogenetic patterns in bluefish (*Pomatomus saltatrix*) feeding ecology and the effect on mercury biomagnification. Environmental Toxicology and Chemistry 30 (6): 1447-1458.

Taylor, D.L., Kutil, N.J., Malek, A.J., and Collie, J.S. 2014. Mercury bioaccumulation in cartilaginous fishes from Southern New England coastal waters: Contamination from a trophic ecology and human health perspective. Marine Environmental Research 99: 20-33.

Terceiro M. 2012. Stock assessment of scup (*Stenotomus chrysops*) for 2012. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 12-25; 104 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026, or online at http://www.nefsc.noaa.gov/nefsc/publications/

Todd, B.J., and Greene, H.G. 2007. Mapping the seafloor for habitat characterization. Geological Association of Canada, Special Paper 47, 519 pp.

Trenkel, V.M., Huse, G., MacKenzie, B.R., Alvarez, P., Arrizabalaga, H., Castonguay, M., Goñie, N., Hátúng, H., Jansen, T., Jacobsen, J.A., Lehodey, P., Lutcavage, M., Mariani, P., Melvin, G.D., Neilson, J.D., Nøttestadb, L., Óskarssonk, G.J., Payned, M.R., Richardson, D.E., Seninah, I., and Speirs, D.C. 2014. Comparative ecology of widely distributed pelagic fish species in the North Atlantic: implications for modelling climate and fisheries impacts. Progress in Oceanography 129: 219-243.

Ullman, D.S., Codiga, D.L., 2010. Characterizing the physical oceanography of coastal waters off Rhode Island, Part 2: New observations of water properties, currents and waves. Technical Report #3 for the Rhode Island Ocean Special Area Management Plan. Coastal Resources Management Council, Wakefield, RI.

Vander, M.J., and Vadeboncoeur, Y. 2002. Fishes as Integrators of Benthic and Pelagic Food Webs in Lakes. Ecology 83 (8): 2152–2161.

Vander Zanden, M.J., and J.B. Rasmussen. 2001. Variation in δ15N and δ13C trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography 46: 2061-2066.

Vinagre, C., and Costa, M.J. 2014. Estuarine-coastal gradient in food web network structure and properties. Marine Ecology Progress Series 503: 11-21.

Warwick, R.M., 1984. Species size distributions in marine benthic communities. Oecologia 61: 32-41.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397

Williams, A., and Bax, N.J. 2001. Delineating fish-habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. Marine and Freshwater Research 52 (4): 513-536.

Wilson, J.B. 1999. Guilds, functional types and ecological groups. Oikos 86: 507-522.

Wisner, R. L. 1962. Midwater trawl surveys. Limnology and Oceanography 7 (suppl): xxxix-xli.

Witherell, D., Pautzke, C., and Fluharty, D. 2000. An ecosystem-based approach for Alaska groundfish fisheries. ICES Journal of Marine Science 57 (3): 771-77

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., Enquist, B. J., 2007. Relationships between body size and abundance in ecology. Trends in Ecology and Evolution 22: 323–330.

Woolnough, D.A., Downing, J.A., and Newton, T.J. 2009. Fish movement and habitat use depends on water body size and shape. Ecology of Freshwater Fish 18 (1): 83-91.

Wuenschel, M.J., Able, K.W., Byre, D., 2009. Seasonal patterns of winter flounder *Pseudopleuronectes americanus* abundance and reproductive condition on the New York Bight continental shelf. Journal of Fish Biology 74: 1508-1524.

Zamon, J.E. 2003. Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. Marine Ecology Progress Series 261: 243-255.