

Data Science Final–NECC Proposal

Nate Hermann

10 December, 2021

Contents

Executive Summary	1
Introduction	2
Methods	3
Discussion	4
References	7
Figures	9

Executive Summary

The western Atlantic is a productive environment with great social, ecological, and commerical value, but which is experiencing community-wide changes due to climate change. As the waters warm, faster than most global oceans, species adapt to novel conditions. One observed response is to relocate to cooler waters, primarily by shifting poleward or offshore. Due to multi-directional responses and species-specific rates of movement, there is a high potential for inter-specific interactions to change. Using the historical diet data collected by the National Marine Fisheries Service dating back to 1973, I propose to characterize the feeding behaviors, and their changes along with the drivers of change, in a selection of important, focal predators. In this document, I provide context for the proposed project along with an introduction to the data available and possible approaches. The included figures represent examples of important dietary metrics that will be used and provide a template for partitioning data into spatio-temporal groups to observe changes. The impetus for this work is the threat marine communities face due to climate change driven by anthropogenic activity. As such, the objective for this work is to provide an assessment of risk to a range of niches and behavioral responses. In doing so, I hope to inform the management, as these species have high commercial value, and conservation of marine fishes throughout the western Atlantic.

Introduction

The western Atlantic is a highly productive ecosystem with diverse environments. It holds very high economic value as well with commercial fisheries cumulatively generating \$1.3 billion in annual revenue (Fisheries 2021a, 2021b). However, while the region is a focal point for marine commerce, it is also a central location in the progressive climate change occurring around the world. The Gulf of Maine, the northern end of the Northwest Atlantic, is warming faster than 99.9% of the world's oceans (Pershing et al. 2015). The water body is fed primarily by cool Arctic waters, a region showing strong signals of climate change, that circulate in the deep basins, allowing them warm further. The Gulf of Maine is also linked to the south to the regions of the Georges Bank and Long Island Sound of Southern New England and the Mid-Atlantic Bight further south. These waters have historically been connected transiently, but have shown increasing homogenization in recent years (Langan et al. 2021).

As the Gulf of Maine circulating waters allow it to warm more quickly than its southern neighbors, the thermal conditions of this northern region have become more similar to past and present conditions of those areas (Lucey and Nye 2010). As such, recent decades have shown a rapid onset of species encroaching into the Gulf of Maine that had, historically, been seasonal visitors at most. New arrivals or expanding populations include those of the Atlantic blue crab (*Callinectes sapidus*), black sea bass (*Centropristes striata*; McMahan et al. (2020)), butterfish (*Peprilus triacanthus*), tautog (*Tautoga onitis*), and longfin squid (*Doryteuthis pealeii*) among many more. Similarly, species that have been historically abundant and important contributors to the Gulf of Maine ecosystem have shown appreciable declines due, at least in part, to climate change. These struggling species of the region include Atlantic cod (*Gadus morhua*; Alexander et al. (2009); Mieszkowska et al. (2009); Pershing et al. (2016)), Northern shrimp (*Pandalus borealis*; Richards and Hunter (2021)), Atlantic salmon (*Salmo salar*; Teichert et al. (2017)), with the collapse of American lobster (*Americanus homarus*) on the horizon in the eyes of many researchers (Le Bris et al. 2018; Pershing et al. 2021). The reason for these changes in species' abundance within the region is due to the widespread pattern of range shifts experienced by marine organisms.

Species, both in marine and terrestrial ecosystems, rely on habitable conditions that are specific to their needs. Due to progressive climate change, the conditions of a local area may become uninhabitable for a species or individual that previously were. This change can result in contractions of a population's range. However, as condition changes are global, it is probable that an area previously uninhabitable becomes habitable for that same species allowing an expansion of their range. These two components, a push and pull on a population's range, can happen simultaneously resulting in another shift in the areas used by a species. Work has shown that the expansion or leading edge of range shifts responds more quickly to climate change than does contraction or the lagging edge (Fredston-Hermann et al. 2020). While the general case, this directional shift in population ranges is species-specific (Fredston-Hermann et al. 2020) with species moving at different rates and even different directions (Chen et al. 2011; Pinsky et al. 2020). Even further, many species instead seek cooler water temperatures by deepening their distribution (Dulvy et al. 2008). This plurality of responses exists both around the globe as well as within a shared community (Pinsky et al. 2020); disconnecting previously interconnected communities that had been based on overlapping distributions of species. It is theorized that climate influences marine habitat suitability more strongly at the cold, leading edge whereas biotic interactions dominate at warmer, trailing edges (Fredston-Hermann et al. 2020). These two components of species range may, additionally, interact to produce a 'double whammy' for marine populations.

Fish, like many marine organisms, are poikilothermic meaning their body temperatures are able to range widely, pre-dominantly due to changes in their environmental temperature. Due to this substantial influence of climate conditions on the internal conditions of the individual, the physiology of fishes can range widely. Though non-linear and species-specific (Clarke and Johnston 1999; Clark et al. 2013), a universally positive interaction of temperature and metabolic demand exists for fish. Therefore, with the rising temperatures fish experience, they are expected to increase their metabolism. Such increases require additional forage to maintain consistent individual growth and broader population biomass, though adaptations exist to reduce this pressure (Auer et al. 2015). However, forage may also be struggling to maintain biomass with increased metabolisms, declining in energy density, or shifting to new locations that are less accessible for a predator. Therefore, as a global phenomenon climate change can influence predators both directly—by physiological

demands of the species—and indirectly—by similarly impacting lower trophic levels. As such, predators are expected and shown to feel greater threats due to climate change than species lower in trophic level and/or with shorter generation times (Thackeray et al. 2010).

As marine communities are subject to a variety of changes with complex interactions, there is potential for changes in diets of the fish predators within these communities. My objective is to conduct retrospective analyses on the diets of important predators that represent a variety of taxa and showcasing a range spatial responses. Using historical diet contents from these predators across a broad spatial area allows spatio-temporal analyses to characterize the magnitude and direction of foraging changes. Defining the patterns in dietary shifts can provide additional metrics—beyond reproductive, mobility, and habitat traits previously employed (Hare et al. 2016)—to characterize the vulnerability of niches or taxa to climate change. Ultimately, informing fishers and managers about how community-wide dietary changes impact the vulnerability of those large predatory fishes that are commonly harvested can aid in their conservation and help to stabilize the community in the future.

Methods

Diet contents for species were collected by the National Marine Fisheries Service Annual Spring-Fall Bottom Trawl Survey. The survey has been conducted throughout the western Atlantic each spring (March-June) and fall (September-November) since 1968, with targeted species being subset to collect and analyze diets starting in 1973. The geographic extent of the survey is from Cape Hatteras, NC to the Bay of Fundy, Nova Scotia offshore to the continental shelf (Figure 1). The survey follows a stratified sampling design, with trawl locations being binned by the statistical areas (Figure 1). Due to the sampling of captured fish at trawl sampling locations, a two-stage clustering design was used to evaluating means and variances in statistical groups, such as by region or time period.

The number of diets is highly variable across species over time (Figure 2). Variation is a reflection of a variety of interacting elements: abundance and accessibility together represent the actual capture rate of the species, trawling effort and diet collection quotas together represent procedural elements. Quotas were defined as the number of individual diets that should be collected from each trawl binned to different fish length intervals, e.g., 1 diet per 10 cm. Diets collected were then either analyzed in the lab in all cases before 1981 or but only 2 cases after 1981, the rest being collected and analyzed at sea (Link and Almeida 2020).

Diet contents for an individual were first analyzed together with either the total weight or volume being recorded, with the other being calculated by a 1.1:1 ratio (Link and Almeida 2020). Empty diets were recorded accordingly. The individual components of occupied diets were identified to the greatest resolution possible by visual inspection. A total of 964 unique prey items were identified. To simplify analyses, distinct prey were grouped at varying levels of specificity: **General** represents the coarsest resolution often at the phylum or class of identifiable items, **Analytical** represents mid-level resolution grouping generally at order or family, and **Collection** represents the lowest resolution and is often the genus or species. Fish were categorized with more specificity than invertebrates. A fourth method of grouping is included that is a functional blend of other categories utilized by Garrison and Link (2000a) in defining feeding guilds for the entire community. Namely, common prey fish species combined with broad categories of invertebrates. The number of distinct prey categories named in each level of grouping is shown in Figure 3.

Data Summaries

To initiate the exploration of dietary structure changes in time and space, it is first important to characterize species diets through a variety of metrics. These metrics may rely on a significant number of diets to be calculated accurately, but can otherwise be calculated for subsets across regions, seasons, and years for each of the species. The simplest method of assessing diet is to compare the size of the diet, either by the volume or mass. When using the mass, it is common that such a value is made relative to the mass of the fish to better compare the magnitude of feeding. Related to feeding magnitude, the mere presence of stomach contents can help to approximate the frequency of feeding. As such, the proportion of stomachs

found empty can be used in characterizing foraging strategies and success. The second metric commonly used to characterize a fish diet is to calculate an index of diversity, such as Levin's Breadth. The formula for Levin's breadth is:

$$B_a = \frac{\sum \frac{1}{p_j^2} - 1}{n - 1}$$

where p_j is the proportion of the diet represented by diet item j , and n is the total number of diet items to standardize the breadth measures between 0-1. A third metric for diets reflects the sizes of prey items, both by relating prey size to predator size and evaluating the distributions of relative prey size. Beyond a simple linear regression of the mean prey length against predator length, a regression for the 5th and 95th prey length percentiles can reveal the scope of prey size at different predator sizes (Scharf et al. 2000). Relative prey size indicates what type of prey a species may select beyond prey identification; such as only feeding on items much smaller than oneself, taking primarily large prey near ones own size, or showing no preference for prey size. These patterns can be summarized by calculating skewness of the relative prey size distributions where higher skew represents higher selectivity. Finally, predators can be compared to each other and intra-specifically by calculating dietary overlap. Again, a variety of indices exist for calculating overlap, but one popularly used due to its simplicity is Schoener's Overlap (Schoener 1970) calculated as:

$$S_a = 1 - 0.5 * \sum |p_{1,j} - p_{2,j}|$$

where p_1 and p_2 represent the proportions of the j th diet item in predators 1 and 2, respectively. A matrix of overlap comparisons across all relevant groups can be constructed, then clustering is used to partition out similar groups.

Discussion

A total of 265698 diets were collected from the focal predators between 1973-2019. These diets provide considerable insight into the foraging ecology of these predators both in comparison to each other and intra-specific differences on spatial and temporal scales.

Across all species, the range of relative consumption values was 0.000003-0.61, with the median being 0.008. All species showed heavy skew towards small diets, but the hakes (*Urophycis tenuis*, *Merluccius bilinearis*, and *Urophycis chuss*) showed the highest medians (Figure 4). Every species exceeded 10% body mass at least sometimes, but Silver and White Hake exceeded 10% more than 6% of the time (Figure 4). This is a relevant point in relative consumption as this level of consumption is rarely achieved and widely considered a conservative understanding of binge-feeding (Essington et al. 2000; Green et al. 2011; Armstrong et al. 2013; Furey et al. 2016; Hermann et al. 2020). A true definition of this metabolic standard requires closer observations of digestion rates that is species-specific and environmentally dependent. Closer work on the geographic location and trawl-recorded water temperatures of possible binge-feeding instances can help to refine these definitions. Larger predators are also considered more prone to binge-feeding due to relatively lower metabolisms than larval and juvenile fishes (Furey et al. 2016; Deslauriers et al. 2017). As my focal predators are all large-bodied and the bottom trawl survey favors capture of large adults, the prevalence of binge-feeding observed here may be reasonable though high. Ultimately, without additional work on the physiology of species, no definitive classification can be made on the status of this feeding behavior.

As an exhibition of the influence geographic region can have, patterns in diet presence were broken apart by both species and region (Figure 5). The frequency of empty stomachs can be roughly reflective of true foraging heterogeneity which is common across fishes (Arrington et al. 2002; Armstrong and Schindler 2011). Consistent with a broader review, inter-species diversity in niches contributed more variation to feeding frequency than geographic region [Figure 5; Arrington et al. (2002)]. Though piscivores have been seen to have empty stomachs more often than other predators due to the size and patchy distribution of their prey (Arrington et al. 2002), there does not appear to be a direct link between the proportion of empty stomachs

and median relative consumption. Continued efforts may make these populations more comparable in time and space, but spatial impacts were minor compared to species. It does appear, however, that a response toward less frequent emptiness occurred in more northern regions such as the Gulf of Maine and Scotian Shelf (Figure 5), consistent with theoretical understanding of fish feeding (Clarke and Johnston 1999; Godby et al. 2007). The cooler waters of these regions can slow fish metabolisms leading to slower digestion simultaneously increasing the probability of having stomach contents even with the same frequency of feeding and reducing the demand for foraging. Patterns observed for species foraging are likely to reflect their preferred prey, with those seeking large prey being expected to feed at higher levels, less frequently. Additionally, the degree of specialization by a predator may influence the frequency of feeding as the opportunity for feeding may be less common among specialists than for those willing and able to consuming “anything.”

To address the possibility of this link between feeding behavior and specialization, an index of diversity was used to calculate breadth. The metric of Levin’s breadth was used here and resulted in breadths between 0.04 and 0.22. In line with proportions empty, the most broad diets corresponded to the least empty stomachs, namely Haddock, Little Skate, and Red Hake that were the only species to exceed 0.2 (Figure 6). This general observation should be further assessed consistently across seasons as not all species showed the same diet breadth in Spring and Fall, most notably Haddock that showed a difference of 0.07 between the two seasons. Dietary specialization need not be restricted to just prey type, but characteristics of the prey may also contribute to predator preferences. One important feature of prey that predators may select for is prey size.

Predators may exhibit selectivity toward particular prey sizes for many reasons. Larger prey will be more nutritious, often not just absolutely but also relatively (Hartman and Brandt 1995), but are typically less difficult to find and consume due to lower availability and higher mobility. Additionally, as most fish predators consume prey whole, they may be gape-limited even as they grow longer. Due to these trade-offs to prey quality, the relationship of predators to their prey sizes may be species influenced. Previous work has shown that predators increase their consumption of larger prey as they grow, but they continue to consume small prey (Scharf et al. 2000). Mimicking the procedure from this work, I again see all predators increasing their average prey size as they grow larger, but the rate of increase in the smallest prey is lower (Figure 7a). The mean rate of increase varies between species, suggesting some species may be less likely to incorporate larger prey as they grow. This is assessed more directly by calculating the ratio of prey to predator length and assessing their distributions (Figure 7b). Across all species, the widespread consumption of small prey items is shown by the skew toward low ratios. Though consistently skewed towards small prey, the strength of skew varies greatly, from 0.1343 for Silver Hake to 3.1944 for Little Skate. Higher skew indicates higher size selectivity, but interestingly those most selective predators by size were the most generalist by prey type (Figure 7b). This shows that there are multiple ways to be a diverse predator, size and type being just two of many. Even further, even predators that look very similar by simple metrics may actually be very different if they feed on very different things. For example, two predators may each consume 10 different small prey items in the same proportions, but one could be consuming fish and the other invertebrates showing very little similarity in diet. To address this possibility, the species need to be directly compared.

Unlike comparing independently calculated species metrics, dietary overlap is a direct measure of how similar two predators are to each other. Though Schoener’s overlap is calculated pairwise, the complete matrix of values that exist for a community can serve to summarize the community structure as the level of competition or total overlap. The mean overlap from the focal predators was 0.39 which is more than the complete northwestern Atlantic community and in line with other small communities (Garrison and Link 2000a). The highest overlap between two species was 0.7 between Pollock and Silver Hake (Figure 8). The lowest overlap between two species was 0.13 between White Hake and Yellowtail Flounder. Though the full extent of feeding guilds is not represented by these focal species (Garrison and Link 2000a), they span most of the dietary breadth of the northwestern Atlantic and could be representative of the types of changes particular foragers might experience with climate change, e.g., formerly piscivorous fishes are having to incorporate more benthic prey into their diets. Though these analyses require more samples to consistently calculate clusters, breaking out species over time can work to track these possible shifts in guilds, though they may be rare (Garrison and Link 2000b). Beyond the high level of similarity these focal predators share in their diets, they are also interconnected through consumption on each other.

Though these species represent generally large predators, they are still consumed by each other. Each of the focal predators consumed at least one of the other predators in this study, but Little Skate was never consumed by these predators (Figure 9). The most consumed of the species for all predators was Silver Hake, even by Silver Hake cannibals (Figure 9). The average proportion of the diets consisting of the focal predators was just 0.01, of which 82.6% was due to Silver Hake.

References

- Alexander, K.E., Leavenworth, W.B., Cournane, J., Cooper, A.B., Claesson, S., Brennan, S., Smith, G., Rains, L., Magness, K., Dunn, R., Law, T.K., Gee, R., Bolster, W.J., and Rosenberg, A.A. 2009. Gulf of maine cod in 1861: Historical analysis of fishery logbooks, with ecosystem implications. *Fish and Fisheries* **10**(4): 428–449. doi:10.1111/j.1467-2979.2009.00334.x.
- Armstrong, J.B., and Schindler, D.E. 2011. Excess digestive capacity in predators reflects a life of feast and famine. *Nature* **476**: 84–88. doi:10.1038/nature10240.
- Armstrong, J.B., Schindler, D.E., Ruff, C.P., Brooks, G.T., Bentley, K.E., and Torgersen, C.E. 2013. Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology* **94**(9): 2066–2075. doi:10.1890/12-1200.1.
- Arrington, D.A., Winemiller, K.O., Loftus, W.F., and Akin, S. 2002. How often do fishes "run on empty"? *Ecology* **83**(8): 2145–2151. doi:10.2307/3072046.
- Auer, S.K., Salin, K., Rudolf, A.M., Anderson, G.J., and Metcalfe, N.B. 2015. Flexibility in metabolic rate confers a growth advantage under changing food availability. *Journal of Animal Ecology* **84**(5): 1405–1411. doi:10.1111/1365-2656.12384.
- Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., and Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**(6045): 1024–1026. doi:10.1126/science.1206432.
- Clark, T.D., Sandblom, E., and Jutfelt, F. 2013. Aerobic scope measurements of fishes in an era of climate change: Respirometry, relevance and recommendations. *Journal of Experimental Biology* **216**(15): 2771–2782. doi:10.1242/jeb.084251.
- Clarke, A., and Johnston, N.M. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology* **68**(5): 893–905. doi:https://doi.org/10.1046/j.1365-2656.1999.00337.x.
- Deslauriers, D., Chipps, S.R., Breck, J.E., Rice, J.A., and Madenjian, C.P. 2017. Fish bioenergetics 4.0: An r-based modeling application. *Fisheries* **42**(11): 586–596. doi:10.1080/03632415.2017.1377558.
- Dulvy, N.K., Rogers, S.I., Jennings, S., Stelzenmüller, V., Dye, S.R., and Skjoldal, H.R. 2008. Climate change and deepening of the north sea fish assemblage: A biotic indicator of warming seas. *Journal of Applied Ecology* **45**(4): 1029–1039. doi:10.1111/j.1365-2664.2008.01488.x.
- Essington, T.E., Hodgson, J.R., and Kitchell, J.F. 2000. Role of satiation in the functional response of a piscivore, largemouth bass (*micropterus salmoides*). *57*: 9.
- Fisheries, N. 2021a. 2021 state of the ecosystem: Mid-atlantic.
- Fisheries, N. 2021b. 2021 state of the ecosystem: New england.
- Fredston-Hermann, A., Selden, R., Pinsky, M., Gaines, S.D., and Halpern, B.S. 2020. Cold range edges of marine fishes track climate change better than warm edges. *Global Change Biology* **26**(5): 2908–2922. doi:10.1111/gcb.15035.
- Furey, N.B., Hinch, S.G., Mesa, M.G., and Beauchamp, D.A. 2016. Piscivorous fish exhibit temperature-influenced binge feeding during an annual prey pulse. *The Journal of animal ecology* **85**(5): 1307–1317. doi:10.1111/1365-2656.12565.
- Garrison, L.P., and Link, J. 2000a. Dietary guild structure of the fish community in the northeast united states continental shelf ecosystem. *Mar. Ecol. Prog. Ser.* **202**: 231–240. doi:10.3354/meps202231.
- Garrison, L.P., and Link, J.S. 2000b. Fishing effects on spatial distribution and trophic guild structure of the fish community in the georges bank region. *ICES Journal of Marine Science* **57**(3): 723–730. doi:10.1006/jmsc.2000.0713.
- Godby, N.A., Rutherford, E.S., and Mason, D.M. 2007. Diet, feeding rate, growth, mortality, and production of juvenile steelhead in a lake michigan tributary. *North American Journal of Fisheries Management* **27**(2): 578–592. doi:10.1577/m06-077.1.
- Green, S., Akins, J., and Côté, I. 2011. Foraging behaviour and prey consumption in the indo-pacific lionfish on bahamian coral reefs. *Mar. Ecol. Prog. Ser.* **433**: 159–167. doi:10.3354/meps09208.
- Hare, J.A., Morrison, W.E., Nelson, M.W., Stachura, M.M., Teeters, E.J., Griffis, R.B., Alexander, M.A., Scott, J.D., Alade, L., Bell, R.J., Chute, A.S., Curti, K.L., Curtis, T.H., Kircheis, D., Kocik, J.F., Lucey, S.M., McCandless, C.T., Milke, L.M., Richardson, D.E., Robillard, E., Walsh, H.J., McManus, M.C., Marancik, K.E., and Griswold, C.A. 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast u.s. Continental shelf. *PLoS ONE* **11**(2): e0146756. doi:10.1371/journal.pone.0146756.

- Hartman, K.J., and Brandt, S.B. 1995. Estimating energy density of fish. *Transactions of the American Fisheries Society* **124**(3): 347–355. doi:10.1577/1548-8659(1995)124<0347:EEDOF>2.3.CO;2.
- Hermann, N.T., Chaloner, D.T., Gerig, B.S., and Lamberti, G.A. 2020. Ecological consequences of great lakes salmon subsidies for stream-resident brook and brown trout. *Can. J. Fish. Aquat. Sci.* **77**(11): 1758–1771. doi:10.1139/cjfas-2020-0086.
- Langan, J., Puggioni, G., Oviatt, C., Henderson, M., and Collie, J. 2021. Climate alters the migration phenology of coastal marine species. *Mar. Ecol. Prog. Ser.* **660**: 1–18. doi:10.3354/meps13612.
- Le Bris, A., Mills, K.E., Wahle, R.A., Chen, Y., Alexander, M.A., Allyn, A.J., Schuetz, J.G., Scott, J.D., and Pershing, A.J. 2018. Climate vulnerability and resilience in the most valuable north american fishery. *Proceedings of the National Academy of Sciences of the United States of America* **115**(8): 1831–1836. doi:10.1073/pnas.1711122115.
- Link, J.S., and Almeida, F.P. 2020. An overview and history of the food web dynamics program of the northeast fisheries science center, woods hole, massachusetts. : 64.
- Lucey, S., and Nye, J. 2010. Shifting species assemblages in the northeast US continental shelf large marine ecosystem. *Mar. Ecol. Prog. Ser.* **415**: 23–33. doi:10.3354/meps08743.
- McMahan, M.D., Sherwood, G.D., and Grabowski, J.H. 2020. Geographic variation in life-history traits of black sea bass (*centropristes striata*) during a rapid range expansion. *Front. Mar. Sci.* **7**: 567758. doi:10.3389/fmars.2020.567758.
- Mieszkowska, N., Genner, M.J., Hawkins, S.J., and Sims, D.W. 2009. Chapter 3 effects of climate change and commercial fishing on atlantic cod *gadus morhua*. In *Advances in marine biology*. Elsevier. pp. 213–273. doi:10.1016/S0065-2881(09)56003-8.
- Pershing, A.J., Alexander, M.A., Brady, D.C., Brickman, D., Curchitser, E.N., Diamond, A.W., McClenachan, L., Mills, K.E., Nichols, O.C., Pendleton, D.E., Record, N.R., Scott, J.D., Staudinger, M.D., and Yanjun Wang. 2021. Climate impacts on the gulf of maine ecosystem: A review of observed and expected changes in 2050 from rising temperatures. *Elementa: Science of the Anthropocene* **9**: 1–18. doi:10.1525/elementa.2020.00076.
- Pershing, A.J., Alexander, M.A., Hernandez, C.M., Kerr, L.A., Bris, A.L., Mills, K.E., Nye, J.A., Record, N.R., Scannell, H.A., Scott, J.D., Sherwood, G.D., and Thomas, A.C. 2016. Response to comments on "slow adaptation in the face of rapid warming leads to collapse of the gulf of maine cod fishery. *Science* **352**(6284): 423–423. doi:10.1126/science.aae0463.
- Pershing, A.J., Mills, K.E., Record, N.R., Stamieszkin, K., Wurtzell, K.V., Byron, C.J., Fitzpatrick, D., Golet, W.J., and Koob, E. 2015. Evaluating trophic cascades as drivers of regime shifts in different ocean ecosystems. *Phil. Trans. R. Soc. B* **370**(1659): 20130265. doi:10.1098/rstb.2013.0265.
- Pinsky, M.L., Selden, R.L., and Kitchel, Z.J. 2020. Climate-driven shifts in marine species ranges: Scaling from organisms to communities. *Annu. Rev. Mar. Sci.* **12**(1): 153–179. doi:10.1146/annurev-marine-010419-010916.
- Richards, R.A., and Hunter, M. 2021. Northern shrimp *pandalus borealis* population collapse linked to climate-driven shifts in predator distribution. *PLoS ONE* **16**(7): e0253914. doi:10.1371/journal.pone.0253914.
- Scharf, F., Juanes, F., and Rountree, R. 2000. Predator size-prey size relationships of marine fish predators: Interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.* **208**: 229–248. doi:10.3354/meps208229.
- Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* **51**(3): 408–418. doi:10.2307/1935376.
- Teichert, M.A.K., Foldvik, A., Einum, S., Finstad, A.G., Forseth, T., and Ugedal, O. 2017. Interactions between local population density and limited habitat resources determine movements of juvenile atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **74**(12): 2153–2160. doi:10.1139/cjfas-2016-0047.
- Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J., and Wanless, S. 2010. Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* **16**(12): 3304–3313. doi:10.1111/j.1365-2486.2010.02165.x.

Figures

Figure 1

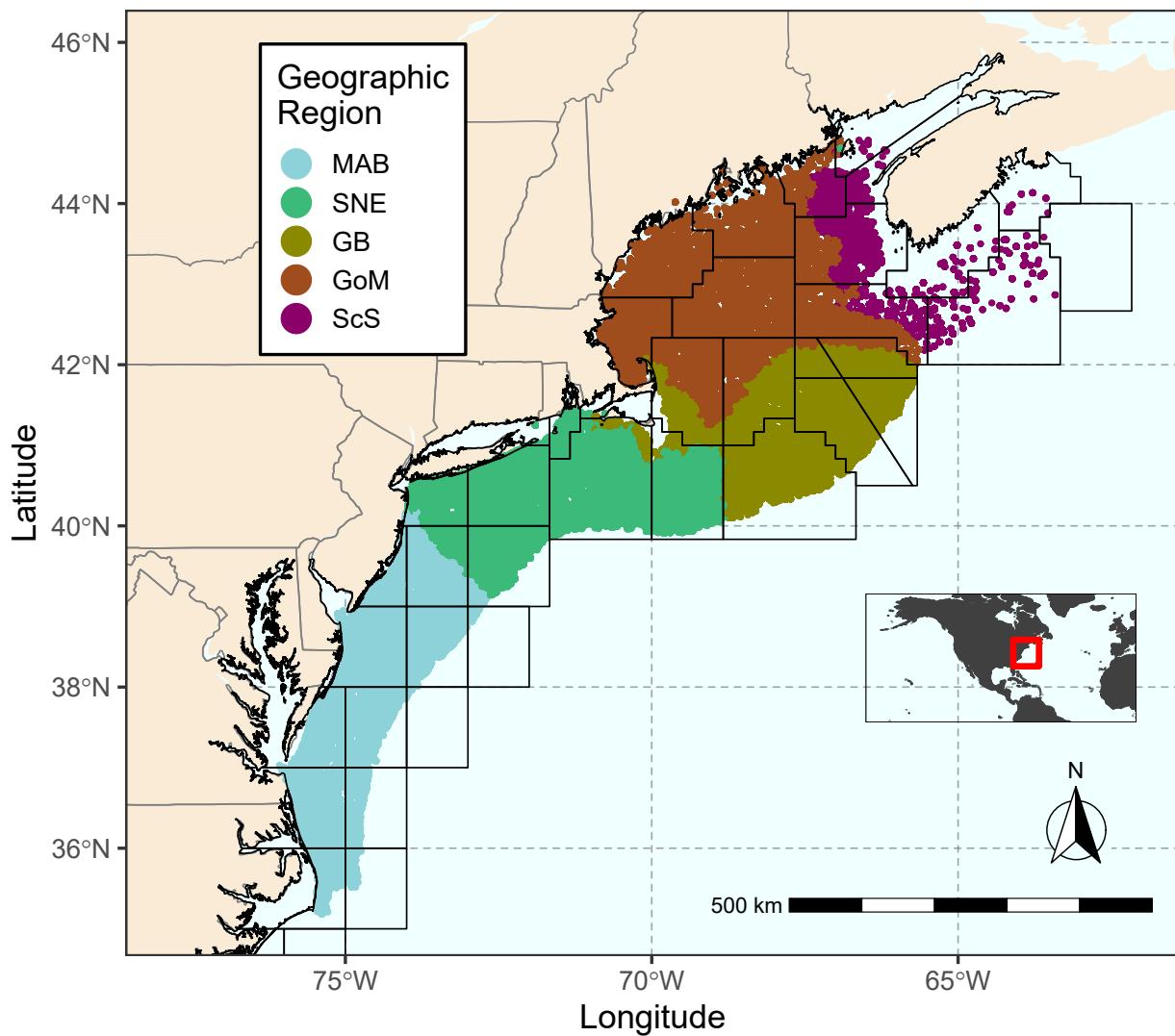


Figure 1: Map of the starting points for all trawls from across all years and dates from the Annual Spring-Fall Bottom Trawl Survey. Point colors correspond to broad geographic regions: the Mid-Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB), Gulf of Maine (GoM), and Scotian Shelf (ScS). Black outlines show the NMFS Statistical areas used to stratify sampling.

Figure 2

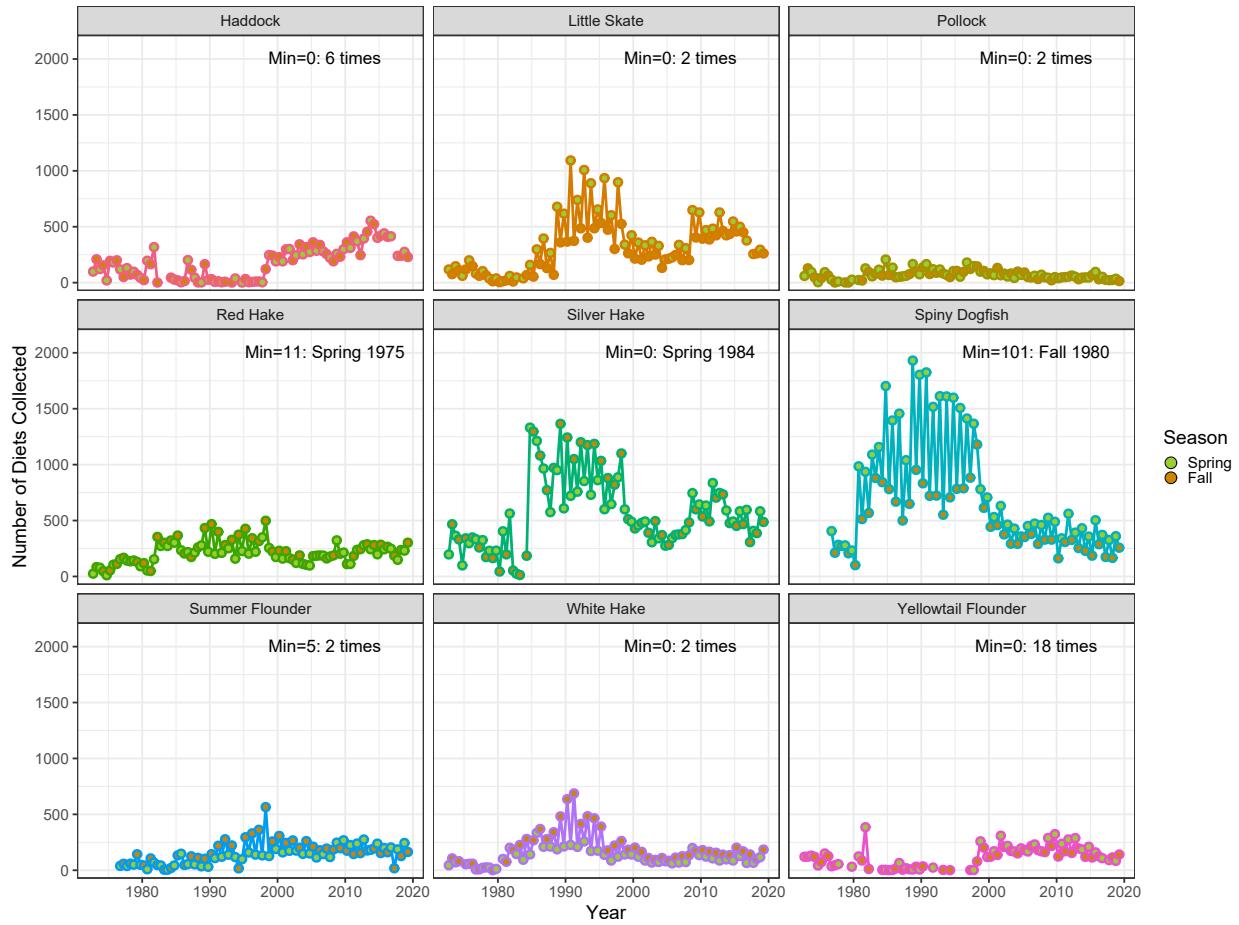


Figure 2: Number of diets for each focal predator species collected by the National Marine Fisheries Service from the Annual Spring-Fall Bottom Trawl Survey. Diet collection began in 1973, though not for all species. Once a species was included for collection it was included in all years. Variability between predators and over time represent availability as well as research prioritization, both of which have varied over time. The minimum number of diets collected by a season of trawls is noted in each panel, along with the season in which it occurred. If the minimum number of diets for a species occurred in multiple seasons, the number of seasons is listed instead. When zero diets were collected in a season, no point is included and a break in the line is added.

Figure 3

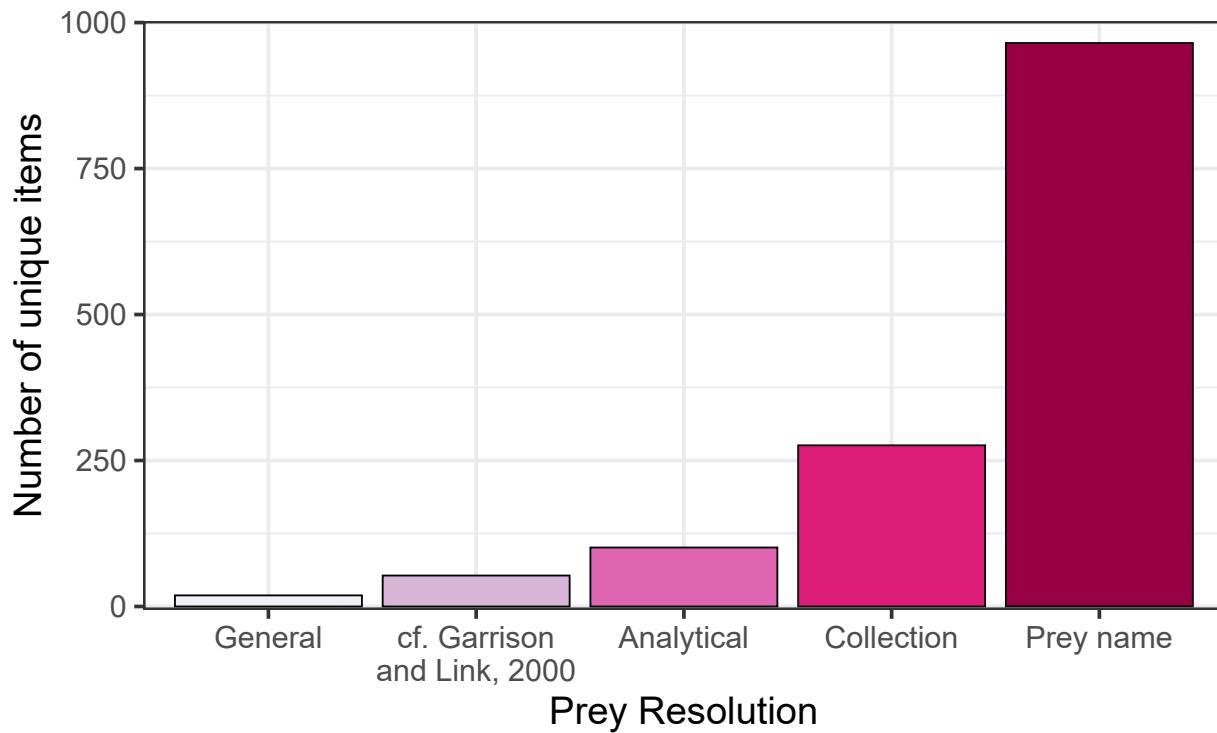


Figure 3: Number of unique prey items named at each level of resolution within the NOAA Food Habits Database. General, Analytical, and Collection resolution refer to those provided by the National Marine Fisheries Service at roughly phylum and class, order and family, and genus and species, respectively; Prey name is the most specific a visual observer could identify an item to; and cf. Garrison and Link, 2000 refers to that grouping used in their feeding guild analyses.

Figure 4

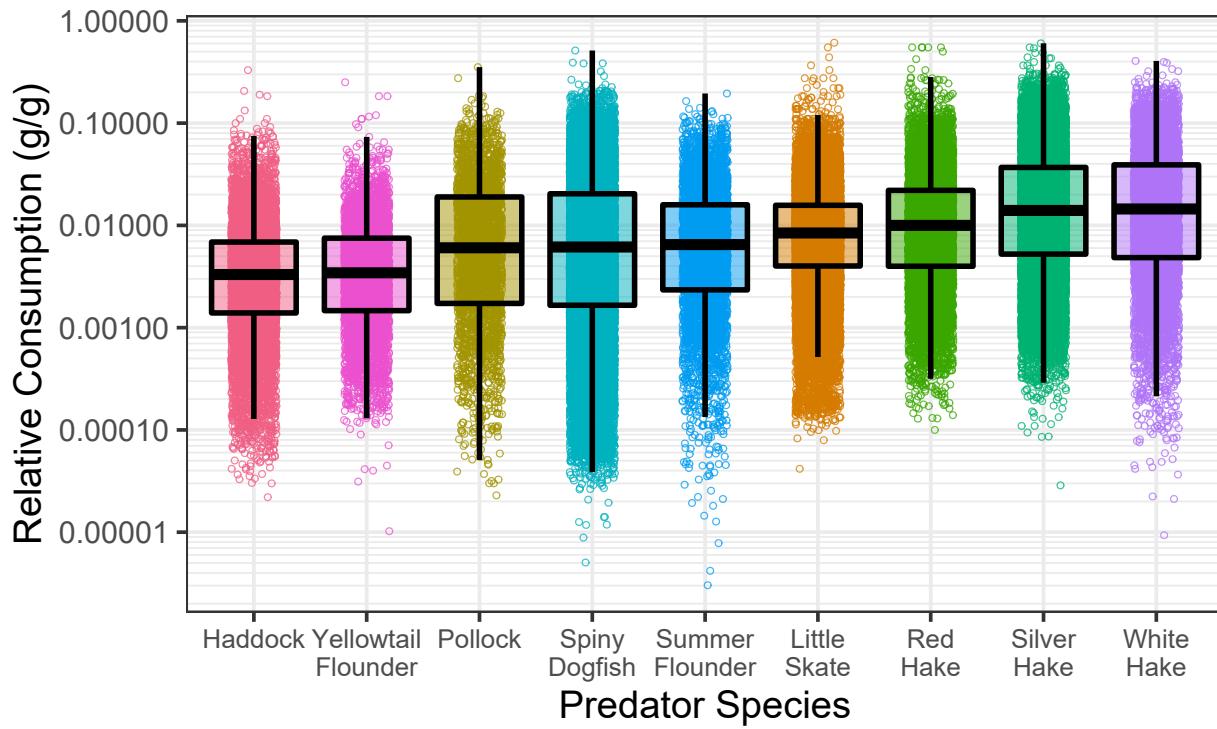


Figure 4: Relative consumption, that is the mass of the total diet divided by the mass of the fish, for each of the focal predators. All empty diets were removed. Note the log-scale for the y-axis.

Figure 5

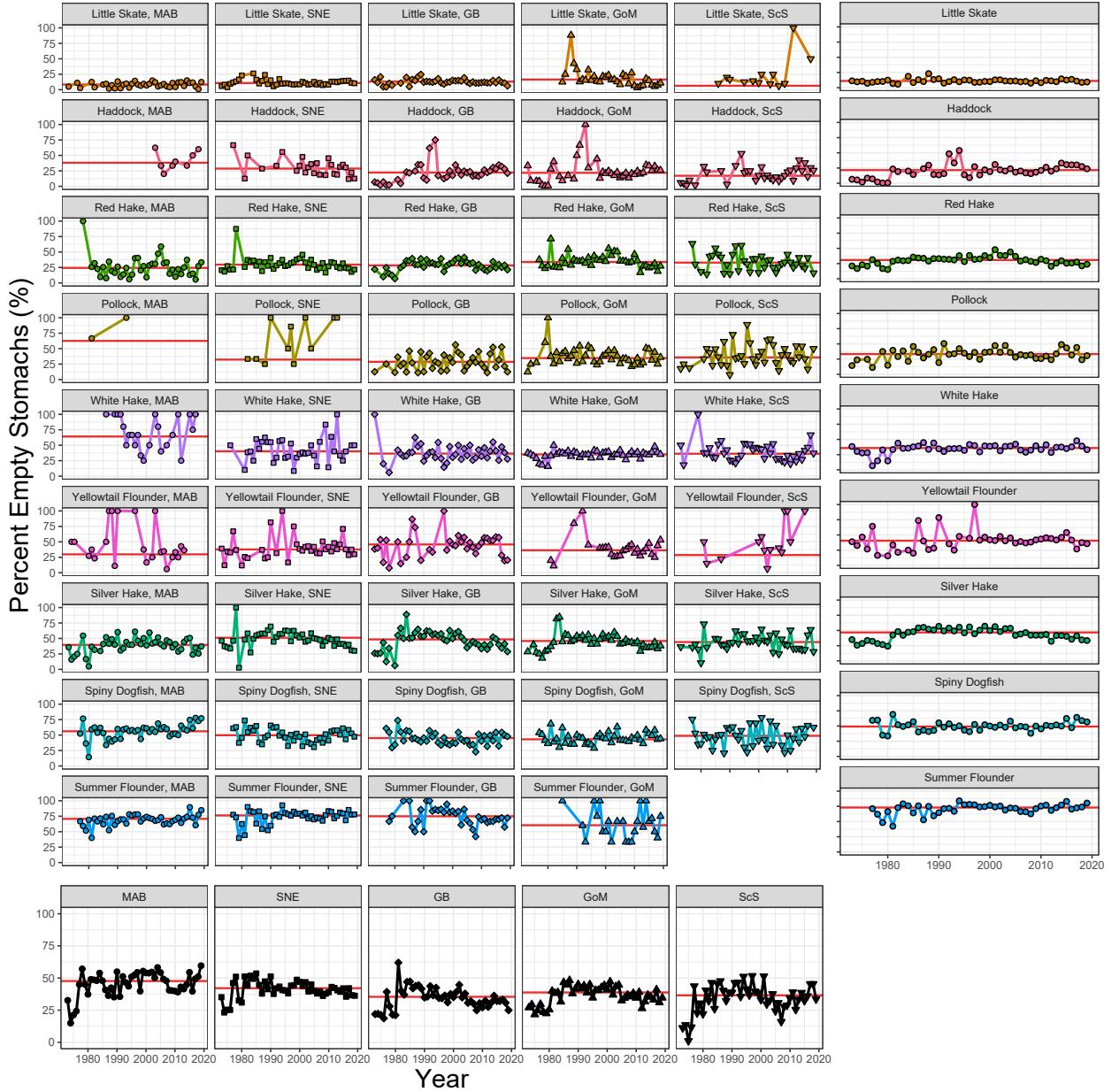


Figure 5: Percentage of stomachs that are empty over time for each of the predator species in each of the geographic regions. The rightmost column represents the cumulative across regions for each species. The bottom row represents the cumulative across species for each region. Horizontal red lines in each panel show the mean across all years for that subset of diets. Regions are ordered by increasing latitude from left to right, species are ordered by increasing percentage of empty stomachs from top to bottom.

Figure 6

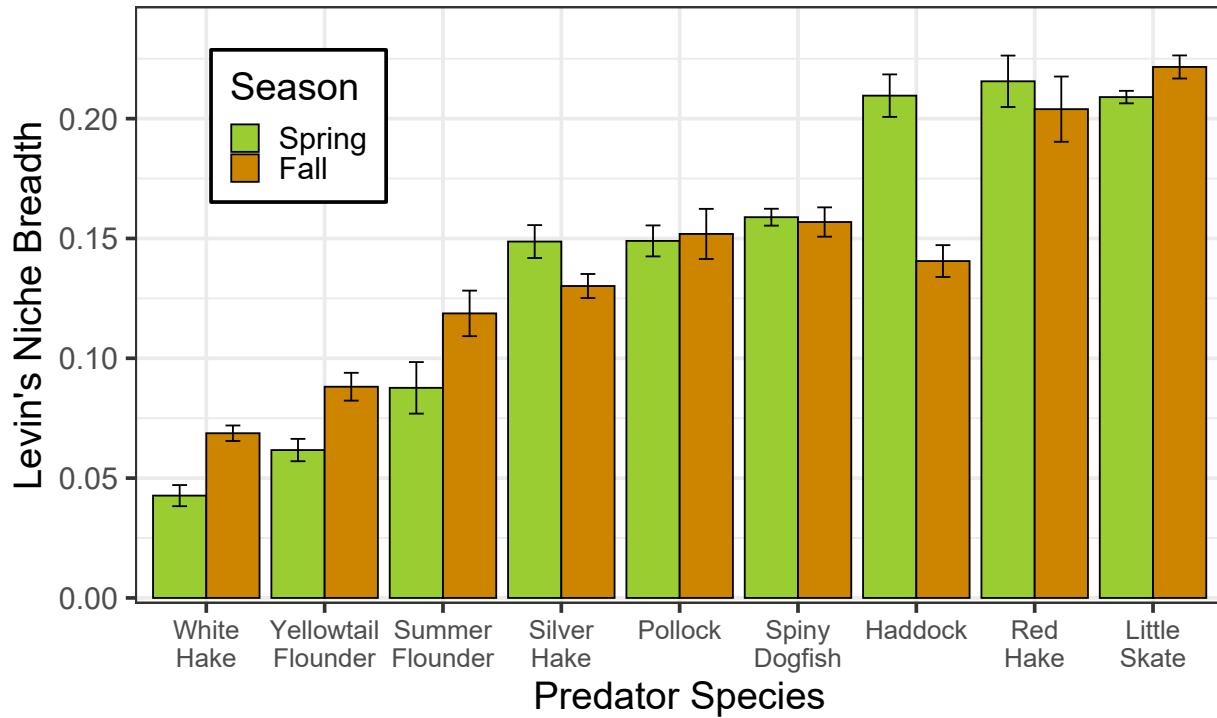


Figure 6: Mean Levin's Niche Breadth for each focal predator in the two major seasons collected, spring (green) and fall (orange). Errorbars represent standard deviation as calculated from 100 bootstrap resamples. Higher values for Levin's Niche Breadth, ranging from 0-1, indicate more diverse diets. Species are ordered left to right by increasing breadth.

Figure 7

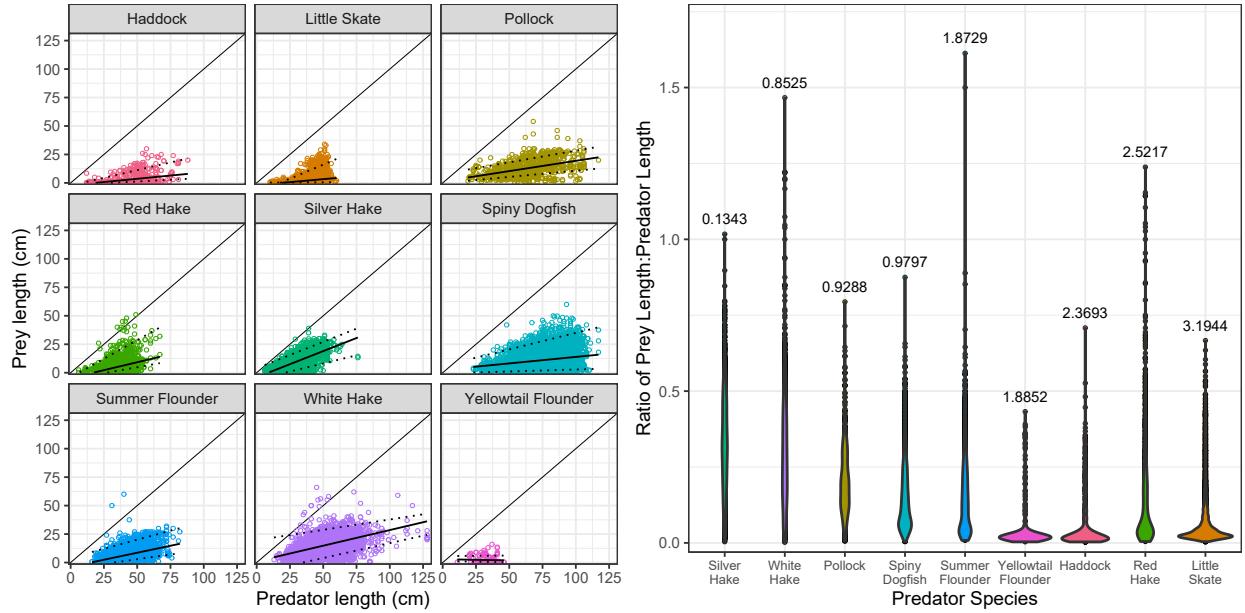


Figure 7: Relationship of the sizes of predators to the sizes of their prey. (Left) Prey sizes tend to increase with predator size on average (solid line), though the range of prey consumed often increases as well shown by higher slopes at the 95th than 5th percentile (dashed lines). (Right) The ratio of prey length to predator length is generally less than 0.5, though skewness scores listed for each species, and increasing left to right, show differing levels of size selectivity by predators. Higher skew indicates greater selectivity for prey size.

Figure 8

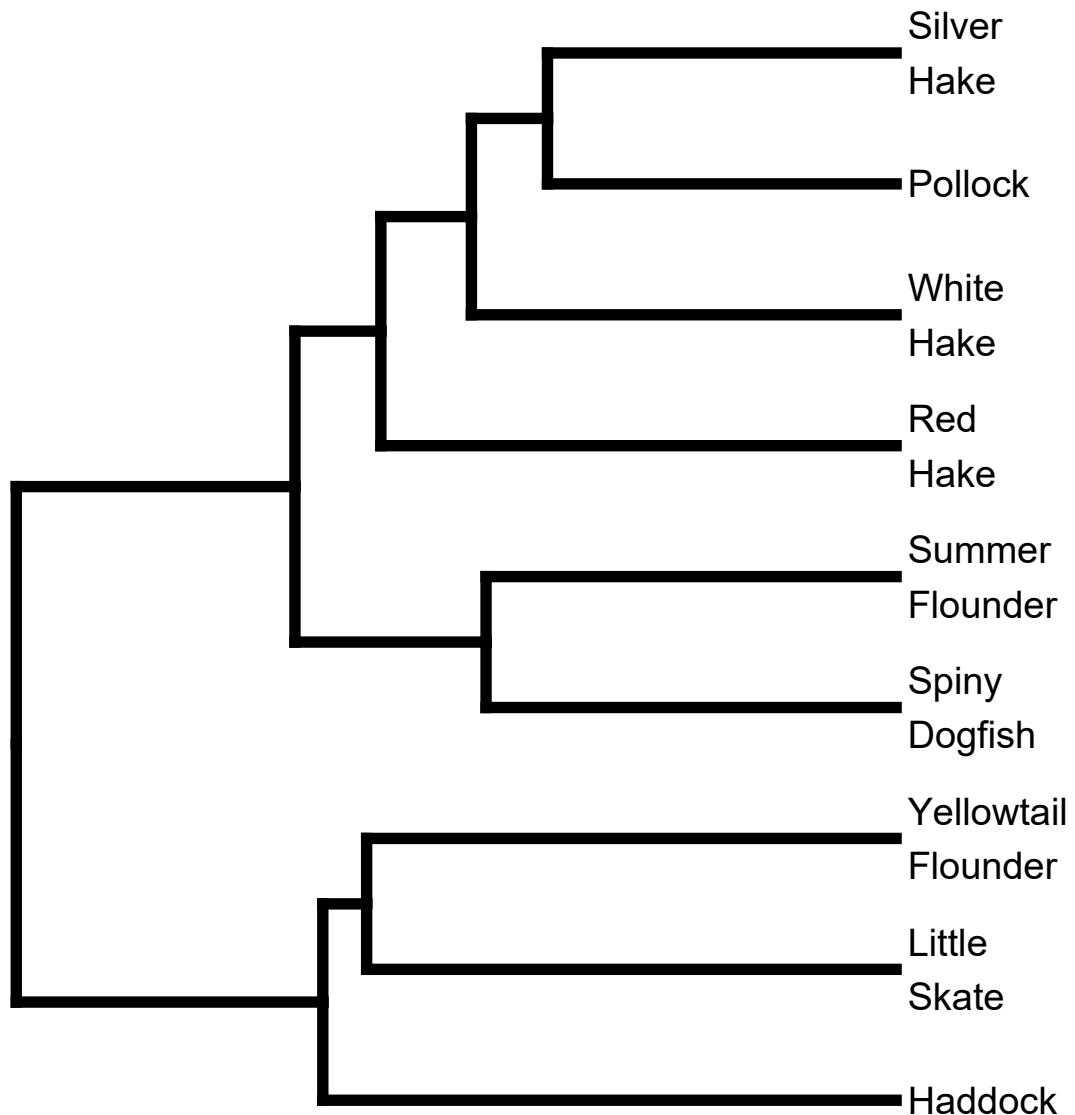


Figure 8: Focal predators clustered by similarity in diet composition. Species closer together have more similar diets with the height of a branch, distance from the right, being the average degree of dissimilarity. Hierarchical agglomerative clustering using the group average was performed from a matrix of Schoener's dietary overlap to generate this dendrogram.

Figure 9

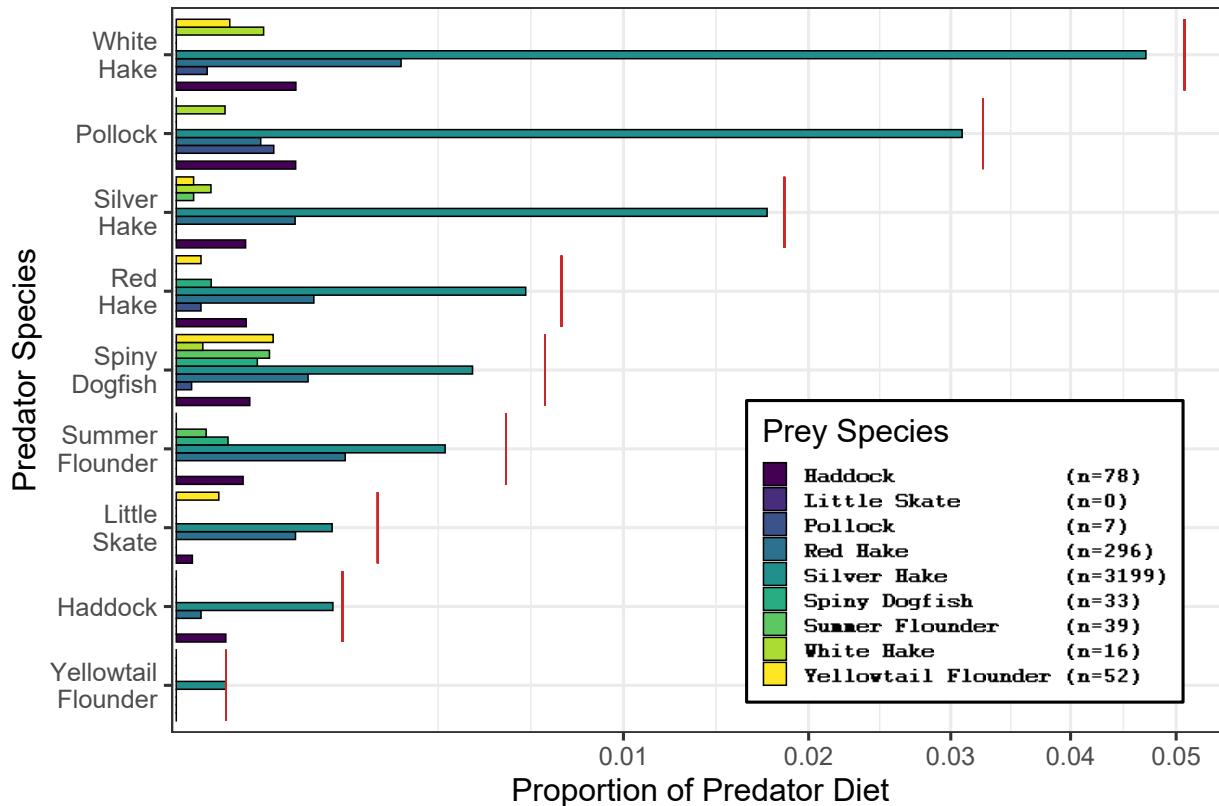


Figure 9: Proportion of total diet mass for each focal predator occupied by other focal predators, including cannibalism. Red lines represent the total proportion on self and other focal predator, making the remaining proportion (1-the total) equal to the proportion of consumption on non-focal predators. The total number of instances of predation on a species are included in the figure legend. Note square-root scale on x-axis.