Stability in the feeding ecology of four demersal fish predators in the US Northeast Shelf Large Marine Ecosystem

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ABSTRACT: Evidence of species interactions are generally well understood over broad temporal and spatial scales, particularly for commercially valuable species. Yet species that are not as commercially valuable may nonetheless be ecologically important in stabilizing trophic interactions in large marine ecosystems. We examined the diets for 4 of these demersal fish species: black sea bass *Centropomus striata*, scup *Stenotomus chrysops*, Northern searobin *Prionotus carolinus*, and striped searobin *P. evolans*. We examined food habits data across size class, season, 5 yr time block, and geographic region to evaluate the major determinants of diet composition. We used multivariate statistics, specifically canonical correspondence analysis, as the primary method to explore diet determinants. Our results showed that the scup and 2 searobin species are primarily benthivorous, whereas black sea bass notably shifts towards piscivory with ontogeny. Our results also showed that the diet of these predators was mainly influenced by size class, region, and (to a lesser extent) season, whereas 5 yr time block did not notably influence diet composition, a surprising observation given the well-documented changes to benthic habitat in this ecosystem. These results suggest that these species feed opportunistically in proportion to the relative abundance of available prey given the constraints of their morphology, which implies that despite notable impacts to benthic habitat, the prey field for these understudied species has been consistent (within seasonal variation) over the past 3 decades. Stable feeding dynamics such as these may act to enhance resilience in large marine ecosystems.

KEY WORDS: Black sea bass · Scup · Northern searobin · Striped searobin · Benthic · Ontogenetic shifts · Northwest Atlantic · Canonical correspondence analysis

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INTRODUCTION

There have been numerous calls to adopt an ecosystem approach to fisheries (EAF)—a governance framework using principles grounded in fisheries management and ecosystem-based management (EBM) (Link 2002a,b, Garcia et al. 2003). Adopting such an approach requires an understanding of the ecological dynamics and processes operating in an ecosystem, namely, the trophic ecology among the fish community in the food web of a large marine ecosystem (LME). Since most fisheries are managed at large scales, examining trophic ecology of fish at large scales is also prudent (Sherman 1991).

Any manageable system is made up of a multitude of ecological dynamics and processes. Some of these processes may remain stable over space or time. Other processes may change dynamically under varying environmental conditions or with anthropogenic disturbances. Stable ecosystem processes act to enhance overall system resilience whereas unstable processes act to deteriorate it (Holling 1973, Levin & Lubchenco 2008). A key part in designing appropriate EAF management in a system requires examining these processes over varying scales for stability.

In the specific context of trophic ecology, a point of focus to examine process stability is in predator–prey interactions. Stable predator–prey interactions are

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thought to enhance stability of the food web, which can then enhance the stability and resilience of the entire system (Holling 1973). Predator–prey relationships may differ at different spatial and temporal scales and with varying degrees of disturbance. The scale at which these stabilizing mechanisms take place and the severity of disturbance may determine the extent to which the system can be managed, or at least its resilience for management assumptions, functionally speaking (Auster & Link 2009). Therefore, examining a system and the interactions with that system at the same scale at which it is managed is critical (Sherman 1991, 1994, 2006).

The US Northeast Shelf (NES) LME has had an actively managed fishery for more than 3 decades and has experienced a wide range of impacts and disturbances (Fogarty & Murawski 1998, Garrison & Link 2000a,b, Link et al. 2008, 2009, Auster & Link 2009). These include fishing effects that directly (targeting) and indirectly (bycatch) impact populations, fishing effects that directly and indirectly impact benthic habitats, and climate change. Long-term trawling has permanently altered benthic habitat and prey community for parts of this and other marine ecosystems (Collie et al. 1997, Greenstreet et al. 1999a,b, Garrison & Link 2000a,b, Kaiser & de Groot 2000, Kaiser et al. 2000, 2002, Hermsen et al. 2003). Perturbations such as trawling may have additional unexpected impacts in the wake of climate change (Anthony et al. 2009). Fish populations respond to temperature and other environmental influences associated with climate change (Murawski 1993, Klyashtorin 1998, Ehrich & Stransky 1999, Perry et al. 2005) and are expected to undergo further changes in the next 50 yr (Graham & Harrod 2009). Little is known about how compounding impacts such as fishing and climate change will influence the trophic ecology of fish populations.

Elucidation of stable relationships in an ecosystem will enhance EAF by closing gaps in our understanding of ecological processes. Species interactions are generally understood at broad temporal and spatial scales for many fish species in the NES system (e.g. Garrison & Link 2000a,b,c, Link & Almeida 2000, Link & Garrison 2002, Link et al. 2002, Link 2007). Most of those species studied are prominent, valuable, and ecologically dominant fish. Yet there are species that are not as commercially valuable that do have ecological value in their trophic role as predators, but are often not as typically studied or associated with a region. These less valuable, less prominent species are relatively understudied compared to more commercially valuable species, such as gadids, pleuronectids, or clupeids. For instance, Atlantic cod *Gadus morhua* is one of the most historically valuable gadids in the NES system. A recent (May 2009) ISI Web of Sci-

ence literature search for '*Gadus morhua*' and 'food or feeding or diet' yielded 1488 publications. The same search for the 4 understudied species noted here (see next paragraph) resulted in a total of 41 publications. Thus we wanted to examine these understudied species' food habits to ascertain whether they have consistent food habits and thus a stabilizing role in the food web. We also did so in the context of how impacts to demersal and benthic processes have changed over time in this ecosystem.

These understudied species include black sea bass *Centropristis striata*, scup *Stenotomus chrysops*, Northern searobin *Prionotus carolinus*, and striped searobin *P. evolans*. Food habits of these, or similar, species have been generally reported before, both in the NES and other ecosystems (Richards et al. 1979, Atkinson & Percy 1992, Hood et al. 1994, Lindquist et al. 1994, Manderson et al. 1999, Steimle et al. 1999, Garrison 2000, Nakai et al. 2001, Perez-Espana et al. 2005, Jaworski & Ragnarsson 2006, Drohan et al. 2007). These species are generalist carnivores consuming mostly crabs, amphipods, polychaetes, mollusks, and small fish (Hood et al. 1994, Lindquist et al. 1994, Steimle et al. 1999, Nakai et al. 2001, Drohan et al. 2007). Studies of related species in other systems suggest that temporal, spatial, or ontogenetic variation exists in the diet (Kingsford 1992, Greenstreet et al. 1998, St. John 1999, Steimle et al. 2000, St. John et al. 2001). Furthermore, the understudied species in the present study could potentially have a large impact on their prey field and thus also on competing predators, as other benthic predators with similar foraging strategies have been shown to remove a large portion of benthic production (Collie 1987). Understanding mechanisms and the stability of these mechanisms that influence the foraging ecologies of these 4 species are important for LME management. Thus we simultaneously examined the determinants of diet for these species across a range of factors that have been shown to influence fish feeding for other species. Diet composition of each species is examined across: season, 5 yr block, geographic region, and size class. Characterizing the diet of these fish across different temporal, spatial, and ontogenetic factors will help to elucidate an important part of the NES LME food web for these relatively understudied species.

MATERIALS AND METHODS

Data collection. Data were collected from seasonal bottom-trawl surveys conducted by the Northeast Fisheries Science Center (NEFSC). Surveys are conducted 4 times a year (spring, March and April; summer, June to August; fall, September to November;

Fig. 1. Major geographic regions and sampling areas of the Northwest Atlantic continental shelf off the USA and Canadian coasts

winter, February) and extend from 33° to 45° N (Fig. 1). These seasonal surveys have been ongoing since 1963. Food habits data collection began in 1973 for scup and 1977 for black sea bass, Northern searobin, and striped searobin. Between 300 and 400 stations were surveyed in each of the main seasonal surveys (spring and fall), with 100 to 200 stations intermittently in other seasonal surveys. Stations occupied ranged from depths between 8 and 400 m, approximately 1 per 2.5' latitude by 2' longitude rectangular unit, and were selected using a stratified random sampling design. At each station, a 36 Yankee (or similar) bottom trawl was deployed for 30 min and towed at 6.5 km h⁻¹. Total catch weight, subsampled individual body weight and lengths, and total numbers of each species were recorded for each tow. Details of the survey sampling design, execution, and efficiency are available in Azarovitz (1981) and Northeast Fisheries Center (1988).

A subset of species during each seasonal cruise was examined for age and food habits data. The present study includes 7375 stomach samples from the 4 selected species (Table 1). Fish stomachs were sampled based on fish size and strata-station quotas irrespective of species abundance. Prior to 1981, stomach contents were preserved and returned to the laboratory for identification of prey. Total stomach content weight and the weight of each prey were measured to the nearest 0.1 g. Since 1981, stomach contents have been examined at sea. The total volume of stomach contents was measured by comparing the stomach bolus to a calibrated volumetric gauge (to

the nearest 0.1 g). The proportion of stomach contents comprised by each prey item was then estimated after separating each prey item from the entire stomach contents and measuring these with the volumetric gauge (relative to the total stomach volume).

We converted all stomach content and prey units into weights. In some cases, both weights and volumes were measured of the same stomachs. A linear regression was performed to convert volumes to weights and resolve the differences in prey quantification during the 2 periods. The regression was highly significant ($r^2 = 0.906$, $p < 0.0001$), and prey volumes from the post-1981 time period were multiplied by 1.1 to convert volumes to weights based on this analysis (Link & Almeida 2000). Further details of the food habits sampling methodology are available in Link & Almeida (2000).

Prey and predator categories. Prey items were identified to the lowest taxonomic resolution possible. Since stomach contents were identified in the laboratory prior to 1981, the taxonomic resolution of invertebrate prey is generally higher in these samples. In the present study, most fish and invertebrate prey were grouped to family or order to account for these sampling differences. The high abundance of some prey items allowed grouping at lower taxonomic levels than less abundant prey items for the purpose of statistical analysis. For example, the group 'miscellaneous fish' contains all fish species consumed except for those otherwise noted (bay anchovies, Engraulidae anchovies, scup, and sand lance). Similarly, the category 'Engraulidae anchovies' includes all Engraulidae anchovies except for bay anchovies, which were identified more precisely. The same is true for both 'decapod crab' and '*Cancer* spp. crab'. We also included a group of unidentifiable well-digested prey, which is a notable amount of the diets of some of the demersal species examined in the present study. There are 15 different prey groups in our analysis, including a group called 'other prey' that consists of all identifiable scarce prey items not included in any of the other 14 specified groups (Table 2).

Table 1. Sample size and summary metrics for the fish species studied

Predator	Number of stomachs sampled	Mean stomach weight (g)	Mean predator weight (g)	Mean predator length (cm)
<i>Centropristis striata</i>				
Black sea bass (BSB)	2400	2.20	366	25.40
<i>Stenotomus chrysops</i>				
Scup (SCP)	3886	0.44	109	15.40
<i>Prionotus carolinus</i>				
Northern searobin (NSR)	727	0.54	93	19.99
<i>P. evolans</i>				
Striped searobin (SSR)	362	2.82	264	24.89

Table 2. Prey item categories and abbreviations (codes) used in Figs. 2 to 6

Code	Prey item
AMP	Amphipods Order Amphipoda
MAR	Miscellaneous arthropods Phylum Arthropoda
BAN	Bay anchovy <i>Anchoa mitchilli</i>
CCR	<i>Cancer</i> spp. crabs <i>Cancer</i> spp.
DCR	Decapod crabs Order Decapoda
DSH	Decapod shrimp Order Decapoda
EAN	Engraulidae anchovies Family Engraulidae
MFS	Miscellaneous fish
LSQ	Longfin squid <i>Loligo pealeii</i>
MOL	Mollusks Phylum Mollusca
OPR (identifiable)	Other prey
PLY	Polychaetes Class Polychaeta
SLC	Sand lance <i>Ammodytidae</i> spp.
SCP	Scup <i>Stenotomus chrysops</i>
WDP (unidentifiable)	Well-digested prey

The fish predators were divided into length categories to account for suspected ontogenetic shifts in diet (Garrison & Link 2000a,b). Diet composition shifted at similar length categories among different species. These length categories are: <25 cm (small), 25–50 cm (medium), and >50 cm (large) for black sea bass; <20 cm (small), 20–50 cm (medium), and >50 cm (large) for scup; <20 cm (small), 20–30 cm (medium), and >30 cm (large) for Northern and striped searobins (Garrison & Link 2000b).

Diet analysis. Mean and variance of prey amount (weight) per stomach were calculated using a weighted, 2-stage cluster design to account for survey sampling design and included empty stomachs (Link & Almeida 2000). Mean stomach contents within a tow were weighted by the number of fish of that species in a size category captured in that tow. We assessed general trends in means and 95% CIs of relative prey amounts (% of diet by weight) by size category (small, medium, large), geographic region (Fig. 1), season, and 5 yr time blocks (1973–1975, 1976–1980, 1981–1985, etc. to 2006–2008) for each species. The 5 yr time block provided sufficient resolution of temporal trends while maintaining adequate sample size for each period. The

first and last time blocks are only 3 yr and include the most recent data available at the time of the study.

For each species, a canonical correspondence analysis (CCA; ter Braak 1986) was used to assess the diet response across the 4 explanatory factors noted in the previous paragraph. CCA is a multivariate equivalent to a multiple, unimodal regression (ter Braak 1986, 1987). It is a direct gradient method whereby canonical axes that are combinations of explanatory variables are correlated to weighted averages of multivariate response variables (prey amounts) within cells. The statistical significance of explanatory factors in the ordination was evaluated using 499 Monte Carlo permutation tests (ter Braak 1986). Rare prey items were downweighted to reduce the otherwise unduly large influence on the analysis. The results of the CCA are best understood by examining prey–environment biplots, the correlation between the canonical axes and the explanatory variables, and the amount of variance in the prey matrix explained by the canonical axes (ter Braak 1986, 1987). CCA is an effective method to statistically assess the quantitative relationship between multivariate response and explanatory variables and is robust to violations of assumptions (e.g. non-normality, ter Braak 1986; Palmer 1993). The CCA ordination was performed using CANOCO version 4.5 (Microcomputer Power).

RESULTS

Black sea bass

Across all factors and species, crabs comprised a large portion of the diet composition (Fig. 2). Overall, arthropods comprised 45.5% of the diet of black sea bass with *Cancer* spp. crabs representing 19.0% of the diet and decapod crabs 16.5% of the diet (Fig. 2). Fish comprised 28.8% of the diet, which was mostly made up of several miscellaneous species (25.9%).

Geographic region and size significantly influenced the diet of black sea bass and generally corresponded to the first ($p = 0.012$) and second ($p = 0.016$) CCA axes, respectively (Fig. 3A). The first and second CCA axes explained 45.6 and 26.5%, respectively, of the explainable variance, which was 6.7% of the total variation in the diet data (Fig. 3A). The most important regional dietary shift was from Engraulidae anchovies in the South-Atlantic Bight to miscellaneous arthropods and other prey in the Gulf of Maine (Fig. 3A,B). Black sea bass exhibited a clear ontogenetic shift in diet. They consumed more polychaetes, miscellaneous arthropods, and decapod shrimp at the small size class and switched to sand lance and other fish at the large size class (Fig. 3A,C).

Fig. 2. Percent composition by weight of prey items of each predator. Error bars represent 95% CI. See Tables 1 & 2 for abbreviations

Scup

Well-digested prey comprised 46.5% and polychaetes comprised an additional 14.1% of the diet of scup (Fig. 2). Predator size significantly influenced the diet of scup, despite the lack of a large scup size class and corresponded to CCA Axis 1 ($p = 0.002$), which explained 51.0% of the total explainable variance (Fig. 4A). Thus, like black sea bass, scup also exhibited an ontogenetic shift in diet composition (Fig. 4A,B). The largest dietary shift was decapod shrimp and miscellaneous fish at small size classes to sand lance, anchovies, *Cancer* spp. crabs and other prey at the medium size class (Fig. 4A,B). Seasonal changes were also evident. Season generally corresponded to CCA Axis 2, which explained 21.9% of the total explainable variance, but was marginally significant ($p = 0.118$). Both CCA axes explained 6.2% of the total diet variation. Scup switched from anchovies and *Cancer* spp. crabs in the fall to (other) decapod crabs and miscellaneous fish in the winter and to sand lance in the summer (Fig. 4A,C). Scup consumed amphipods and miscellaneous arthropods throughout the year and did not have a major influence on seasonal shifts in diet (Fig. 4A,C).

Northern searobin

In general, polychaetes comprised 38.4% of the diet of Northern searobin (Fig. 2). Decapod crabs and well-digested prey comprised an additional 16.7 and 13.2%, respectively (Fig. 2).

Season and geographic region significantly influenced the diet of Northern searobin and generally cor-

responded to CCA Axis 1 ($p = 0.002$) and Axis 2 ($p = 0.012$), respectively (Fig. 5A). CCA Axis 1 explained 61.0% and CCA Axis 2 explained 33.6% of the explainable variance, and together they explained 12.6% of the total diet variation (Fig. 5A). The greatest dietary shift in season was from polychaetes in the spring to *Cancer* spp. crabs in the fall and *Loligo pealeii* squid and well-digested prey in the winter (Fig. 5A,C). Very few Northern searobin were caught in the summer and as such that season was excluded from the analysis. Regional differences in diet composition were also evident. Miscellaneous fish comprised most of the diet in the South-Atlantic Bight, polychaetes in the Mid-Atlantic Bight, and amphipods in Southern New England (Fig. 5A,B). Miscellaneous arthropods were present in the diet of Northern searobin in all geographic regions and did not have a large influence on seasonal shifts in diet (Fig. 5A,B).

Striped searobin

Striped searobin exhibited a different diet composition than the other 3 species, with 80% of its diet almost equally split between all the fish (bay anchovies, Engraulidae anchovies, scup, sand lance, and miscellaneous fish; 42.8%) and all the arthropods (*Cancer* spp. crabs, decapod crabs and shrimp, amphipods, and miscellaneous arthropods; 39.7%) prey categories (Table 2).

Striped searobin exhibited an ontogenetic shift similar to black sea bass and scup. Size significantly influenced the diet of striped searobin, corresponding to CCA Axis 1 ($p = 0.002$) (Fig. 6A). Striped searobin

Fig. 3. *Centropristis striata*. (A) Canonical correspondence analysis (CCA) biplot. Arrow: significant explanatory factors; the dashed lines are the negative direction and the arrowheads are the positive direction of the variable. A small angle between a variable arrow and a CCA axis indicates a high correlation between the variable and the axis. Three-letter codes indicate CCA scores of individual prey items in ordination space. (B) Percent diet composition by weight in each geographic region. Error bars represent 95 % CI. Geographic regions from north to south: Gulf of Maine (GOM), Georges Bank (GBK), Southern New England (SNE), Mid-Atlantic Bight (MAB), South-Atlantic Bight (SAB). (C) Percent diet composition by weight for different size classes. Error bars represent 95 % CI. Large (LRG): >50 cm, medium (MED): 25–50 cm, small (SML): <25 cm. See Table 2 for prey item abbreviations

Fig. 4. *Stenotomus chrysops*. (A) Canonical correspondence analysis (CCA) biplot. See Fig. 3A legend for CCA explanation. (B) Percent diet composition by weight for different size classes. Error bars represent 95% CI. Medium (MED): 20–50 cm, small (SML): <20 cm. (C) Percent diet composition by weight during different seasons. Error bars represent 95% CI. Arrows signify error bars >80% of diet composition. Seasons: spring (SPR), summer (SUM), fall (FAL), winter (WTR). See Table 2 for prey item abbreviations

Fig. 5. *Prionotus carolinus*. (A) Canonical correspondence analysis (CCA) biplot. See Fig. 3A legend for CCA explanation. (B) Percent diet composition by weight in each geographic region. Error bars represent 95% CI. See Fig. 3B legend for abbreviations. (C) Percent diet composition by weight during different seasons. Error bars represent 95% CI. See Fig. 4C legend and Table 2 for abbreviations

Fig. 6. *Prionotus evolans*. (A) Canonical correspondence analysis (CCA) biplot. See Fig. 3A legend for CCA explanation. (B) Percent diet composition by weight for different size classes. Error bars represent 95% CI. Large (LRG): > 30 cm, medium (MED): 20–30 cm, small (SML): <20 cm. (C) Percent diet composition by weight during different seasons. Error bars represent 95% CI. See Fig. 4C legend and Table 2 for abbreviations

switched from miscellaneous arthropods and amphipods to *Loligo pealeii* squid and scup at larger sizes (Fig. 6A,B). Season was less influential on diet composition than ontogeny. Very few striped searobin were caught in the summer and thus that season was excluded from the analysis. Season generally corresponded to CCA Axis 2 but was marginally significant ($p = 0.078$). CCA Axis 1 explained 56.0% and CCA Axis 2 explained 20.5% of the explainable variance, which was 12.9% of the total diet variation (Fig. 6A). Mollusks comprised most of the diet in spring whereas scup comprised most of the diet in winter seasons (Fig. 6A,C).

DISCUSSION

What proved to be remarkable in our results was that important benthivorous species had a relatively consistent diet through time, despite occupying habitats suspected of having experienced notable impacts from fishing in this ecosystem (Auster et al. 1996, Collie et al. 1997, Watling & Norse 1998, Hermesen et al. 2003). Consistency in the diet over the full range of 5 yr time blocks was somewhat surprising. These results could be due to an artifact of the highly aggregated taxonomic level of our prey, the differential sampling of these fish species relative to major fishing grounds, or similar confounding factors. Yet, we suspect that at a broad level, for major benthic groups at large scales, the prey field has been relatively consistent for these predators, implying that fishing impacts to the benthos are not notably impacting the available food for these understudied species. Such relatively stable predator–prey relationships may act to enhance the resiliency of the NES LME.

Stability in the prey field is confirmed by the observation that the diet of these predators was mainly influenced by size class, region, and, to a lesser extent, season. These same factors have been shown to influence the diet of other benthic predators, such as commercially valuable flatfish (Link et al. 2002) and commercially valuable cod (Link & Garrison 2002). All of these species are demersal predators that are capable of prey switching. The seasonal and regional differences in diet imply that these fish feed opportunistically in proportion to the relative abundance of the prey field. That seasonal and regional differences were more important factors than long time scales (5 yr blocks) implies that the local and seasonal dynamics of the benthos and small demersal fishes were more important than broad-scale impacts like gear effects.

The impacts of trawling may be shorter-lived than some studies suggest (Auster et al. 1996, Fogarty & Murawski 1998, Watling & Norse 1998, Tillin et al. 2006), depending upon habitat type, mobility and pro-

ductivity of organisms (Link et al. 2005). Kaiser et al. (1998) found that the effects of trawling disappeared with a change in season. Rapid recolonization of trawled areas by infaunal species (Kaiser et al. 1998) can stabilize prey availability for demersal predators. In fact, higher abundances of infaunal species have been observed in more frequently trawled areas as compared to lightly trawled areas (Collie et al. 1997, Tillin et al. 2006).

Most of these understudied fish showed an ontogenetic shift in diet. This is common among fish (Scharf et al. 2000, Steimle et al. 2000). Scup, a notable omnivorous benthivore (Steimle et al. 1999), exhibited an ontogenetic shift in diet (despite the lack of a large size class) suggesting that even the transition from small (<20 cm) to medium (20–50 cm) size class greatly impacted feeding behavior. Striped searobin switched from infaunal invertebrates to crabs and scup when they could better accommodate them physically at a larger size class (Persson et al. 1996, Nilsson & Bronmark 2000). However, previous experiments suggest that an ontogenetic shift was not prominent. Striped searobin continued to feed on small prey items even at large sizes (Manderson et al. 1999). Both Northern and striped searobin are known benthivores. Given the constraints on their morphology with size (e.g. gape), these results confirm that species feed opportunistically on the prey field available to them (Michelman 1988). Ontogenic shifts were clearly seen with the piscivorous black sea bass (Fig. 3A,C). Drohan et al. (2007) reported that amphipods and mysids were the major prey items of juvenile (1 to 9 cm) black sea bass. As they grew, they incorporated small crabs and polychaetes (9 to 14 cm) and eventually fish into their diets. Thus, all these species that are mainly benthivorous showed ontogenetic shifts.

The total diet variance in the present study (6.2 to 12.9%) was low but comparable to other studies that have used CCA (12.6 to 18.4%, Garrison & Link 2000c; 10%, Link & Garrison 2002; 8 to 11.7%, Link et al. 2002; 6 to 16%, Jaworski & Ragnarsson 2006). Total diet variance is the amount of variance explained by the factors. This differs from total explainable variance that is explained by both CCA axes. Low total diet variance suggests that other factors may also be influencing diet composition. For example, our findings suggest that diet composition was influenced at a specific temporal scale since prey composition in diets was only influenced by the short-term seasonal scale and not over a broad-term year–block scale. This raises questions as to whether diet composition can also be influenced at a specific geographic spatial scale or across several different spatial scales. Jaworski & Ragnarsson (2006) found that diet composition of demersal fish in Iceland varied at several spatial scales including

depth, latitude, and longitude. Additional studies exploring the effects of spatial scale on diet observations thus seem warranted.

Collectively the results for these understudied species showed that they can be ecologically important in the trophic dynamics of regions and locales that may have historically been overlooked. As we move towards an EAF (Link 2002a,b, Garcia et al. 2003), studies such as the present one will continue to be vital for the successful development and implementation of EBM approaches. An enhanced understanding of trophic ecology and the resilience of food webs to major anthropogenic perturbations will be increasingly important with the added pressure of climate change, especially as the potentially stabilizing influence of the predator–prey relationships of these species becomes more fully appreciated. However, much work has yet to be done towards the understanding of these understudied species. These 4 species represent an interesting and unique part of the fish community in the NES LME. We hope that the present study further elucidates their role in the food web and will be valuable as fisheries management continues to move towards EBM as a component of an EAF.

Acknowledgments. This research was sponsored by National Science Foundation (NSF) Integrative Graduate Education and Research Traineeship (IGERT) grant number 0504103 to the University of Rhode Island (URI) Coastal Institute. Thank you to the URI IGERT faculty and fellows for providing support and the opportunity for collaboration with the Northeast Fisheries Science Center. We thank those dedicated staff, past and present, who have collected and maintained the food habits database at the Northeast Fisheries Science Center, most particularly B. Smith. We thank the anonymous reviewers for their comments on prior versions of this manuscript.

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