Feeding hotspots for four northwest Atlantic groundfish species

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We used predator distribution and stomach content data to estimate the annual per capita rate of consumption for four representative predator species from the northwestern Atlantic Ocean, and considered how consumption is influenced by depth, bottom salinity, sediment grain size, location variables, and species-specific diet components. We found that geographic variables and species-specific prey resources were significantly associated with consumption rates, a pattern consistent with predator-prey theory. Prey categories comprised of fish were particularly important for a more mobile predator (silver hake *Merluccius bilinearis*), whereas benthic invertebrate prey were consistently important for a more sedentary predator (little skate *Raja erinacea*). Hotspots in consumption rates that overlap with particular prey resources were highlighted by the significance of location variables (longitude) for winter flounder *Pseudopleuronectes americanus*, silver hake, little skate, and sea raven *Hemitripterus americanus*. Depth was an important explanatory factor for consumption by little skate, but the explanatory value of abiotic habitat factors was low for the other three species. Greater emphasis on species-specific food habits, migratory patterns, and ecological interactions at the synoptic scales relevant to fisheries is needed for fisheries management.

Keywords: consumption, continental shelf, ecosystem-based fisheries management, essential fish habitat, food web dynamics, Georges Bank, Gulf of Maine, Southern New England, vital rate.

Introduction
Population control mechanisms influence populations by modifying one of several vital population rates including growth, mortality–survivorship, fecundity, reproductive success, migration, and consumption (Caswell, 1989; Metcalfe *et al.*, 2002). Ultimately, changes in these rates on an individual basis can scale up to alter population level processes. Vital population rates may be affected by any number of biotic or abiotic factors that vary across a landscape (Hoffman and Powell, 1998; Buckley *et al.*, 2004), and as such we would expect that the vital rates themselves would be spatially variable. This expectation poses several germane questions. What is the nature of this spatial variability? What factors best delineate the habitat where these rates are maximized? And what are the implications of those habitat-rate relationships for fisheries management?

Vital population rates and the relationships between vital rates and associated habitat factors are often highly dependent upon the scale of observation and measurement (Sundermeyer *et al.*, 2006). Many studies have shown that perceived ecological patterns are quite different on the spatial and temporal scales of tens of square metres and minutes when compared to thousands of square kilometres and weeks (Rahbek, 2005). Integrating from smaller to larger scales in order to capture the full extent of entire free-ranging populations usually poses some difficulties, such as the homogenization of important finer-scale patterns or processes (Levin, 1992). For example, at broad spatial scales, the dispersal of marine fish and their recruitment into populations are influenced by continental scale and regional scale water currents (e.g. the Labrador Current, Pepin and Helbig, 1997). At much finer scales, the roles of swimming behaviour, habitat selection, and post-settlement processes are more evident (Tupper and Boutilier, 1995). Few studies have attempted to estimate or compare vital population rates in the order of thousands of square kilometres on an annual basis, even though these are often the scales at which many living marine resources are managed (NEFSC, 2006).

In the USA, essential fish habitat (EFH) is a significant component of fisheries management (NMFS, 2007), however there are no

known instances where EFH as it relates to vital rates or productivity has been used to manage marine fisheries. Within the EFH framework, there are four different levels of practical application. Level I describes the presence–absence of a species among habitats, level II describes the relative abundance of species among habitats, level III relates to the vital population rates of species among habitats, and level IV to species productivity among habitats (NMFS, 2007). A chief criticism of the EFH approach is that the combined abundance–distribution plots for multiple species suggests that the entire ocean is "essential", implying then that none of it is (Cook and Auster, 2005). Given the increased considerations of spatial management tools for fisheries (Fluharty, 2000), an enhanced understanding of the relationship among vital population rates and habitat is warranted. Knowing where vital rates are maximized and understanding the factors underlying those spatial patterns are useful steps toward better elucidation and use of refined EFH delineations.

Consumption (or more precisely, the rate at which an individual fish acquires energy resources) is one vital rate that can have a direct effect on the distribution, abundance and production of fish populations. This rate may be influenced by the availability of preferred prey in any given prey field at a particular locale, as reflected in the differing diet composition of the prey consumed. Consumption hotspots, or areas where a prey species occurs in greater abundance in the predator's diet relative to its ambient abundance, may reflect preference, whereas prey avoidance may be seen via lower consumption of a prey relative to its ambient abundance (Chesson, 1978). A lower overall consumption rate may suggest maintenance feeding, which can be augmented by periods of time or locations of "gorge" feeding on preferred prey (Link and Burnett, 2001). Such patterns may be indicative of changes in maturity state (Link and Burnett, 2001). Environmental factors can also affect rates of consumption. Depth, bottom temperature, bottom salinity, and bottom substrate type are all important aspects of demersal fish habitat and each has been associated with feeding migrations, prey fields, or ontogenetic shifts in prey preference (Swain, 1993).

Perceived patterns of consumption and other vital rates may be expected to vary with the resolution of the analysis. Spatial resolution is often used synonymously with several other terms including the scale, "grain" (*sensu* O'Neill, 1986), "focus," spatial cell size, or pixel size, and can be described as the area of inference represented by each data point in the analysis (Scheiner, 2003). The extent of the analysis describes the size of the entire inference space in which the analyses are carried out and to which the results apply (Scheiner *et al.*, 2000). The degree to which resolution affects pattern can depend upon how spatially heterogeneous the dataset is. Increasing the spatial cell size tends to average away extreme values, thereby reducing the overall spatial variability among spatial cells (Rahbek, 2005). If the landscape is patchy, increasing the spatial cell size may also increase the spatial variability within a cell as more patch types are included in the cell. For analyses involving fisheries species, an appropriate spatial resolution is one that is consistent with the population extent of the species examined, is able to accommodate the available data, and corresponds to the spatial scales of fisheries management.

Hotspot delineation in marine ecosystems has primarily focused on marine production and biodiversity (Reese and Brodeur, 2006). While foraging hotspots are known for some large marine predators (Hays *et al.*, 2006; Gende and Sigler, 2006), actual rates of consumption at these hotspots and the

ecological explanation(s) underlying their spatial variability are less well understood. Delineating where and why consumption hotspots occur is of general interest ecologically, and of particular interest for EFH-related fisheries management issues. A suite of ecological factors such as predator and prey densities, environmental heterogeneity, and refuge space availability all contribute to the amount of food eaten by fish (Garrison and Link, 2000). Despite the broad range of factors that influence predator consumption rates, there are no studies that examine the relative importance of biotic or abiotic factors simultaneously as they influence consumption. Moreover, none have done so with respect to spatial variability in those factors. Thus, the objective of our study was to evaluate a key vital population rate— consumption—in relation to a host of environmental and ecological factors. We examined the consumption rates of predator species that are representative of various feeding habits, mobility, and life history strategies (chosen across a broad range of functional feeding types) from the northwest Atlantic as they relate to oceanographic habitat features, benthic habitat features, and the realized prey field of each predator.

Methods
Data sources and data manipulation
Environmental data and food habits data for winter flounder (*Pseudopleuronectes americanus*), silver hake (*Merluccius bilinearis*), little skate (*Raja erinacea*), and sea raven (*Hemitripterus americanus*) were obtained from the Northeast Fisheries Science Center (NEFSC) food habits database for both fall and spring for the time period 1994–2003 (Link and Almeida, 2000). This time period was chosen to provide a representative temporal snapshot of feeding relationships. It was desirable to select a large enough time period to provide sufficient spatial coverage of data, yet a small enough period of time to prevent shifts in diet over the timeframe from obscuring patterns. Stomach contents (measured in grams) were examined during the NEFSC surveys which collected data from 350–400 sampling stations per survey, from Nova Scotia to Cape Hatteras, using a stratified–random sampling design (NEFC, 1988). Each sampling station was sampled using a no. 36 Yankee (or comparable) bottom trawl deployed for 30 min at a tow speed of 6.5 km h^{-1}. The surveys also recorded a suite of physiographic and oceanic variables for each tow. A more detailed description of the bottom trawl sampling design is published elsewhere (NEFC, 1988).

We evaluated depth, bottom salinity, and substrate grain size as explanatory environmental variables in the analysis because these factors are often used to delineate species distributions for marine continental shelf fishes (Overholtz and Tyler, 1985). Depth is associated with migratory patterns and life history strategies (Macpherson and Duarte, 1991; Metcalfe *et al.*, 2002) and generally holds the greatest explanatory value for distribution and abundance patterns (Overholtz and Tyler, 1985). Particular bottom types are associated with nursery grounds and refuges for many groundfish species (Gibson and Robb, 1992), and some species may track a salinity gradient with an onshore–offshore seasonal migration. Many flatfish species, for example, have nursery grounds in shallow water estuaries (Swain, 1993). As such, it is strongly suspected that these variables could have an influence on consumption rates. Because temperature was

used to calculate consumption rates, it was not used as an explanatory variable in the analyses.

The substrate data used for the analysis was based on a surficial sediment database for this region that was assembled by the US Geological Survey (Poppe *et al.*, 2003). This data set is a compilation of numerous surveys carried out by multiple investigators that primarily employed grab samplers to collect surficial sediment samples. The spatial extent of the substrate data overlapped with that of the bottom trawl surveys in the Gulf of Maine, Georges Bank, and parts of Southern New England, so we focused our analyses primarily on these regions.

To examine relationships between fish consumption and environmental variables in a spatially explicit manner, a grid composed of spatial cells measuring 30 min of latitude by 30 min of longitude (55.5 km × 55.5 km, or 3080 km^2 per cell) was overlaid on the region. This scale was consistent with the population extent of the species examined, was able to accommodate the available data, and collectively corresponds to the spatial scales of fisheries management. The number of spatial cells in the analysis for a given species ranged from 64 to 116 (median = 69) depending on the extent of each species within our study region. Each sampling station (i.e. tow) was assigned to the spatial cell in which it occurred. The average depth, temperature, salinity, and grain size were calculated by summing samples across the number of stations within a spatial cell and then dividing by the total number of stations within that cell (Figure 1).

The diet composition percentages were based on mass (gram) of each major prey category (Table 1) and determined by summing the weight of each prey category for an individual predator and then dividing by the total weight of that individual's stomach contents (Link and Almeida, 2000). The average diet composition for a predator species was then determined for each spatial cell by summing these percentages across the stomachs sampled for that predator species within a spatial cell and then dividing by the total number of stomachs (including empty stomachs) for that predator species within the spatial cell. Mean stomach contents (irrespective of prey type) were also estimated for each predator for each spatial cell. Because our emphasis was on spatial dynamics rather than temporal dynamics, we averaged across time to obtain a reasonable sample size. Certainly feeding can vary over time, but previous studies have demonstrated that major shifts in diet are detectable over five to ten year time blocks (Garrison and Link, 2000). Seasonal shifts in diet can be pronounced, and we account explicitly for seasonality in our analysis. Cells which contained no tows or in which the species did not occur were not included in the analysis.

Analyses

Based upon the food habits information, the average annual *per capita* rate of consumption for each spatial cell was calculated by using the evacuation rate model (Eggers, 1977; Elliott and Persson, 1978). This model requires two variables and two
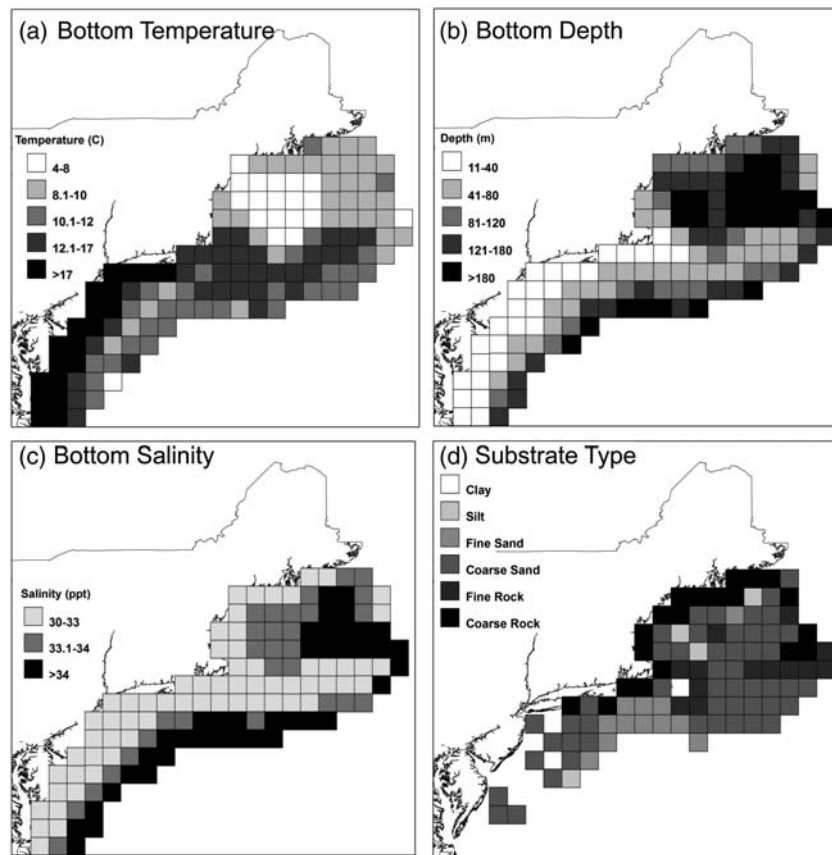

Figure 1. Environmental variables. (a) Bottom temperature (°C). (b) Bottom depth (m). (c) Bottom salinity (parts per thousand, ppt). (d) Substrate type on the northeastern U.S. Continental shelf from the Gulf of Maine to the mid-Atlantic Bight. Sediments were grouped into one of six substrate types based on particle diameter using the Wentworth (1922) scale of geological classification. Spatial cells are 55.5 km × 55.5 km.

Table 1. Identification of major groups within the prey categories for each species.

| Predator	Prey category	Taxonomic groups included
Winter Flounder	Amphipods	Amphipoda
	Annelids	Annelida
	Cnidarians and ascidians	Cnidaria, Ascidiacea
	Decapods	Decapoda
	Molluscs and echinoderms	Mollusca, Echinodermata
Little Skate	Annelids	Polychaeta
	Decapods	Decapoda, other Crustacea, Mysidacea, Euphausiacea
	Bivalves and echinoderms	Bivalvia, Gastropoda, Echinoidea, Ophiuroidea
	Other small benthic invertebrates	Isopoda, Amphipoda, Pycnogonida, Stomatopoda, Cumacea
	Fish and squid	Cephalopoda, demersal fish spp.
Silver Hake	Cephalopods	Cephalopoda
	Shrimp	Euphausiacea, Mysidacea, Crangonid shrimp, Pandalidae, Penaeidae, Decapoda shrimp spp.
	Other arthropods	Amphipods, Crustacea, Decapoda crab spp.,
	Small pelagics	Clupeidae, Myctophidae, Scombridae, Engraulidae
	Other fish	Groundfish spp.
Sea Raven	Benthic invertebrates	Gastropoda, Cephalopoda, Polyplacophora, Scaphopoda, Brachiopoda, Stomatopoda, Cnidaria, Paguroidea, Echinodermata, Porifera, Annelida, Platyhelminthes, Nematoda, Nemertea, Phoronida, Echiuridae, Ascidiacea, Pycnogonia, Amphipoda, Isopoda, Ostracoda, Bryozoa, Cirrepedia, Cumacea
	Flatfish	Pleuronectiformes, Bothidae
	Other demersals	Zoarcidae, Gadidae, Cottidae, Ophidiidae, Rajiformes, Scorpaenidae, Lumpenus spp.,
	Small pelagics	Carangidae, Cryptacanthodes spp., other demersal fish spp.
		Clupeidae, Myctophidae, Scombridae, Engraulidae, Cepholopoda, Mallotus, Atherinidae
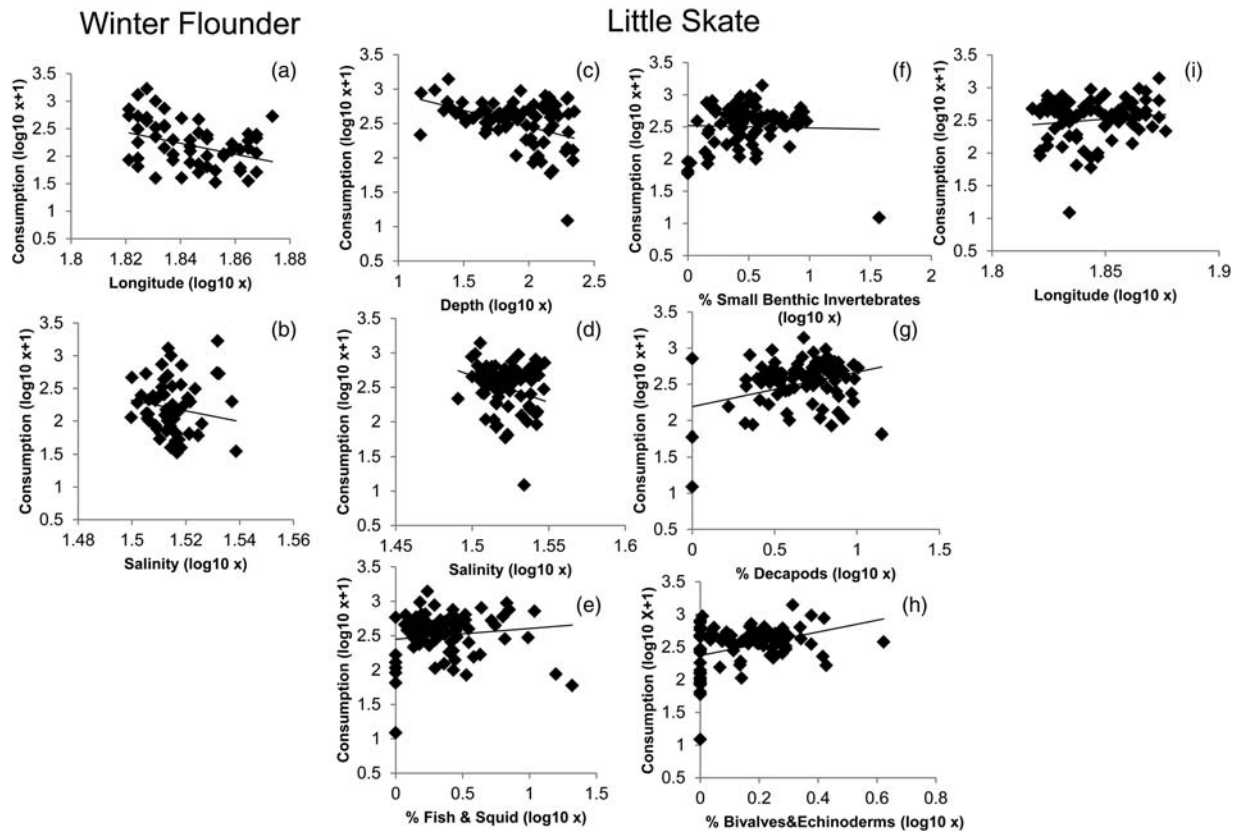
Figure 2. Linear regressions showing the relationship between significant explanatory variables and annual per capita consumption for two relatively sedentary species, winter flounder and little skate. The first two panels show the relationship between consumption and (a) longitude, and (b) salinity for winter flounder. The last seven panels represent the relationship between consumption and (c) depth, (d) salinity, (e) percentage fish and squid, (f) percentage small benthic invertebrates, (g) percentage decapods, (h) percentage bivalves and echinoderms, and (i) longitude for little skate. Percentages indicate the proportion by weight of each prey in the predator's diet.

parameters. The *per capita* consumption rate, C_{it} is calculated as:

$$C_{it} = 24 \cdot E_{it} \cdot \overline{S_{it}}^{\gamma},$$

where 24 is the number of hours in a day and the evacuation rate E_{it} is:

$$E_{it} = \alpha e^{\beta T};$$

and is formulated such that estimates of mean stomach contents (S_{it}, see Link and Almeida, 2000 for estimators) and ambient temperature [T; here used as bottom temperature from the NEFSC bottom trawl surveys for each cell and season (Taylor *et al.*, 2005)] are the only data required. This was done for each predator species (i) for each time period (t) (fall and spring during 1994–2003) and was independent of any prey item (j). The values for α (0.04) and β (0.11) were chosen from the literature (Tsou and Collie, 2001). The parameter γ is a shape function and is almost always set equal to 1 (Gerking, 1994).

For each spatial cell, the summation of consumption across individual predators of a given species for each season was calculated as:

$$C_{i\_Annual} = \sum_{t} C_{it} \cdot 182.5$$

where 182.5 is the number of days in a season [where spring (March–May) proxies for winter and autumn (September–November)

proxies for summer]. Thus, for each spatial cell, fall and spring consumption were summed to obtain the annual *per capita* rate of consumption C_{i_Annual}, hereafter referred to as consumption. There have been copious applications of this approach in this ecosystem (e.g. Tsou and Collie, 2001; Methratta and Link, 2006; Link *et al.*, 2008; Overholtz *et al.*, 2008).

A stepwise linear regression approach was used to model *per capita* annual consumption calculated for each spatial cell using the predictor variables of depth, bottom salinity, bottom substrate grain size, location (latitude and longitude), and the top 4–5 main prey groups specific to each predator's diet (Table 1). Linear regression assumes that the response variable is a function of a linear combination of the predictor variables plus an error term. The stepwise regression method systematically added each parameter into the model in a forward stepwise manner with an entry criteria of $p = 0.15$ and exit criteria of $p = 0.085$. Predictor variables that described diet (i.e. proportional data) were arcsin square root transformed, the environmental and geographic predictor variables were log base 10 (x) transformed, and consumption, the response variable, was log base 10 ($x + 1$) transformed to meet the assumptions of heteroscedasticity for a generalized linear model (Zar, 1996; McCune *et al.*, 2002; Sokal and Rohlf, 2012). The arcsin square root transformation is a commonly used transformation for proportional data and has been applied previously to fish stomach data (e.g. Arrington *et al.* 2002). We also explored other linear and non-linear statistical modelling approaches including generalized additive modelling (GAM),
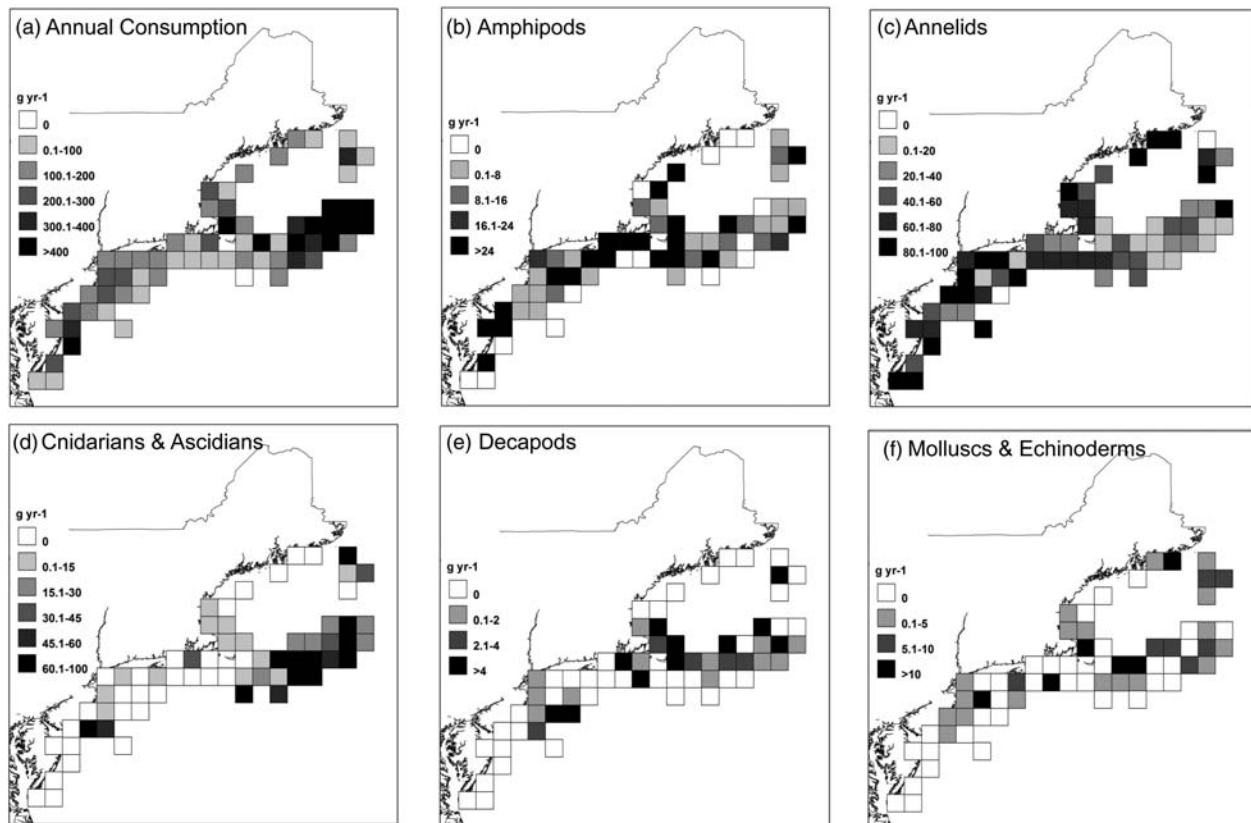

Figure 3. Spatial distribution of consumption and diet for winter flounder on the northeastern US Continental Shelf from the Gulf of Maine to the mid-Atlantic Bight. Panel (a) shows the annual per capita consumption (g yr^{-1}). The remaining panels depict diet percentages: (b) percentage amphipods, (c) percentage annelids, (d) percentage cnidarians and ascidians, (e) percentage decapods, and (f) percentage molluscs and echinoderms, in winter flounder diets. Spatial cells are 55.5 km × 55.5 km.

Table 2: Linear regression model resulting from the stepwise procedure for winter flounder, little skate, silver hake, and sea raven.

Species	Regression model	d.f.	F-ratio	Model p-value	Significant factors	Partial r^2 (p-value)
Winter Flounder	C = − 13.71 (longitude) − 17.26 (salinity) + 53.64	2, 54	5.27	<0.0081	longitude	0.089 3 (0.024)
					salinity	0.074 (0.033)
Little Skate	C = −1.19 (depth) + 13.69 (salinity) + 0.92 (% fish and squid) + 0.41 (% small benthic inverts) 0.92 (% decapods) + 0.79 (% bivalves & echinoderms) − 9.49 (longitude) + 0.17	7, 82	8.50	<0.000 1	depth	0.120 0 (0.000 8)
					% decapods	0.066 6 (0.009 1)
					% fish & squid	0.106 7 (0.000 5)
					% small benthic invertebrates	0.028 1 (0.064 3)
					% bivalves & echinoderms	0.035 1 (0.035 3)
					longitude	0.025 8 (0.060 7)
					salinity	0.025 3 (0.059 5)
Silver Hake	C = 0.53 (% small pelagics) + 2.03	1, 99	23.3	<0.000 1	% small pelagics	0.190 5 (<0.000 1)
Sea Raven	C = −0.34 (% benthic invertebrates) − 13.50 (longitude) + 27.74	2, 65	7.07	0.001 7	longitude	0.134 0 (0.002 1)
					% benthic invertebrates	0.044 6 (0.064 7)

p, probability.
C, per capita annual consumption.
All percentages refer to the proportion of that prey category in the diet. Diet variables were arcsin, square root transformed, and all other variables were log10 x or x + 1 transformed.

which allows for non-linear relationships between predictor and response variables. Best fit GAMs indicated that relationships between predictor variables and consumption were linear in most instances. Thus we report only the results from the stepwise linear regression model here. To alleviate our concerns about collinearity among predictor variables, we explored variance inflation factors and found that such relationships were not influential. Statistical analyses reported were carried out using proc glm and proc reg in SAS version 8 (SAS Institute Inc., 1989).

Results

Winter flounder (*P. americanus*)

The most significant variables for winter flounder consumption from the stepwise procedure were longitude and salinity (Figures 2, 3). Both variables were negatively associated with consumption and the resultant linear model including these variables explained 16.3% of the variance in consumption by winter flounder (Table 2). The association between consumption and geographic location reflects the relatively higher rates of consumption on the northeast portion of Georges Bank, which is toward the central-east of the study extent, and relatively lower consumption rates along the shelf of Southern New England. The relationship between consumption and salinity also highlights this pattern. No one prey species was associated with the high consumption rates on Georges Bank, indicating a mixed species diet for winter flounder in areas of high consumption.

Little skate (*R. erinacea*)

Seven factors were retained in the regression model for little skate. Depth, salinity, and percentage small benthic invertebrates were all negatively associated with consumption, while percentage fish and squid, percentage decapods, percentage bivalves and echinoderms, and longitude were all positively associated with consumption (Figure 2, Table 2). Together, these variables explained 40.8% of the variation in consumption, however, depth and percentage fish and squid were the only variables that explained more than 10% of the variation while the other variables were of less importance. The relationship with depth was reflective of greater rates of consumption occurring at shallower depths along the coast. The significance of longitude and salinity in the model reflects higher consumption in the western portion of the study extent along the coast of Southern New England where salinity levels are lower (Figure 4). Decapods made up a greater proportion of little skate diet along the coast of Southern New England and portions of Georges Bank. Fish and squid contributed to a large proportion of little skate diet along the coast of the Gulf of Maine, portions of Georges Bank, and the outer shelf of Southern New England. Bivalves and echinoderms were large components of the diet in Southern New England and parts of Georges Bank, while small benthic invertebrates made their contribution to little skate diet primarily in Southern New England.

Silver hake (*M. bilinearis*)

Stepwise regression retained only the proportion of small pelagics in the diet as a significant predictor of silver hake consumption rates ($r^2 =19.1$%) reflecting greater overall consumption by silver hake where diets were composed of large amounts of small pelagics (Figure 5, Table 2). Small pelagics represented a large diet component on parts of Georges Bank, coastal Southern
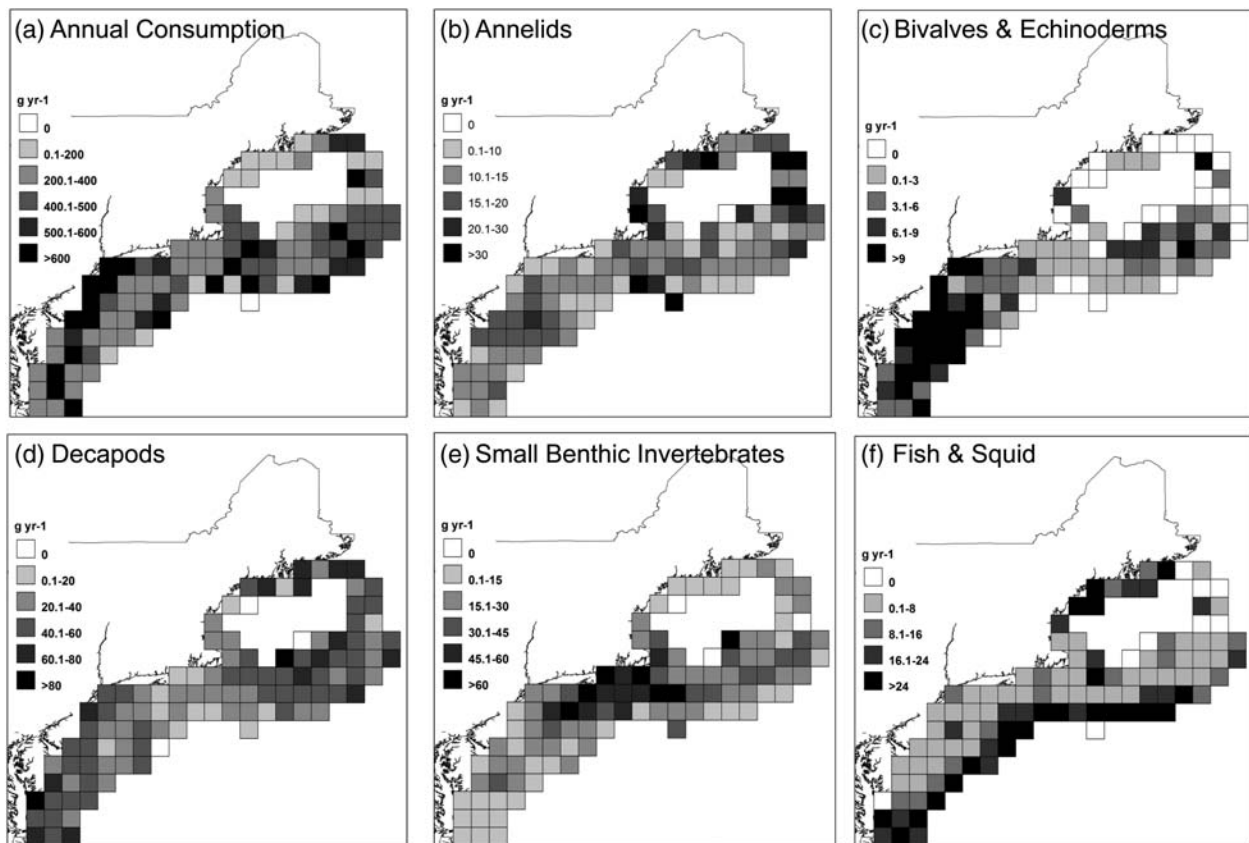
Figure 4. Spatial distribution of consumption and diet for little skate on the northeastern US Continental Shelf from the Gulf of Maine to the mid-Atlantic Bight. Panel (a) shows the annual per capita consumption (g yr^{-1}). The remaining panels show diet percentages : (b) percentage annelids, (c) percentage bivalves and echinoderms, (d) percentage decapods, (e) percentage small benthic invertebrates, and (f) percentage fish and squid, in little skate diets. Spatial cells are 55.5 km $\times$ 55.5 km.

New England, and coastal Gulf of Maine where overall consumption rates were high (Figure 6).

Sea raven (*H. americanus*)

The two significant factors in the linear regression from the stepwise procedure were longitude and the percentage of diet represented by benthic invertebrates (Figure 5, Table 2). This model explained 17.9% of the variation in the consumption for sea raven. Longitude had the largest partial r^2 (Table 2), with consumption highest east of 70° longitude (Figure 7). Consumption was negatively associated with benthic invertebrate prey. This pattern was driven by the low proportion of benthic invertebrates in the diet of sea raven on Georges Bank where overall consumption by this predator was relatively high.

Discussion

The relative importance of the factors affecting consumption was unique to each species, emphasizing the important role of the spatially-explicit feeding ecology for individual species . For the four species we examined, the major determinants of consumption rates were primarily diet components, location variables, and depth. However, no single factor consistently explained consumption for the five species examined. Most notably, benthic sediment type contributed little explanatory value to the models.

The species-specific influence of diet on consumption is consistent with traditional predator–prey model predictions, in which food consumed increases as predators encounter and eat preferred prey (Stephens and Krebs, 1986). For example, silver hake consumed more food on average when they were eating small pelagic prey as opposed to other prey in their diet. Similarly, the increased proportional contribution of decapods to the predator's diet resulted in increased consumption rates for little skate. This positive effect of particular prey groups on consumption suggests preference for these groups by the predator.

Conversely, there were some instances where a large amount of a particular prey in the diet was associated with low consumption rates, presumably indicating poor feeding conditions. For example, where sea raven and little skate ate a high proportion of benthic invertebrates, they were generally not consuming that much food. This suggests maintenance or suboptimal feeding to maintain metabolism and basic body function with little surplus energy available for allocation to growth, reproduction, and other vital rates (Li *et al.*, 2005). Maintenance feeding may be offset by times or locales where the predators augment their diet with preferred prey (Link and Burnett, 2001). However, if this maintenance strategy is maintained over long periods, it could have important implications for other vital population rates and overall fitness (Opstad *et al.*, 2006).

The significant effect of diet on consumption rates should not be unexpected. But determining *a priori* which prey are significant
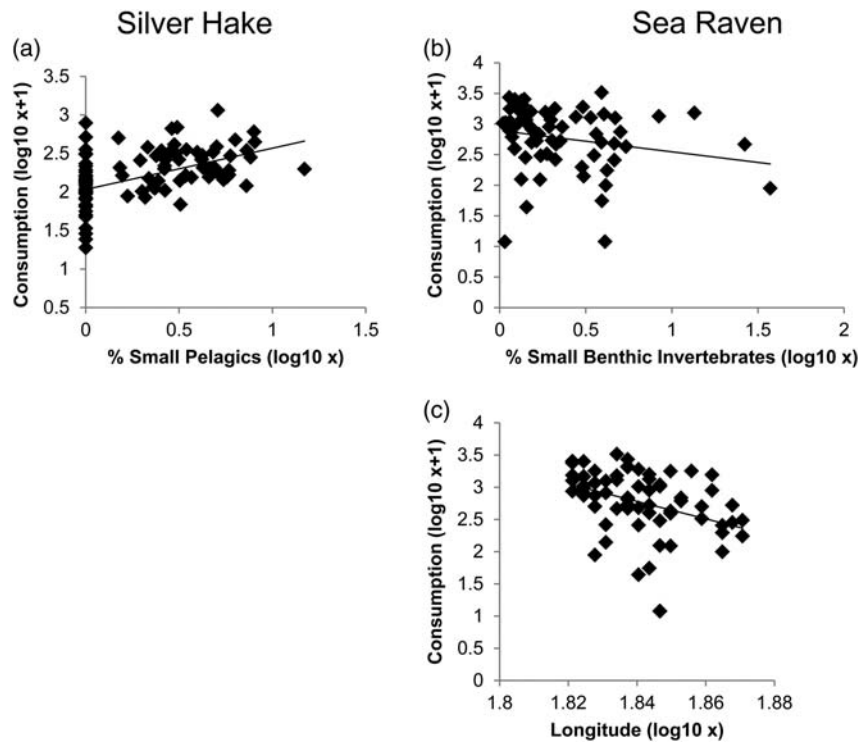
Figure 5. Linear regressions showing the relationship between significant explanatory variables and annual per capita consumption for silver hake and sea raven. The first panel shows the relationship between consumption and (a) percentage small pelagics for silver hake. The next two panels depict how consumption is related to (b) percentage benthic invertebrates, and (c) longitude, for sea raven. Percentages indicate the proportion by weight of each prey in the predator's diet.

in terms of limiting or enhancing this vital population rate poses a challenge due to the high spatial and temporal variation in prey populations. For example, small pelagics are seasonally migratory and occur in dense schools distributed heterogeneously in the seascape. This prey category was associated with higher consumption for silver hake in a pattern similar to that for some Bering Sea predators (Livingston, 1993). Benthic invertebrates, which can also have a patchy distribution (Stokesbury and Himmelman, 1995), comprised another key prey category that significantly affected consumption by sea raven and little skate. Because populations fluctuate over space and time, repeating these analyses for the same species in different systems or over a different temporal range may yield patterns distinct from those reported here. Thus, we assert that evaluations of consumption and likely other vital rates in an EFH context require a reasonable and spatially-explicit understanding of fish feeding ecology.

Location variables were important determinants of consumption, as they identified the location of particular prey resources and/or hotspots of consumption. For instance, sea raven had greater consumption in the eastern portion of the region. The significance of longitude for sea raven reflected the hotspots in consumption located on Georges Bank and coastal Gulf of Maine, which in turn are related to the particular prey consumed there. In contrast, winter flounder had higher consumption on Georges Bank and lower consumption in Southern New England, indicated by a significant negative relationship between consumption and longitude. Winter flounder was the only species for which longitude and salinity, but no diet variables, explained the variability in consumption, largely due to their benthic feeding nature, limited gape width, lack of clearly-preferred

prey, and availability of their most common prey taxa across those regions. Spatial patterns in feeding can have implications for other vital rates and could be strongly linked to the proximity and availability of these hotspots for fish populations.

Depth and, to a lesser extent, salinity were important factors for consumption by little skate, reflecting high consumption rates in shallow areas near the coast where salinities are lower. We expected depth and salinity to be representative of major oceanographic features and to play a larger role for each of the species examined (Macpherson and Duarte, 1991). The relatively low explanatory value of these oceanographic factors for the other species examined is consistent with studies of how these factors relate to the abundance and distribution of fishes in this and similar ecosystems (Overholtz and Tyler, 1985). Substrate grain size was also not an important factor influencing consumption rates. Several studies have noted or suggested the importance of this aspect of habitat for marine fishes (Tupper and Boutilier, 1995; Cook and Auster, 2005), yet it was not a critical component here. Particularly for species such as winter flounder and little skate whose diet is composed of a large proportion of benthic invertebrates, we expected bottom type to be influential. Yet for these fishes, the role of habitat factors was overshadowed by the importance of diet. The extreme patchiness of habitat, the diurnal variation in habitat use, and the mobility of these species all likely contributed to this lack of significance. Other studies are increasingly noting that bottom type is a poor delineator of habitat for temperate marine fishes on continental shelves (Methratta and Link, 2006; Sundermeyer *et al.*, 2006; Methratta and Link, 2007). Considering that habitat associations shift with ontogenetic stage (Swain, 1993), that habitat is spatially patchy, and that marine
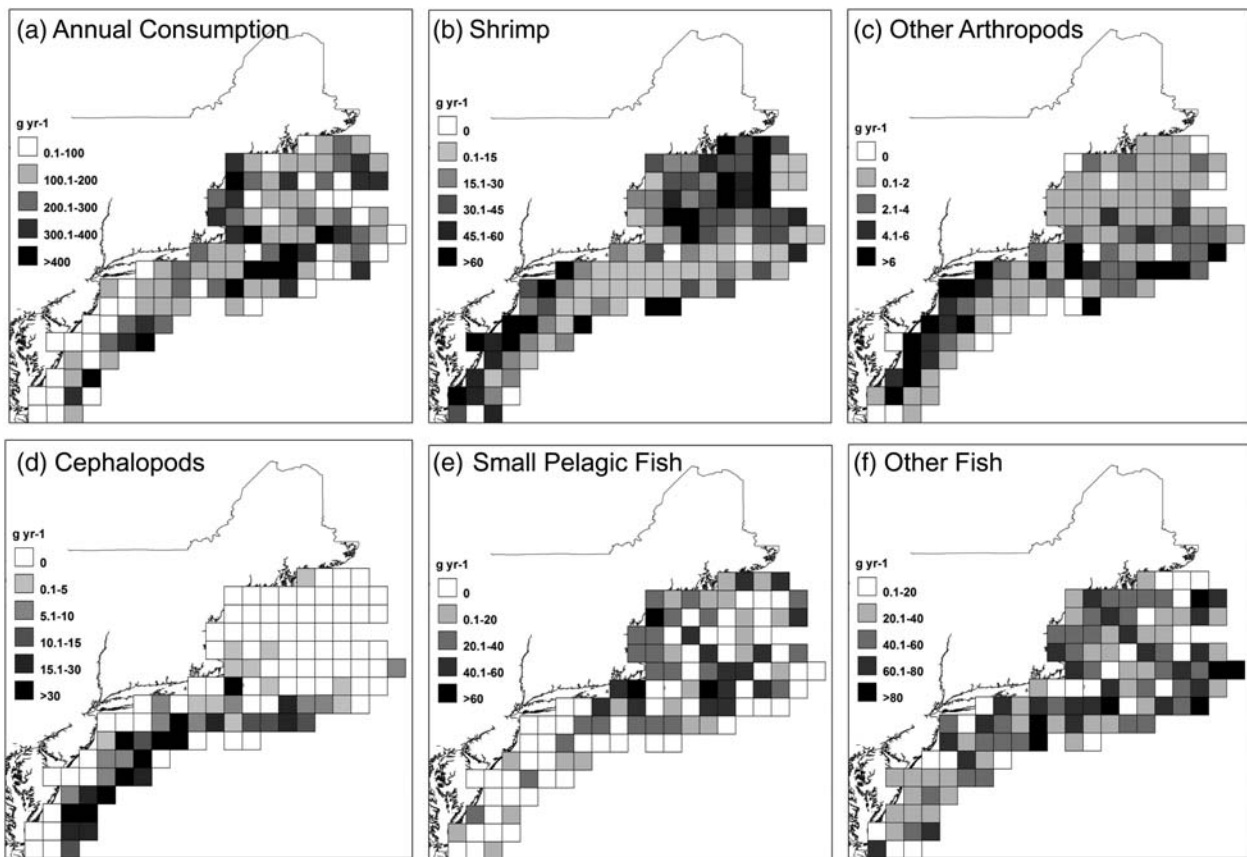
Figure 6. Spatial distribution of consumption and diet for silver hake on the northeastern US Continental Shelf from the Gulf of Maine to the mid-Atlantic Bight. Panel (a) shows the annual per capita rate of consumption (g yr^{-1}). The remaining panels depict the diet percentages : (b) percentage shrimp, (c) percentage other arthropods, (d) percentage cephalopods, (e) percentage small pelagic fish, (f) percentage other fish, in silver hake diets. Spatial cells are 55.5 km × 55.5 km.

fish migrate diurnally and seasonally (Metcalfe *et al.*, 2002), perhaps this is not surprising.

The large amount of unexplained variance was similar to that found by related studies of marine fishes in continental shelf systems (Overholtz and Tyler, 1985). There are numerous factors that could contribute to this low explanatory value. For example, all of the species we examined are opportunistic omnivores whose diets change with ontogeny, size, season, and region. In most cases, their diets are dominated by small invertebrates and other benthos in early life history, but more by fish later in ontogeny (Link and Almeida, 2000). A previous paper explored fish abundance–habitat associations for demersal species at large spatial scales along a gradient in fish size, and found stronger relationships with depth (fish increased in size with depth) and temperature (a reflection of seasonal migration patterns) (e.g. Methratta and Link 2007). There is also considerable variation in feeding behaviour and mobility that may have contributed to the unexplained variance. For the relatively more mobile species examined here (i.e. silver hake), piscivory had a significant influence on consumption rates. Consumption rates may also vary with maturity stage. Some iteroparous fish species have been shown to increase feeding during the ripe and running stages of reproduction while others increase feeding post-spawning (Link and Burnett, 2001). While understanding differences among population strata is important (Garrison and Link,

2000), understanding the factors that influence *per capita* differences within entire populations is also relevant from a management perspective. Perhaps subsequent analyses that explore spatial patterns in association with ontogeny, season, behaviour, or somatic condition would better explain the variability in this vital rate.

Despite its relevance to fisheries management, little is known about consumption rates at broad spatial scales (i.e. shelf wide) in marine ecosystems, although many *in vivo* studies for the purposes of bioenergetic analyses have been conducted. Some studies have made important strides, but further progress has been impeded by the difficulties in collecting the necessary data. Eastern Pacific dolphinfish (*Coryphaena hippurus*), for example, exhibit sex- and size-based differences in consumption rates that vary regionally (Olson and Galvan-Magana, 2002). In the eastern Bering Sea, Livingston (1993) showed that consumption of walleye pollock (*Theragra chalcogramma*) by its predators depended on predator age, whereas predation on herring (*Clupea pallasi*) depended on the rate at which predators encountered herring schools. The foraging hotspots of leatherback turtles in the Atlantic have been linked with high densities of their preferred zooplankton prey (Hays *et al.*, 2006). Similar patterns have been recognized for stellar sea lions and patches of forage fish in southeast Alaska (Gende and Sigler, 2006). Consumption by predators can have a large and significant
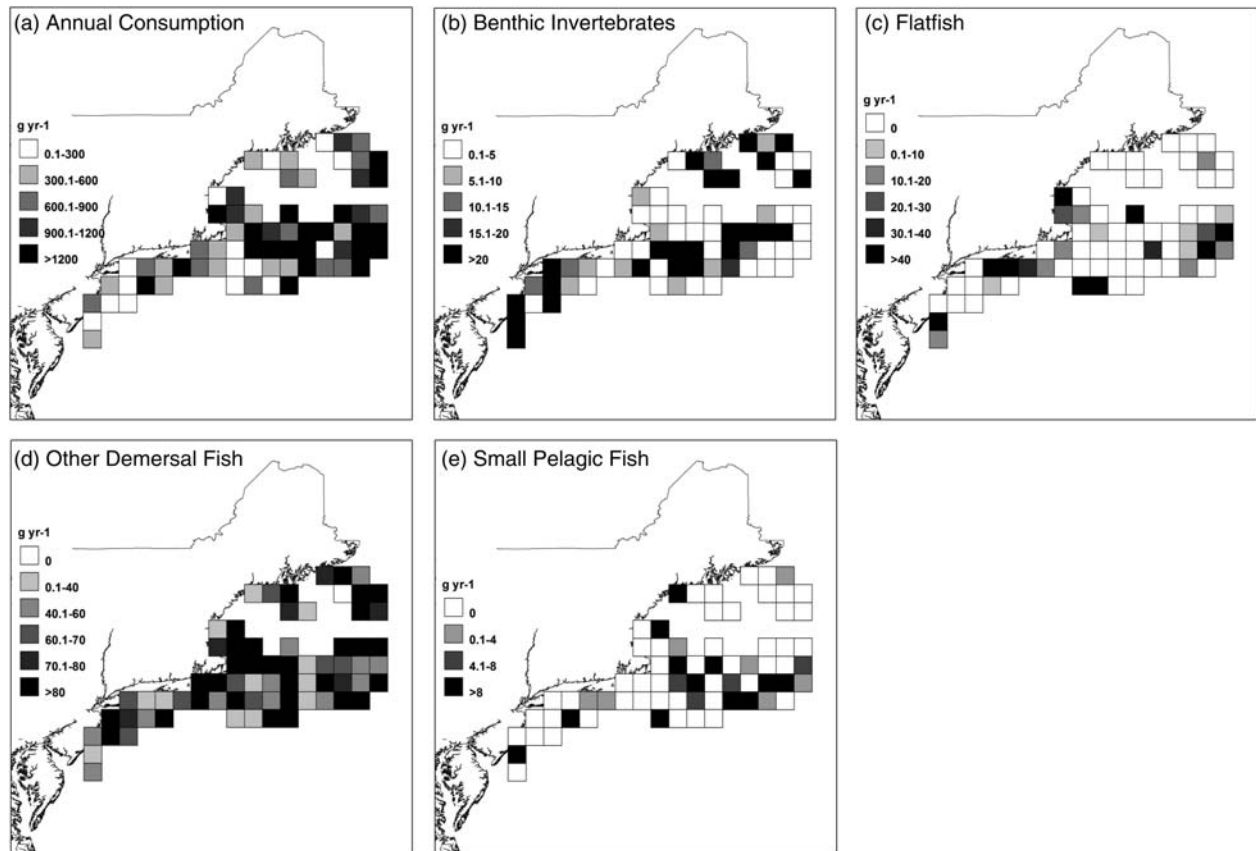
Figure 7. Spatial distribution of consumption and diet for sea raven on the northeastern US Continental Shelf from the Gulf of Maine to the mid-Atlantic Bight. Panel (a) shows the annual per capita rate of consumption (g yr^{-1}). The remaining panels depict the diet percentages : (b) percentage benthic invertebrates, (c) percentage flatfish, (d) percentage other demersal fish, (e) percentage small pelagic fish, in sea raven diets. Spatial cells are 55.5 km × 55.5 km.

effect on the vital rates of prey populations. Such was the case in the North Sea where an aggregate of predatory whiting (*Merlangius merlangus*) consumed an aggregate of more than 50 million juvenile cod (*Gadus morhua*), accounting for the major source of juvenile cod mortality in this ecosystem (Temming *et al.*, 2007). More localized studies have demonstrated the importance of regional differences in prey quality (Cross *et al.*, 2005), habitat complexity (Talman *et al.*, 2004), and discards (Bozzano and Sarda, 2002). Besides consumption, broad-scale spatial variability in other vital rates, such as recruitment, remains coarsely resolved, although much work has examined stock-recruitment relationships and the factors underlying the variability in recruitment for the purpose of constructing population dynamic models (Brodziak and Legault, 2005). The dearth of research on vital population rates at fisheries-relevant spatial scales is primarily due to the practical challenges of gathering sufficient information to support such analyses. Data-mining techniques such as those employed here may provide an alternative approach for further addressing the spatial heterogeneity of vital rates at informative and appropriate scales.

Fisheries managers may wish to consider the possibility that higher-level EFH approaches used to help manage a multi-species fishery may not be fully feasible. In one of the most well-studied and data-rich marine ecosystems (NEFC, 1988; Link and Almeida, 2000), the relationships we uncovered were generally weak. This would indicate that attempting to establish level III

(and above) EFH considerations may be difficult due to scaling issues and the lack of process knowledge. The EFH mandate has contributed little towards the management of exploited fish stocks in terms of operational management advice. Other criteria besides EFH that incorporate spatial considerations may be worth considering.

We examined a vital population rate that has consequence for fisheries management, the balancing of ecosystem energy budgets, and the development of population dynamic modelling at broad spatial scales. While the role of habitat at finer spatial scales is evident for many species, our work suggests that a narrow focus on habitat considerations at the exclusion of other factors may obscure the larger picture for vital rates. Careful consideration of other aspects of the biology (e.g. feeding ecology, reproduction, mortality, production) of focal species at the synoptic scales relevant to those at which fisheries operate is needed.

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