



FEATURE ARTICLE

It takes guts to locate elusive crustacean prey

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ABSTRACT: Mobile crustacean prey, i.e. crangonid, euphausiid, mysid, and pandalid shrimp, are vital links in marine food webs. Their intermediate sizes and characteristic caridoid escape responses lead to chronic underestimation when sampling at large spatial scales with either plankton nets or large trawl nets. Here, as discrete sampling units, we utilized individual fish diets (i.e. fish biosamplers) collected by the US National Marine Fisheries Service and Northeast Fisheries Science Center to examine abundance and location of these prey families over large spatial and temporal scales in the northeastern US shelf large ecosystem. We found these prey families to be important to a wide variety of both juvenile and adult demersal fishes from Cape Hatteras to the Scotian Shelf. Fish biosamplers further revealed significant spatial shifts in prey in early spring. Distributions of mysids and crangonids in fish diets shoaled significantly from February to March. Distributions of euphausiids and pandalids in fish diets shifted northward during March. Of multiple hypotheses for these shifts, prey migration is most strongly supported. Rather than only the classic ontogenetic shift from feeding on shrimp to piscivory, of the 25 identified diet shifts in fish predators, 12 shifts were toward increased shrimp feeding frequency with increasing body length.

KEY WORDS: Fish feeding · Northwest Atlantic · Pandalidae · Mysidae · Euphausiidae · Crangonidae · Migration

INTRODUCTION

The ability to understand ecological roles of important prey species at large spatial scales relies heavily on the observational tools in use. In the northeastern US shelf large ecosystem (NESLE), tools used to sample organisms at the scale of 100s of km are primarily



NOAA scientist displaying a 'shrimp-sampling device': a goosefish *Lophius americanus* caught by the Northeast Fisheries Science Center Trawl Survey.

Photo: Anne Byford

limited to large trawl nets and small plankton sampling devices. Overlap between these tools is imperfect, and some prey species vital to marine food webs are sampled ineffectively. Caridoid or 'shrimp-like' crustaceans such as members of the families Crangonidae, Pandalidae, Mysidae and Euphausiidae can be easily missed or grossly underestimated with these common sampling techniques.

Most crustaceans belonging to these groups are too small to be effectively sampled by large trawl nets with mesh and liner openings of approximately 10 and 1.25 cm, respectively (NEFC 1988). Furthermore, standard plankton nets are usually towed quite slowly, approximately 1 to 2 knots or 2 to 4 km h⁻¹ (UNESCO 1968), and the 'caridoid escape responses' exhibited

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by these organisms allow them to evade nets in many cases (Fleminger & Clutter 1975). Some species form dense schools or swarms that are patchily distributed (Mauchline 1980), and often individuals occur within a few meters of the substratum during the day (Hurlburt 1957, Haynes & Wigley 1969, Brown et al. 2005, Sato & Jumars 2008), below the area swept by most plankton sampling devices (Hardy 1926, UNESCO 1968, Reid et al. 2003). Sled samplers that are towed faster more effectively sample epibenthic organisms but are often tailored to a given bottom type or habitat, making comparisons difficult (Hessler & Sanders 1967). Their filling with sediments further undermines reliable quantitative estimates of abundance. Additionally, sediment-containing samples are more logistically cumbersome and time consuming and therefore less commonly used over large spatial scales (but see Wigley & Burns 1971, Theroux & Wigley 1998).

Although information on broad-scale distribution patterns of these taxa may be limited, regional and local studies consistently indicate that they are important prey for many commercially important fishes and for baleen whales in the northwest Atlantic. Crangonidae are important prey organisms in adult flounder diets and also important predators of larval flounder (Witting & Able 1995). Euphausiidae dominate diets of whales (Ryan et al. 2014) and are important diet items of migrating salmon smolts in estuary mouths (Renkawitz & Sheehan 2011). Pandalidae include the commercially important northern shrimp *Pandalus borealis*, which has experienced record low numbers recently in the Gulf of Maine, resulting in fishery closures. *P. borealis* is also a major diet species for commercially important fishes such as cod and is subjected to top-down control by cod predation (Worm & Myers 2003). Finally, Mysidae dominate diets of cod <10 cm long (Link & Garrison 2002) and serve as prey for adults and juveniles of other commercially important species (Greccay & Targett 1996, Buchheister & Latour 2011).

These families perform additional vital ecosystem functions. They are highly omnivorous, with most species feeding on phytoplankton, holo- and merozooplankton, as well as benthos. Some Mysidae can digest detritus, including cellulose (Zagursky & Feller 1985, Friesen et al. 1986). This high degree of trophic connectivity, coupled with extensive mobility, means that they play an important role in nutrient import and export through spatially decoupled foraging, somatic growth and excretion (Steinberg et al. 2002, Jumars 2007). Given their obvious importance in marine food webs at regional scales, particularly for the NESLE (Smith & Link 2010), added under-

standing of their large-scale distribution patterns will fill knowledge gaps and may be useful in predicting effects of global stressors on their distributions and abundances.

Here we utilize a long-term diet study conducted by National Marine Fisheries Service (NMFS) and Northeast Fisheries Science Center (NEFSC) to determine the occurrence of our 4 target prey families in the diets of fishes in the NESLE. Using gut contents of individual fishes as the sampling unit (i.e. a fish biosampler) has been an effective tool for surveying prey distribution. This technique has been applied to a diverse array of prey species, from isopods (Rachlin & Warkentine 1997) to ctenophores (Link & Ford 2006), and has been used to measure benthic species richness (Frid & Hall 1999, Link 2004). Further, this approach has been used to sample capelin through cod diet analysis (Fahrig et al. 1993) and to detect effects of mobile bottom fishing gear (Smith et al. 2013). For each prey family we asked the following questions. (1) How important are these families to fish species of the NESLE? (2) Is there a fish size threshold above which they are no longer eaten? Finally, (3) Can this sampling method resolve known or putative patterns in the seasonal distribution of these shrimp?

METHODS

Fish collection

Fish used for diet analysis were collected as part of the seasonal bottom trawl survey conducted by NEFSC. This survey uses a stratified random sampling design and samples depths from 8 to 400 m (Azarovitz 1981, NEFC 1988). Each survey samples between 350 and 400 stations on the continental shelf between Cape Hatteras, NC, USA and Nova Scotia, Canada, and lasts approximately 8 to 10 wk. Further details are given in Azarovitz (1981) and NEFC (1988).

Diet analysis

Specific information regarding food-habits sampling and data for the NESLE can be found in Link & Almeida (2000) and Smith & Link (2010). To summarize, a subset of collected fish species was analyzed for food habits from 1973 to present. From 1973–1981, stomach contents were preserved and returned to the laboratory for identification, and organisms were identified to the lowest possible taxon (often to

species). From 1981–present, stomach contents were examined at sea. Approximately 25 to 40% of the fish stomachs were empty, varying by species (Link & Almeida 2000). Surveys from 1973–2012 were conducted in autumn and spring. Winter trawls were conducted in 1978 and 1992–2007. Summer trawls were conducted 1977–1981 and 1991–1995 (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m538p001_supp.pdf).

Prey family importance

Given the changes in prey identification methods and species resolution over the time span of the survey, we chose to group shrimp by family (Table S2 in the Supplement). The total number of fish stomachs containing each prey family was compiled. These values are affected by encounter rates between predators and prey, predator preference, and also the numbers of predator individuals sampled, which is unequal among predator and prey species (Table 1). They are

also affected by uncontrolled physiological variables, such as temperature effects on ingestion and digestion. To determine the importance of each prey family in the diet of a given predator species, we calculated

$$P_{ijr} = \frac{S_{ijr}}{S_{ir}}$$

Where P_{ijr} is the proportion of prey j in predator i stomachs in region r . S_{ijr} is the number of i predator stomachs containing prey j in region r . S_{ir} is the total number of stomachs sampled for predator i in region r (including empty stomachs). We report diet proportions for the top 10 fish predators of each prey family, which correspond to species where prey of interest are found in at least 5% of the diets analyzed.

Statistical analysis

Statistical tests were conducted using Matlab R2014b and R (R Core Development Team 2009). To test the hypothesis that there is a predator size

Table 1. Numbers of fish stomachs collected across regions in the Northwest Atlantic as part of the National Marine Fish Service Trawl Survey from 1973–2012

Common name	Species name	Number sampled in each region					
		Scotian Shelf	Gulf of Maine	Georges Bank	Southern New England	Mid-Atlantic Bight	South-Atlantic Bight
Acadian redfish	<i>Sebastes fasciatus</i>	831	4788	255	3	0	0
Atlantic cod	<i>Gadus morhua</i>	4131	12805	15572	2241	73	0
Atlantic herring	<i>Clupea harengus</i>	732	7859	3360	5629	4661	22
Atlantic mackerel	<i>Scomber scombrus</i>	255	878	1764	3035	3033	1
Butterfish	<i>Peprilus triacanthus</i>	103	455	843	3147	4248	437
Fourspot flounder	<i>Paralichthys oblongus</i>	9	975	4325	9359	6789	15
Goosefish	<i>Lophius americanus</i>	253	3902	1287	4887	2794	53
Haddock	<i>Melanogrammus aeglefinus</i>	6250	7499	11632	472	79	0
Little skate	<i>Leucoraja erinacea</i>	538	2929	19679	25541	19107	6
Longhorn sculpin	<i>Myoxocephalus octodecemspinosus</i>	1113	4256	10680	3618	26	0
Ocean pout	<i>Zoarces americanus</i>	298	1067	1966	2895	408	0
Pollock	<i>Pollachius virens</i>	1441	4198	2102	77	8	0
Red hake	<i>Urophycis chuss</i>	1066	10863	6999	7628	1715	0
Sea raven	<i>Hemitripterus americanus</i>	1018	2553	4655	1236	117	0
Silver hake	<i>Merluccius bilinearis</i>	2848	24796	10739	13441	6575	24
Smooth dogfish	<i>Mustelus canis</i>	0	17	507	3860	10606	1075
Smooth skate	<i>Malacoraja senta</i>	574	3084	416	11	13	0
Spiny dogfish	<i>Squalus acanthias</i>	3623	18090	17364	17662	23916	818
Spotted hake	<i>Uropycis regia</i>	0	39	465	5593	12536	358
Summer flounder	<i>Paralichthys dentatus</i>	0	71	826	7227	11711	265
Thorny skate	<i>Amblyraja radiata</i>	993	5341	1521	34	9	0
Weakfish	<i>Cynoscion regalis</i>	0	0	3	1091	5078	492
White hake	<i>Urophycis tenuis</i>	1983	14006	2240	693	108	1
Windowpane flounder	<i>Scophthalmus aquosus</i>	1	841	5755	6493	6401	19
Winter flounder	<i>Pseudopleuronectes americanus</i>	1309	3676	6053	7209	1162	0
Winter skate	<i>Leucoraja ocellata</i>	135	1072	19894	9381	5249	0
Witch flounder	<i>Glyptocephalus cynoglossus</i>	2050	6029	761	952	956	0
Yellowtail flounder	<i>Limanda ferruginea</i>	242	1912	5805	5563	342	0

threshold above which fewer target prey are consumed, we conducted multiple Wilcoxon rank sum tests comparing average lengths of fish containing the target prey family with those fish not containing the target prey family. We chose a Wilcoxon rank sum test to accommodate unequal sample size between groups and non-normal distribution of fish lengths. This process yielded 40 separate comparisons, so we used a Bonferroni correction for multiple comparisons to generate a list of fish predators in which there was a significant difference between the sizes of fish with and without prey families. For these fish species, we identified the size cutoff at which it becomes less (or more) likely to find the target prey family in the diet by using a classification and regression tree, CART (Breiman et al. 1984).

To visualize distribution patterns for each prey family, we constructed a grid spanning NESLE with a 15 km² box size. We then compiled latitudes and longitudes where target prey were found in fish diets to produce prey distribution maps. Prey distribution maps are presented as the proportion of fish diets containing the prey family of interest out of the total number of analyzed diets from the 15 km² box.

To address changes in the seasonal distribution of Crangonidae and Mysidae, we selected a time of year with good sampling resolution and a time in which these families are reported to migrate into estuaries (Bamber & Henderson 1994, Jumars 2012). Working around poor historical coverage in some years (see Table S1 in the Supplement), we selected a 15 yr block for which the region was sampled during the months of interest (February and March). For statistical analyses, we grouped all fish biosamplers by station to avoid inflating our degrees of freedom. Therefore, analyses were conducted on the number of stations in which target prey were found in fish diets out of the total number of stations. We tested the hypothesis that stations where fish contained Crangonidae or Mysidae are significantly shallower in March than in February using a 2-way ANOVA, with month and diet (i.e. presence of a Crangonidae, Mysidae, or neither) as our explanatory variables. The analysis was conducted on log-transformed depth values and followed with a Tukey-Kramer pairwise test.

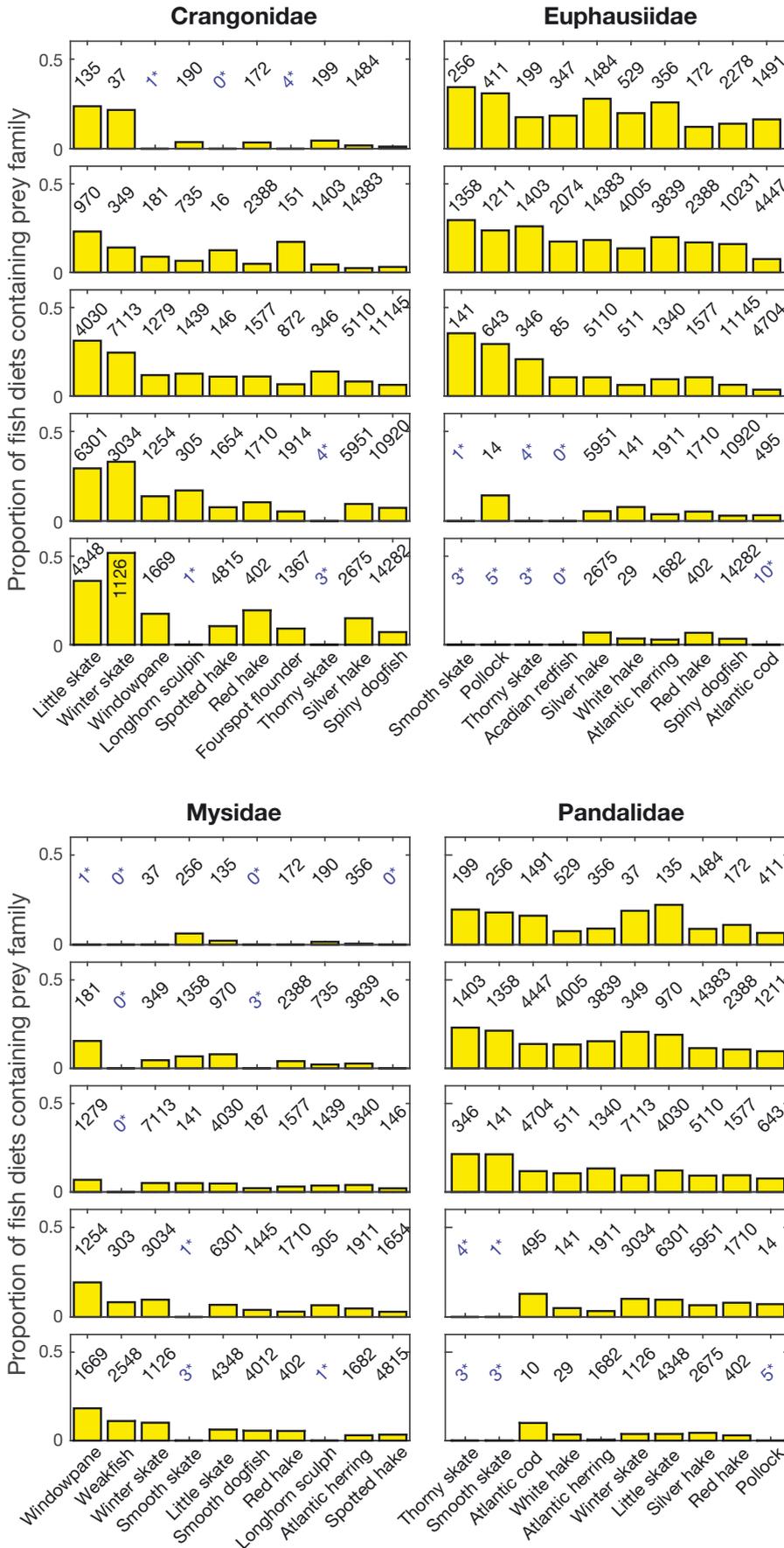
To address seasonal distribution in Euphausiidae and Pandalidae, we had no *a priori* selection criterion, so we looked for months that had the most consistent sampling. We compiled data of the latitude and longitude where Euphausiidae and Pandalidae were found in fish diets and grouped these data by station. We then calculated the distance from a refer-

ence point located near Pamlico Sound along the shortest arc (to account for the curvature of the earth). This technique is similar to that used by Nye et al. (2009) to address movement patterns of fish stocks. One confounding factor is that the trawl survey moves up the northeastern coast in March. Therefore, due to sampling location alone, one would expect a northward trend in the site of prey capture over time within year. To account for this sampling bias, we conducted an ANCOVA to determine whether the slope of the distance from reference point versus date differs significantly between fish biosamplers containing Euphausiidae, Pandalidae, or neither.

RESULTS

The 4 prey families varied in dietary importance across species and region (Fig. 1). Overall, Euphausiidae and Pandalidae were prevalent in diets from the Gulf of Maine, Scotian Shelf and Georges Bank, whereas Crangonidae and Mysidae were common in diets from Georges Bank, southern New England, and the Mid-Atlantic Bight. All prey families were found primarily in the diets of benthivores such as flounder, skate, and hake species (Fig. 1.), although diel vertical migration of both the shrimp (Jumars 2012) and some of the fishes such as Atlantic herring *Clupea harengus* (Gong et al. 2010) and silver hake *Merluccius bilinearis* (Bowman & Bowman 1980) leave open the possibility of pelagic encounter.

In 25 out of 40 cases, predator size varied significantly between individuals with and without target prey in their diets (Fig. 2). In 13 out of these 25 cases, fish containing target prey families were significantly smaller than fish without the prey family. In the remaining 12 cases, however, fish containing target prey families were significantly larger than fish without the prey family. For both euphausiids and pandalids, 5 out of 7 of the size thresholds indicate that larger fish were eating these prey families significantly more frequently. Median lengths that represent a transition to a euphausiid and pandalid diet (across all predators) were 29.5 and 37.5 cm, respectively. Size thresholds for fish eating mysids all indicated that smaller fish were consuming significantly more mysids. The median length that marked the transition away from a mysid diet was 29.5 cm. Four out of 6 of the size thresholds indicated that smaller fish took significantly more crangonids, with a median length of 23 cm. Winter skate and spiny dogfish had the largest size at transition (ranging from 66.5 to 73.5 and 63. to 79.5 cm, respectively). The ma-



A The proportion of fish eating Crangonidae and Mysidae was higher near the coast in March compared to February (Fig. 3).
B Both month and diet content (i.e. diet containing Crangonidae, Mysidae, or neither) had significant effects on depth of occurrence (Fig. 4, Month: $F_{1,4497} = 314$, $p < 0.001$, Diet: $F_{2,4497} = 70.47$, $p < 0.001$, 2-way ANOVA).
C The depth of fish ingesting Crangonidae and Mysidae was reduced by 41 and 36%, respectively, from February to March, while the reduction in the depth of fish bio-samplers without these prey families was 31%.

The proportion of fish eating Euphausiidae and Pandalidae shifted northward from early to late March (Fig. 5). The slope of the relationship of time (in days) versus distance from the Pamlico Sound reference point was significantly steeper for fish containing Euphausiidae and Pandalidae than for fish without these prey families (Table 2, Fig. 6, Euphausiidae, $p < 0.0001$; Pandalidae, $p < 0.0001$).

A Scotian Shelf, **B** Gulf of Maine, **C** Georges Bank, **D** Southern New England, and **E** Mid-Atlantic Bight. Numbers over bars indicate the total number of diets analyzed for each fish species. Numbers in blue with an asterisk indicate a sample size <10 and the proportion is not shown because of its imprecision. Fish were collected as part of the National Marine Fish Service Trawl Survey from 1973–2012

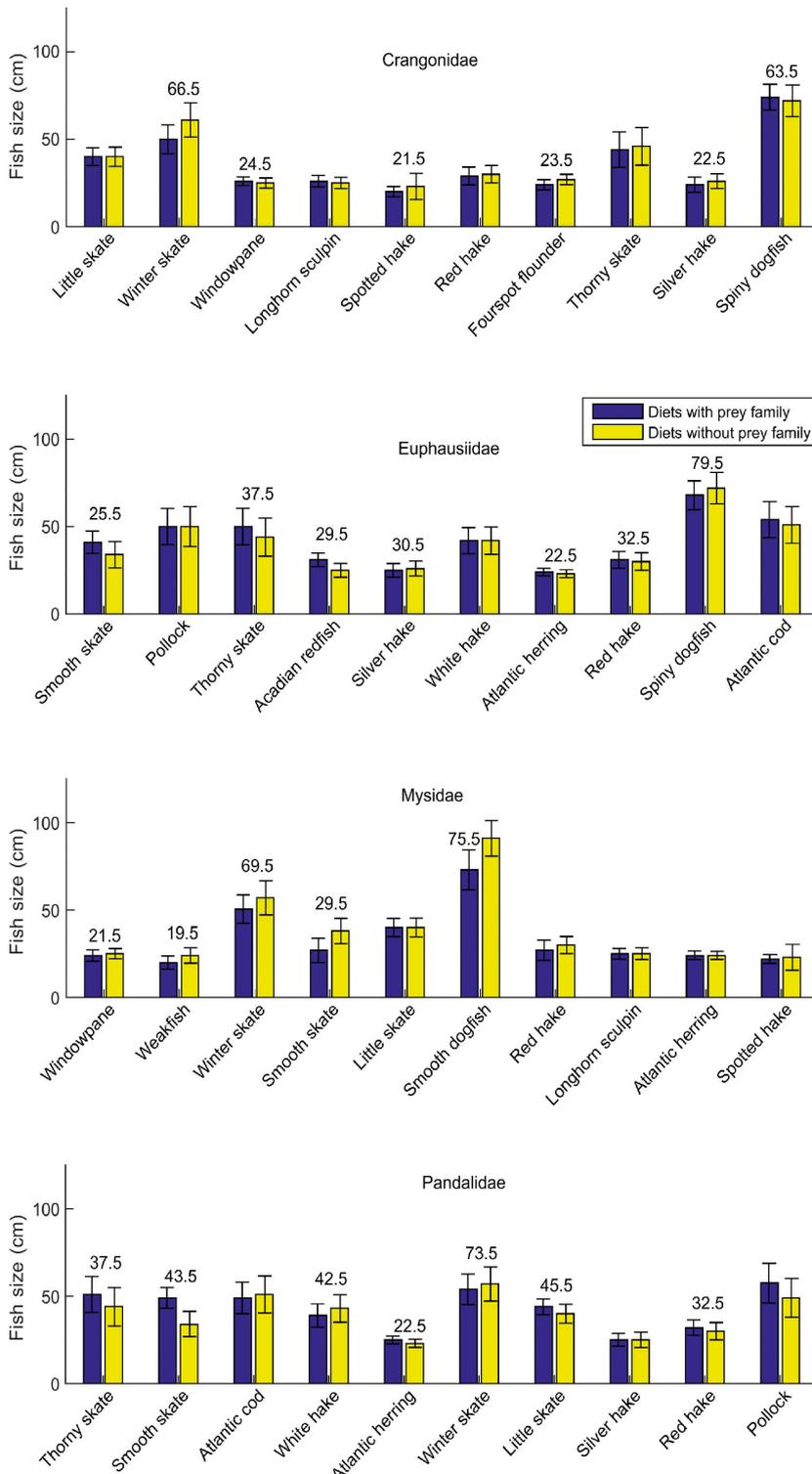


Fig. 2. Mean size (\pm SE) of fish biosamplers with and without prey species of Crangonidae, Euphausiidae, Mysidae, and Pandalidae in their diets. Fish were collected as part of the National Marine Fish Service Trawl Survey from 1973–2012. Bar pairs with a number are significantly different (Wilcoxon rank sum test followed by Bonferroni correction). Numbers correspond to the size threshold (cm) at which a predator becomes less or more likely to contain the prey family of interest (as determined by a classification and regression tree, CART)

DISCUSSION

Our results show that the 4 prey families are important diet components of many demersal predators, especially Gadiformes (cod, hake and pollock), Pleuronectiformes (flounder) and Elasmobranchii (skates and dogfish). These results corroborate findings from several studies demonstrating the importance of these families to demersal fish communities (Garrison & Link 2000b, Link & Garrison 2002, Worm & Myers 2003, Smith & Link 2010). Additionally, these prey families were common in the diet of pelagic Atlantic herring.

These prey families play an important role throughout the NESLE ecosystem. Most NESLE regions contained all prey families, with some families being more important in certain areas and seasons. Pandalidae and Euphausiidae made up a particularly large proportion of the diets of fishes in the Gulf of Maine, on the Scotian Shelf and on Georges Bank. Within our regions of focus, the range of Crangonidae and Mysidae extended from the Mid-Atlantic Bight to the Scotian Shelf, yet they were particularly important in the diets of fishes in southern New England, in the Mid-Atlantic Bight, and on Georges Bank.

Our results suggest that these shrimp families are eaten by fishes of a broad size range. While we did find significant predator length thresholds that marked differences in the propensity to consume shrimp, about half of these thresholds (13/25) indicated smaller fish eating shrimp whereas the other half indicated shrimp being consumed by larger fish. This result was surprising given evidence from previous diet studies suggesting that these shrimp species are important prey for young fish before they transition to piscivory (Garrison & Link 2000a, Sherwood et al. 2007). Fish size thresholds all indicated that smaller fish eat more mysids, highlighting their importance in the diet of juvenile fish (Grecay & Targett 1996, Link & Garrison 2002, Buchheister & Latour 2011).

Detecting size thresholds below which smaller fish eat these shrimp families was expected because this result supports the idea that these shrimp are important prey

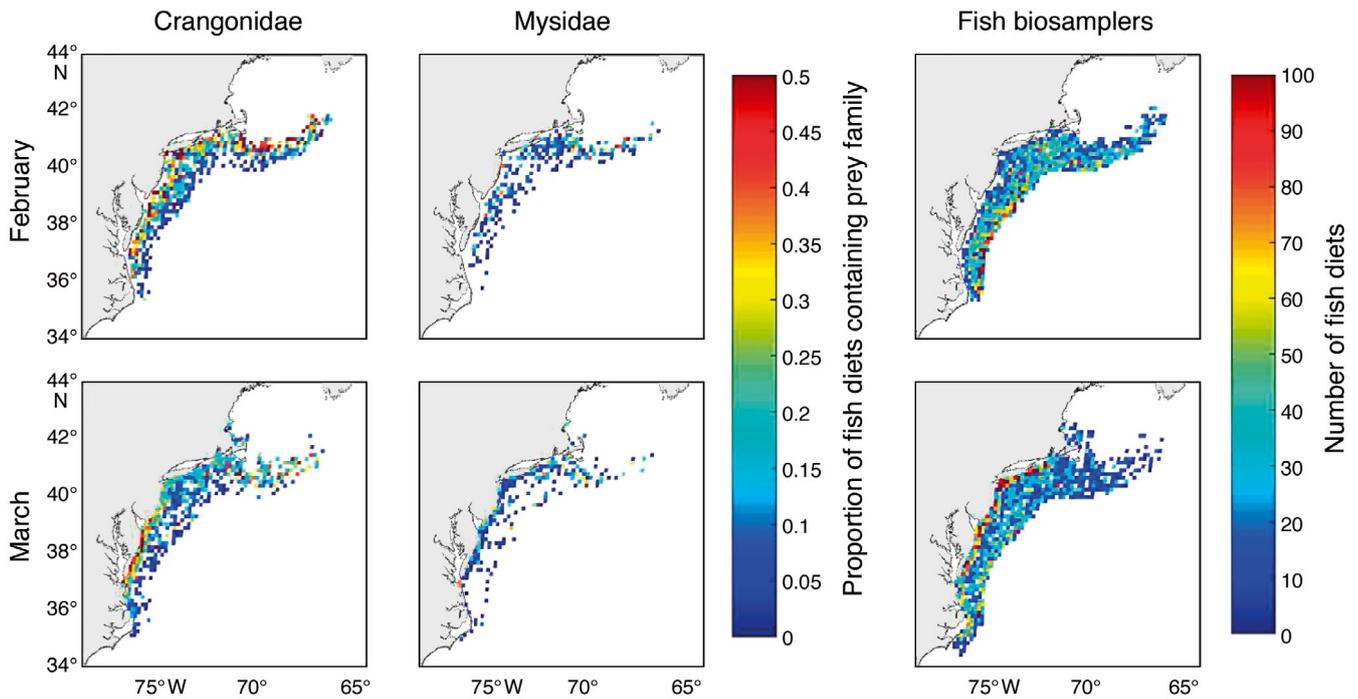


Fig. 3. Proportion of fish diets containing Crangonidae and Mysidae, and the total number of analyzed fish diets. Data from 1992–2007 are shown to illustrate shoaling from February to March

for juvenile fish. As fish get larger, they become more equipped to capture and process larger prey (reviewed by Juanes 1994). From an energetic standpoint, there is a point at which the energy returns of small prey become sub-optimal, and fish must switch to larger prey (Sherwood et al. 2007). So, why do we see a pattern of larger acadian redfish, red hake, as well as thorny, smooth, and little skate consuming more euphausiids and pandalids than the small fish of these species? We cannot identify the mechanism at work here, but one possible scenario is that larger fish may incidentally (or opportunistically) ingest

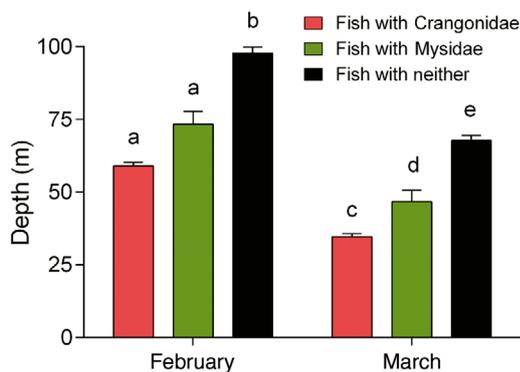


Fig. 4. Average depth (+SE) of Mysidae, Crangonidae, and fish biosamplers collected in February and March from 1992–2007. Letters over bars indicate significant differences (Tukey-Kramer pair-wise comparisons)

crustacean prey while preying on small, planktivorous fish foraging on shrimp aggregations. Opportunistic generalist feeding is common among demersal fishes of the NESLE (Smith & Link 2010). Regardless of the mechanism at work, the fact that prey families were effectively caught by a diverse array of predators spanning the entire NESLE ecosystem indicated that the best approach for using fish as biosamplers was to collectively use all fish species that had ever contained the prey family of interest. In this case, all 28 predators listed in Table 1 were used as samplers for all 4 prey families.

Diet proportion maps suggest that fish consuming Crangonidae and Mysidae become more concentrated nearshore from February to March. Importantly, there is also an apparent distributional change by the fish biosamplers without Crangonidae or Mysidae. Our analysis indicates, however, that the mean water depth of fish feeding on Crangonidae and Mysidae is significantly shallower than the mean water depth of the fish not feeding on Crangonidae or Mysidae. Furthermore, the percent change in the distribution of fish containing Mysidae and Crangonidae is greater than the percentage change by the fish biosamplers. Therefore, fish are generally found in shallower water from February to March, but this pattern is more pronounced for fish with Crangonidae and/or Mysidae in their diets. We interpret this

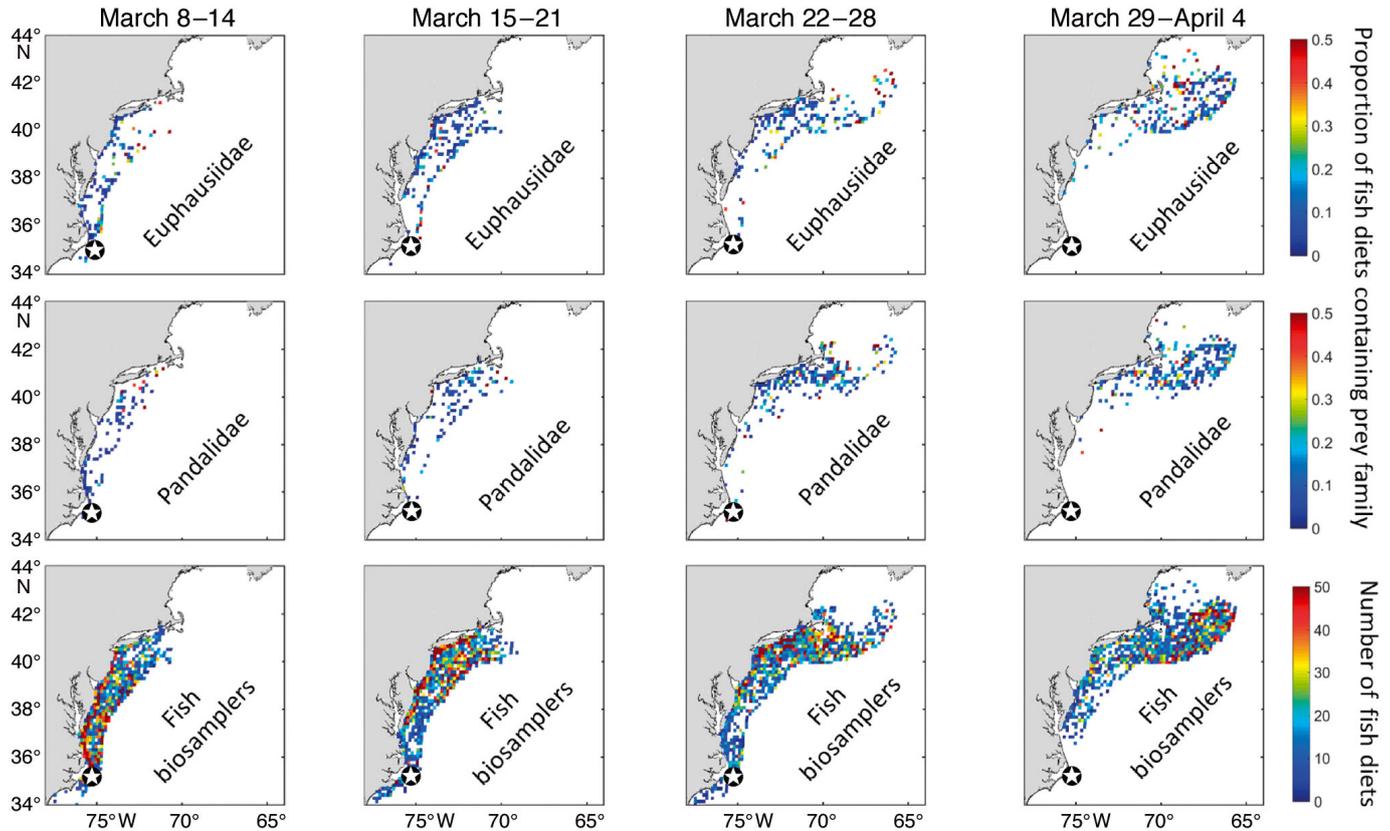


Fig. 5. Proportion of fish diets containing Euphausiidae, Pandalidae, and the total number of analyzed fish diets from early to late March, showing a northward shift. Star represents the location of the reference point from which distances were calculated

pattern to mean that there is a significant change in the distribution of Mysidae and Crangonidae even after controlling for the sampling bias. We note that our approach to aggregate data across predators does not account for variable prey selectivity among predators for the targeted prey families. Despite the coarse prey resolution, however, the reported feeding patterns were observed for the majority of predator species considered individually. It is also important to mention that we cannot detect the actual mechanism responsible for this shift in distribution, but we can provide potential hypotheses.

A distributional shift in Mysidae and Crangonidae from offshore into shallow coastal waters could be

caused by changes in species dominance within each prey family, asynchronous population growth, or the migration of individuals. For a change in species dominance to account for the observed pattern, a species of mysid and crangonid would need to decline in abundance in shelf waters in February while other species increase in abundance in March in nearshore environments. When we look at the species present in fish diets from 1973–1981 (the time period over which prey were preserved and identified to species), however, we find that Crangonidae and Mysidae are each represented by only a few species. *Crangon septemspinosa* made up 99% of the individuals in Crangonidae, and *Neomysis americana*

Table 2. ANCOVA describing the relationship between day and distance from reference point (Pamlico Sound). Euphausiidae and Pandalidae were collected from the stomachs of fish biosamplers. All comparisons are relative to fish not containing the prey family of interest. na: not applicable

Organism	Best fit line (distance from Pamlico Sound vs. day)	95% CI of slope	p-value comparing slope	95% CI interval of intercept	p-value comparing intercept	r ²	n
Fish with Euphausiidae	$y = 26.79x - 1430.56$	±0.76	<0.0001	±62.58	<0.0001	0.59	857
Fish with Pandalidae	$y = 25.54x - 1292.50$	±0.92	<0.0001	±76.64	<0.01	0.56	603
Fish with neither	$y = 19.93x - 979.13$	±0.44	na	±34.56	na	0.34	4144

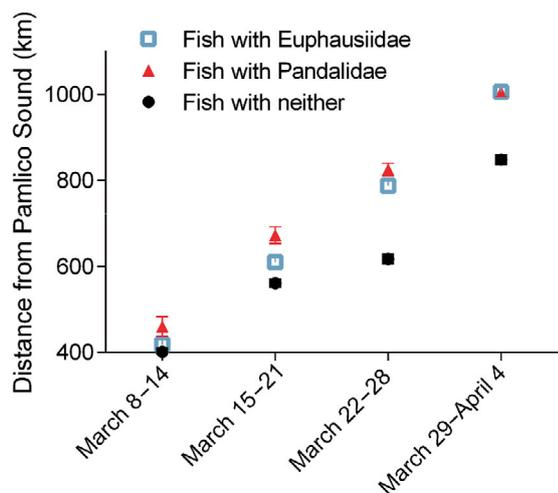


Fig. 6. Average distance (\pm SE) of Euphausiidae and Pandalidae found in fish diets from a reference point near Pamlico Sound from early to late March (see Fig. 5). Slopes and intercepts differ significantly for fish with Euphausiidae and Pandalidae versus fish with neither (see Table 2)

made up 93% of the individuals in Mysidae in fish diets from 1973–1981 in late winter to early spring. This dominance corroborates results from a field survey by Wigley & Burns (1971). There have been no large-scale surveys that have identified these prey families to the species level in recent years, which limits our ability to confirm the consistency in species dominance over the last 34 yr.

Asynchronous population growth could lead to the observed patterns in the absence of migration between the months of February and March if there were higher birth rates in shallow, nearshore environments. *C. septemspinosus* larvae typically hatch from May to June (Price 1962, Modlin 1980). Therefore, it is unlikely that higher crangonid birth rates cause higher coastal abundances in March. The reproductive cycle of *N. americana* is strongly latitude-dependent. Northern populations in Passamaquoddy Bay, Maine, have 2 reproductive pulses, one in spring and the other in summer, with a non-reproductive overwintering population (Pezzack & Corey 1979). These pulses contrast with their reproductive patterns in Delaware Bay and the coastal waters of New Hampshire, where reproduction is nearly continuous all year (Hurlburt 1957, Grabe 1996). Given the lack of discrete reproductive pulses in our regions of interest (southern New England and the Mid-Atlantic Bight), it is unlikely that the observed pattern is due to increased birth rates in shallow coastal waters in March.

A third explanation is that the observed pattern is due to the migration of individuals. Migration has been suggested for Crangonidae and Mysidae (Pezzack & Corey 1979, Bamber & Henderson 1994, Jumars 2012). Several accounts of these species show them becoming more abundant in nearshore environments in early spring (Price 1962, Hopkins 1965, Modlin 1980, Allen & Allen 1981, Sato & Jumars 2008). The distributional shift is just before the characteristic timing of the spring bloom in the shallow coastal regions of Chesapeake Bay (Harding 1994) and Delaware Bay (Powell et al. 2012). Therefore, it would be advantageous to migrate into shallow water to exploit abundant resources. Elevated phytoplankton concentrations are especially valuable to newly hatched offspring, providing a mechanistic explanation for crangonid and mysid immigration into these shallow waters before releasing young. If migration is occurring, it is important to understand the timing of its onset to predict the prey resources for juvenile fishes that rely on estuaries for the first year of life (Houde & Rutherford 1993).

Given the small sizes of both crangonids and mysids, it may seem unlikely that these animals would be able to achieve migrations of 100s of km until one considers their swimming and sensory capabilities. Both mysids and crangonids are capable of impressive, well-documented tail-flipping escape movements (Neil & Ansell 1995). Less is reported on the sustained swimming behavior of these animals, but mysids are capable of sustained swimming speeds of up to 10 body lengths per second (Mauchline 1980). Furthermore, both families are known to utilize tidal currents to control their horizontal positions (Sato & Jumars 2008, Hufnagl et al. 2014). Finally, both Crangonidae and Mysidae have compound, stalked eyes and rely heavily on visual information. Mysids, along with several decapod species, are capable of detecting light polarization (Bainbridge & Waterman 1957, Goddard & Forward 1991). Polarized light (specifically the e-vector) may provide reliable navigational information (Waterman 2006). It is unclear whether Crangonidae are capable of detecting polarized light, although such capability is known in Palaemonidae (Goddard & Forward 1991). Stalked eyes are one indication of potential to navigate based on polarized light (Jumars 2012).

Occurrences of Euphausiidae and Pandalidae in fish diets also shift in early spring, but unlike Crangonidae and Mysidae, they shift northward. Again, when we look at the most dominant species collected from fish diets in 1973–1981, we find that only a few

species dominate during late winter and early spring. Ninety-two percent of Pandalidae were represented by *Dichelopandalus leptocerus*, and 98% of Euphausiidae were represented by *Meganyctiphanes norvegica*. Therefore, it is unlikely that this pattern is due to a shift in species dominance. It is important to note that there is a strong sampling bias toward detecting a northward shift in the month of March because the NEFSC trawl usually begins in March and moves up the coast. Both euphausiids and pandalids, however, displayed northward shifts significantly stronger than the sampling bias. Fish containing Euphausiidae and Pandalidae showed significantly more northward shifts than fish biosamplers without these prey families in their diets—as well as a different slope in the relationship between time and northward distance.

Given the successive, weekly northward shift in Euphausiidae and Pandalidae distribution, it is unlikely that changes in birth rate explain this shift. The most extensive data on *M. norvegica* reproduction in the northwest Atlantic is in the Gulf of Saint Lawrence (Plourde et al. 2011, 2014), where spawning occurs in early summer. *D. leptocerus*' spawning cycle has been documented in the Penobscot River estuary, Maine (Stevenson & Pierce 1984). Here, ovigerous females were present in the winter with most eggs hatching between December and January (Stevenson & Pierce 1984). Therefore, it is unlikely that reproductive pulses led to the observed pattern. Another potential explanation for Euphausiidae and Pandalidae distributional shift is the migration of individuals.

Euphausiids and pandalids are well known for their vertical migration that can span 100s or even 1000s of meters in a day (Barr 1970, Hudon et al. 1993, Tarling et al. 2010). Seasonal horizontal migration has been described in the commercially important *Pandalus borealis* in the Gulf of Maine, but in this case the migration is an onshore–offshore movement (Apollonio et al. 1986). Furthermore, within the Penobscot River estuary, *D. leptocerus* migrated to the lower portions of the bay into deep water in winter (Stevenson & Pierce 1984). However, we see no evidence in the literature describing any sort of horizontal migration of euphausiids in the NESLE ecosystem. There is evidence of such migration in other areas such as off the coast of Hawaii (Benoit-Bird et al. 2001). Here, the migration occurs on a daily cycle and is thought to allow micronekton to take advantage of abundant resources in shallow water at night while avoiding visual predators (McManus et al. 2008). The benefit to euphausiids

and pandalids from moving northward during the month of March could be to avoid warming spring temperatures in their southerly range. It is important to address this idea of euphausiid thermal intolerance and migration in regards to a changing climate and potential phenological mismatches that have been observed in other migrating species such as *P. borealis* (Koeller et al. 2009).

This study highlights the importance of Crangonidae, Mysidae, Euphausiidae, and Pandalidae to many demersal fishes in the NESLE ecosystem. With due accounting for sampling bias, one can utilize fish diets as discrete sampling units deployed at large spatial and temporal scales to detect changes in distribution patterns among these important (but often elusive) prey families. Future efforts can apply this method to address questions regarding temporal patterns or shifts in prey distribution and abundance that may be driven by large-scale stressors such as food-web shifts or climate change.

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LITERATURE CITED

- Allen DM, Allen WB (1981) Seasonal dynamics of a leech-mysid shrimp interaction in a temperate salt marsh. *Biol Bull* 160:1–10
- Apollonio S, Stevenson DK, Dunton EE (1986) Effects of temperature on biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine. NOAA Technical Report NMFS 42, NOAA/National Marine Fisheries Service
- Azarovitz TR (1981) Bottom trawl surveys. A brief historical review of the Woods Hole laboratory trawl survey time series. *Publ Spec Can Sci Halieut Aquat* 58:62–81
- Bainbridge R, Waterman TH (1957) Polarized light orientation of two marine Crustacea. *J Exp Biol* 34:342–364
- Bamber RN, Henderson PA (1994) Seasonality of caridean decapod and mysid distribution and movements within the Severn Estuary and Bristol Channel. *Biol J Linn Soc* 51:83–91
- Barr L (1970) Diel vertical migration of *Pandalus borealis* in Kachemak Bay, Alaska. *J Fish Res Board Can* 27: 669–676
- Benoit-Bird KJ, Au WWL, Brainard RE, Lammers MO (2001) Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. *Mar Ecol Prog Ser* 217:1–14
- Bowman RE, Bowman EW (1980) Diurnal variation in the feeding intensity and catchability of silver hake (*Merluccius bilinearis*). *Can J Fish Aquat Sci* 37:1565–1572
- Breiman L, Friedman J, Olshen R, Stone C (1984) Classifica-

- tion and regression trees. CRC Press, Boca Raton, FL
- Brown H, Bollens SM, Madin LP, Horgan EF (2005) Effects of warm water intrusions on populations of macrozooplankton on Georges Bank, Northwest Atlantic. *Cont Shelf Res* 25:143–156
- Buchheister A, Latour RJ (2011) Trophic ecology of summer flounder in Lower Chesapeake Bay inferred from stomach content and stable isotope analyses. *Trans Am Fish Soc* 140:1240–1254
- Fahrig L, Lilly GR, Miller DS (1993) Predator stomachs as sampling tools for prey distribution: Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*). *Can J Fish Aquat Sci* 50:1541–1547
- Fleminger A, Clutter RI (1975) Avoidance of towed nets by zooplankton. *Limnol Oceanogr* 10:96–104
- Frid CLJ, Hall SJ (1999) Inferring changes in North Sea benthos from fish stomach analysis. *Mar Ecol Prog Ser* 184: 183–188
- Friesen JA, Mann KH, Novitsky JA (1986) *Mysis* digests cellulose in the absence of a gut microflora. *Can J Zool* 64:442–446
- Garrison LP, Link JS (2000a) Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Mar Ecol Prog Ser* 202:231–240
- Garrison LP, Link JS (2000b) Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. *ICES J Mar Sci* 57:723–730
- Goddard SM, Forward RB (1991) The role of the underwater polarized light pattern, in the sun compass navigation of the grass shrimp, *Palaemonetes vulgaris*. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 169:479–491
- Gong Z, Andres M, Jagannathan S, Patel R, Jech JM, Makris NC, Ratilal P (2010) Low-frequency target strength and abundance of shoaling Atlantic herring (*Clupea harengus*) in the Gulf of Maine during the Ocean Acoustic Waveguide Remote Sensing 2006 Experiment. *J Acoust Soc Am* 127:104–123
- Grabe SA (1996) Composition and seasonality of nocturnal peracarid zooplankton from coastal New Hampshire (USA) waters, 1978–1980. *J Plankton Res* 18:881–894
- Greycay PA, Targett TE (1996) Spatial patterns in condition and feeding of juvenile weakfish in Delaware Bay. *Trans Am Fish Soc* 125:803–808
- Harding LW (1994) Long-term trends in the distribution of phytoplankton in Chesapeake Bay: roles of light, nutrients and streamflow. *Mar Ecol Prog Ser* 104:267–291
- Hardy AC (1926) The Discovery Expedition. A new method of plankton research. *Nature* 118:630–632
- Haynes EB, Wigley RL (1969) Biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine. *Trans Am Fish Soc* 98:60–76
- Hessler RR, Sanders HL (1967) Faunal diversity in the deep sea. *Deep-Sea Res* 14:65–78
- Hopkins TL (1965) Mysid shrimp abundance in surface waters of Indian River Inlet, Delaware. *Chesap Sci* 6: 86–91
- Houde ED, Rutherford ES (1993) Recent trends in estuarine fisheries: predictions of fish production and yield. *Estuar Coast* 16:161–176
- Hudon C, Crawford RE, Ingram RG (1993) Influence of physical forcing on the spatial distribution of marine fauna near Resolution Island (eastern Hudson Strait). *Mar Ecol Prog Ser* 92:1–14
- Hufnagl M, Temming A, Pohlmann T (2014) The missing link: tidal-influenced activity a likely candidate to close the migration triangle in brown shrimp *Crangon crangon* (Crustacea, Decapoda). *Fish Oceanogr* 23:242–257
- Hurlburt SN (1957) The distribution of *Neomysis americana* in the estuary of the Delaware River. *Limnol Oceanogr* 2:1–11
- Juanes F (1994) What determines prey size selectivity in piscivorous fishes? In: Stouder DJ, Fresh KL, Feller RJ (eds) *Theory and application in fish feeding ecology*. University of South Carolina, Columbia, SC, p 79–100
- Jumars PA (2007) Habitat coupling by mid-latitude, subtidal, marine mysids: import-subsidised omnivores. In: Gibson RN, Atkinson RJA, Gordon JDM (eds) *Oceanography and marine biology*, Vol 45. CRC Press-Taylor & Francis Group, Boca Raton, FL, p 89–138
- Jumars PA (2012) Stalk-eyed views of the Gulf of Maine—through a nephroid layer dimly. In: Stephenson R, Annala J, Runge J, Hall-Arbor M (eds) *Advancing an ecosystem approach in the Gulf of Maine*, Book 79. American Fisheries Society, Bethesda, MD, p 1–23
- Koeller P, Fuentes-Yaco C, Platt T, Sathyendranath S and others (2009) Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. *Science* 324:791–793
- Link JS (2004) Using fish stomachs as samplers of the benthos: integrating long-term and broad scales. *Mar Ecol Prog Ser* 269:265–275
- Link JS, Almeida FP (2000) An overview and history of the food web dynamics program of the Northeast Fisheries Science Center, Woods Hole, Massachusetts. NOAA Tech Memo NMFS-NE 159, Woods Hole, MA
- Link JS, Ford MD (2006) Widespread and persistent increase of Ctenophora in the continental shelf ecosystem off NE USA. *Mar Ecol Prog Ser* 320:153–159
- Link JS, Garrison LP (2002) Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. *Mar Ecol Prog Ser* 227:109–123
- Mauchline J (1980) The biology of mysids and euphausiids. *Advances in marine biology*, Vol. 18, Academic Press, London
- McManus MA, Benoit-Bird KJ, Woodson CB (2008) Behavior exceeds physical forcing in the diel horizontal migration of the midwater sound-scattering layer in Hawaiian waters. *Mar Ecol Prog Ser* 365:91–101
- Modlin RF (1980) Life cycle and recruitment of the sand shrimp, *Crangon septemspinosa*, in the Mystic River estuary, Connecticut. *Estuaries* 3:1–10
- NEFC (Northeast Fisheries Center) (1988) An evaluation of the bottom trawl survey program of the Northeast Fisheries Center. NOAA Tech Memo NMFS-F/NEC-52, Woods Hole, MA
- Neil DM, Ansell AD (1995) The orientation of tail-flip escape swimming in decapod and mysid crustaceans. *J Mar Biol Assoc UK* 75:55–70
- Nye JA, Link JS, Hare JA, Overholtz WJ (2009) Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar Ecol Prog Ser* 393:111–129
- Pezzack DS, Corey S (1979) Life history and distribution of *Neomysis americana* (Smith) (Crustacea, Mysidacea) in Passamaquoddy Bay. *Can J Zool* 57:785–793
- Plourde S, Winkler G, Joly P, St-Pierre JF, Starr M (2011) Long-term seasonal and interannual variations of krill spawning in the lower St Lawrence estuary, Canada, 1979–2009. *J Plankton Res* 33:703–714
- Plourde S, McQuinn IH, Maps F, St-Pierre JF, Lavoie D, Joly

- P (2014) Daytime depth and thermal habitat of two sympatric krill species in response to surface salinity variability in the Gulf of St Lawrence, eastern Canada. *ICES J Mar Sci* 71:272–281
- Powell EN, Kreeger DA, Morson JM, Haidvogel DB, Wang ZR, Thomas R, Gius JE (2012) Oyster food supply in Delaware Bay: estimation from a hydrodynamic model and interaction with the oyster population. *J Mar Res* 70:469–503
- Price KS (1962) Biology of the sand shrimp, *Crangon septemspinosa*, in the shore zone of the Delaware Bay region. *Chesap Sci* 3:244–255
- R Development Core Team (2009). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rachlin JW, Warkentine BE (1997) Comments on the population structure of the benthic marine isopod *Politolana concharum* collected by the Atlantic sturgeon, *Acipenser oxyrinchus*. *Crustaceana* 70:368–379
- Reid PC, Colebrook JM, Matthews JBL, Aiken J, Continuous Plankton Recorder Team (2003) The Continuous Plankton Recorder: concepts and history, from plankton indicator to undulating recorders. *Prog Oceanogr* 58:117–173
- Renkawitz MD, Sheehan TF (2011) Feeding ecology of early marine phase Atlantic salmon *Salmo salar* post-smolts. *J Fish Biol* 79:356–373
- Ryan C, Berrow SD, McHugh B, O'Donnell C, Trueman CN, O'Connor I (2014) Prey preferences of sympatric fin (*Balaenoptera physalus*) and humpback (*Megaptera novaeangliae*) whales revealed by stable isotope mixing models. *Mar Mamm Sci* 30:242–258
- Sato M, Jumars PA (2008) Seasonal and vertical variations in emergence behaviors of *Neomysis americana*. *Limnol Oceanogr* 53:1665–1677
- Sherwood GD, Rideout RM, Fudge SB, Rose GA (2007) Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): insights from stable carbon isotopes (d13C). *Deep-Sea Res II* 54:2794–2809
- Smith BE, Link JS (2010) The trophic dynamics of 50 finfish and 2 squid species on the Northeast US Continental Shelf. NOAA Tech Memo NMFS-NE 216, Woods Hole, MA
- Smith BE, Collie JS, Lengyel NL (2013) Effects of chronic bottom fishing on the benthic epifauna and diets of demersal fishes on northern Georges Bank. *Mar Ecol Prog Ser* 472:199–217
- Steinberg DK, Goldthwait SA, Hansell DA (2002) Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. *Deep-Sea Res I* 49:1445–1461
- Stevenson DK, Pierce F (1984) Life history characteristics of *Pandalus montagui* and *Dichelopandalus leptocerus* in Penobscot Bay, Maine. *Fish Bull* 83:219–233
- Tarling GA, Ensor NS, Fregin T, Goodall-Copestake WP, Fretwell P (2010) An introduction to the biology of northern krill (*Meganyctiphanes norvegica*). *Adv Mar Biol* 57:1–40
- Theroux RG, Wigley RL (1998) Quantitative composition and distribution of the macrobenthic intertebrate fauna of the continental shelf ecosystems of the Northeastern United States. NOAA Tech Rep NMFS 140, US Dept of Commerce, Seattle, WA
- UNESCO (1968) United Nations Education, Scientific, and Cultural Organization: zooplankton sampling. UNESCO Monogr Oceanogr Methodol 2:1–174
- Waterman TH (2006) Reviving a neglected celestial underwater compass for aquatic animals. *Biol Rev Camb Philos Soc* 81:111–115
- Wigley RL, Burns BR (1971) Distribution and biology of mysids (Crustacea, Mysidacea) from the Atlantic coast of the United States in the NMFS Woods Hole Collection. *Fish Bull* 69:717
- Witting DA, Able KW (1995) Predation by sevenspine bay shrimp *Crangon septemspinosa* on winter flounder *Pleuronectes americanus* during settlement: laboratory observations. *Mar Ecol Prog Ser* 123:23–31
- Worm B, Myers RA (2003) Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* 84:162–173
- Zagursky G, Feller RJ (1985) Macrophyte detritus in the winter diet of the estuarine mysid, *Neomysis americana*. *Estuar Coast* 8:355–362

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