

Ecology of the oceanic rim: pelagic eels as key ecosystem components

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ABSTRACT: Although 92% of the total volume of the world's oceans occurs below a depth of 200 m, our understanding of deep-sea food webs lags far behind that of continental shelves. In particular, little is known about the exchange of biomass at the interface of continental margins and deep-sea ecosystems. Recent studies suggest that the transport of organic matter from continental shelves may influence deep-sea ecosystems more than previously thought. Here, we present results of a pelagic nekton survey along the southern slope of Georges Bank, NW Atlantic, a transition area between coastal and deep-sea environments. Specimens were collected as part of the Census of Marine Life program Gulf of Maine Area project. Macrocrustacea (primarily sergestid shrimps and large euphausiids) dominated the total nekton (all taxa) numbers and biomass. Of the 85 deep-pelagic fish species collected during this cruise, the slender snipe eel *Nemichthys scolopaceus* (Anguilliformes: Nemichthyidae) ranked first in biomass and second in abundance. Microscopic analysis of *N. scolopaceus* gut contents revealed a predominance of large euphausiid and decapod prey. Other abundant potential prey, such as zooplankton, fish, and cephalopods, were absent from the diet, suggesting discriminatory feeding. Considering the relative biomass dominance of sergestid shrimps, large euphausiids, and pelagic eels in this system, the ecological interaction described here likely represents a major trophic pathway in this and similar 'oceanic rim' ecosystems.

KEY WORDS: Continental margin · Mesopelagic · Pelagic eel · Trophic ecology · Food webs · Gulf of Maine

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INTRODUCTION

The deep-sea environment, comprising ~92% of the total ocean volume (Haedrich 1997), is the largest living space on Earth, totaling more than 1.3×10^9 km³ (Horn 1972, Robison 2004). It is also one of the least known environments (Webb et al. 2010). In order to address this lack of knowledge, several Census of Marine Life (www.coml.org) field projects were developed between 2000 and 2010. One such project, the Gulf of Maine Area (GoMA) program (www.gulfofmaine-census.org), considered the pelagic community structure of the southern slope of

Georges Bank, an 'oceanic rim' ecosystem (sensu Merrett 1986). Some evidence suggests that mesopelagic micronekton communities in these ecosystems differ in species composition, abundance, and diversity from those of adjacent oceanic ecosystems (Reid et al. 1991). Aggregations of meso- and bathypelagic organisms along continental slopes and other abrupt topography have also been reported (Porteiro & Sutton 2007, Gartner et al. 2008, Sutton et al. 2008). Certain mesopelagic fishes, specifically, may often occur in large numbers when associated with these slope ecosystems (Reid et al. 1991). Marshall & Merrett (1977) emphasized the likely trophic significance

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of enhanced abundances of mesopelagic animals in slope ecosystems, though little is known of the transition in carbon flow and energy between coastal and oceanic environments (Company et al. 2008). In a recent synopsis of the GoMA, Kelly et al. (2010, p. 2) state:

Currently, the number of different species inhabiting the deep-sea Gulf of Maine region, their distribution across habitats, or their connection to the faunal communities of the continental shelf is poorly understood.

In this paper, we describe the trophic ecology of the biomass-dominant mesopelagic fish over the southern slope of Georges Bank, the slender snipe eel *Nemichthys scolopaceus* (Anguilliformes: Nemichthyidae).

Nemichthys scolopaceus Richardson 1848 (Fig. 1a) is cosmopolitan in tropical and temperate seas, spanning the Atlantic, Indian, and Pacific Oceans between 55°N to 50°S (Bilecenoglu et al. 2006). After leptocephalus transformation, slender snipe eels are thought to inhabit the mesopelagic and bathypelagic zones exclusively (Nielsen & Smith 1978, Karmovskaya 1982, Fishelson 1994, Inoue et al. 2010), most commonly between 200 and 1000 m (Smith & Tighe

2002). Members of the family Nemichthyidae do not show strict diel migration patterns, though *N. scolopaceus* specifically is known to undergo a very active continual vertical migration in association with prey capture (Karmovskaya 1982). The majority of prior studies of *Nemichthys scolopaceus* focused on systematics, distribution, or life history (Beebe & Crane 1937, Nielsen & Smith 1978, Castonguay & McCleave 1987, Smith & Nielsen 1989, Fishelson 1994, Miller & McCleave 1994, Inoue et al. 2010). There is very little research addressing their trophic ecology (Mead & Earle 1970, Gartner 1981, Appelbaum 1982, Bowman et al. 2000). Furthermore, none of these studies have focused exclusively on *N. scolopaceus* feeding, and the majority of trophic information presented thus far has been based on rather small sample sizes. The overall purpose of this study was to quantify the abundance and feeding of a dominant mesopelagic predatory fish in a shelf-break ecosystem in order to better understand the energy dynamics occurring along the oceanic rim. The topics addressed include prey composition, prey quantity, spatiotemporal feeding dynamics, and diet specialization.

MATERIALS AND METHODS

Study site

Samples were collected from 18 to 23 May 2004 aboard the NOAA research vessel 'Delaware II' along the southern flank of the Georges Bank area as part of the Census of Marine Life Gulf of Maine Area field project. Georges Bank is located at the end of the continental shelf, roughly 100 km off the northeast US coast (40° to 42° N, 71° to 66° W). It is ~150 km wide and 280 km long, runs roughly east–west, and the southern edge is transected by at least 15 submarine canyons (Fig. 2). These canyons can be thought of as highly modified areas of the continental slope, which show a more complex fauna, topography, and hydrography than the surrounding slope area (Cooper et al. 1987).

Trawling and sample handling

A modified International Young Gadoid Pelagic Trawl (IYGPT; see Moore et al. 2001 for details) was used to collect micronektonic (20 mm–20 cm) and nektonic (>20 cm) midwater organisms (nekton hereafter). This net was retrofitted with deepwater floats and a 4 mm mesh liner (stretched). The mouth area

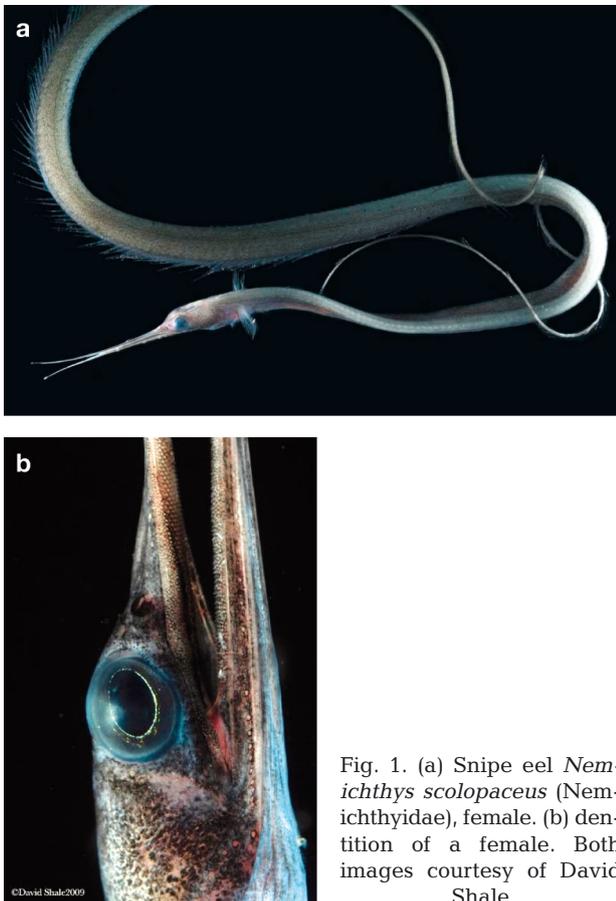


Fig. 1. (a) Snipe eel *Nemichthys scolopaceus* (Nemichthyidae), female. (b) dentition of a female. Both images courtesy of David Shale

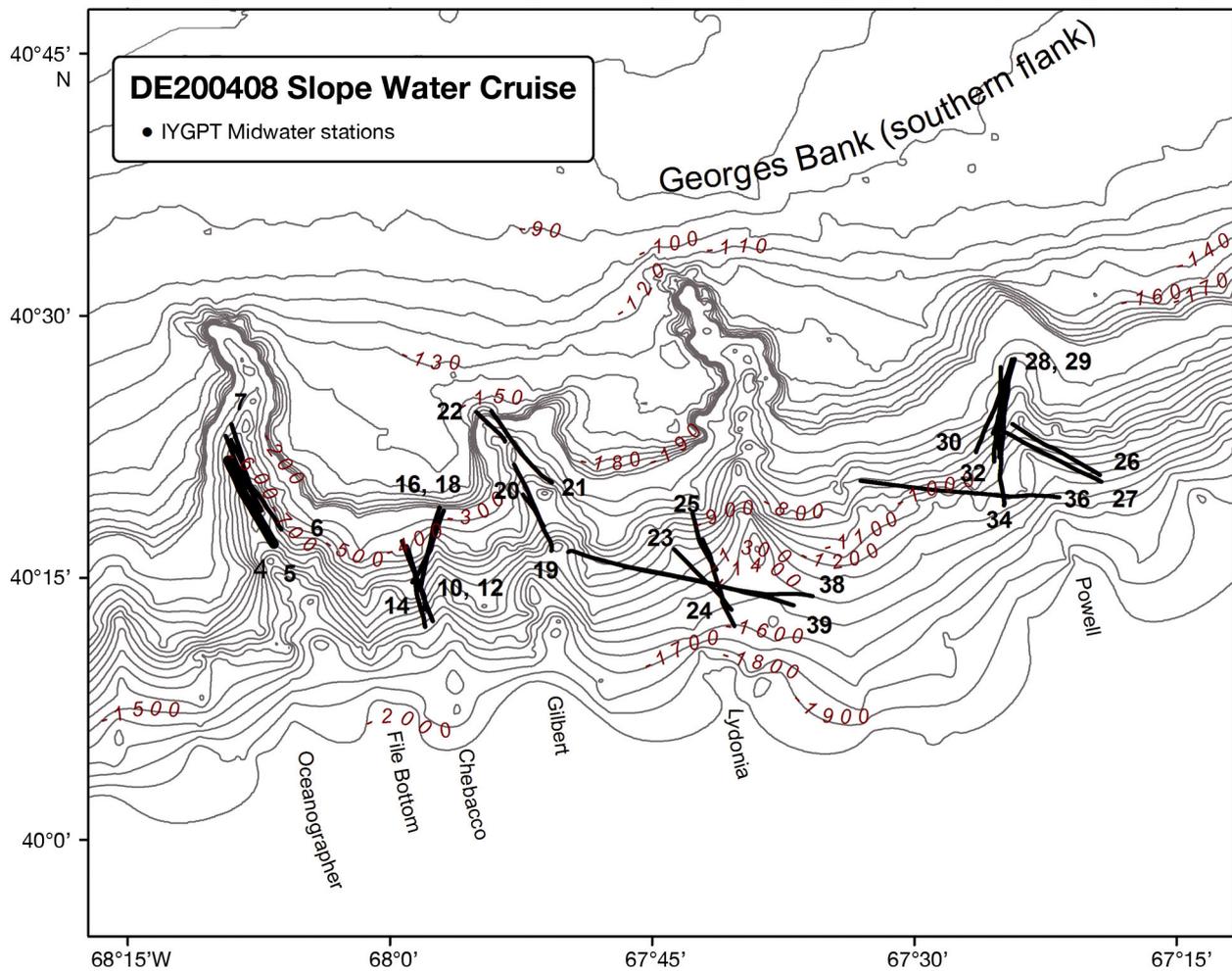


Fig. 2. Bathymetric map (m) of the sample site and locations of trawl tracks

measured 10×10 m when towed at 2.5 knots with a 50 m doorspread. The trawl doors used were 1.8 m² area USA Jet suberkrub-type midwater doors. Fifteen trawl samples were taken in total, 11 during daylight and 4 during nighttime (Table 1), fished open from the surface to the target depths (400–700 m) and retrieved. Net depth (Z) was measured using a Scanmar acoustic link sensor fixed to the headrope of the trawl and recorded using the Hyperterminal feature of Microsoft Windows. Trawl tracks were oriented within canyons and along open slope topography (Fig. 2). Trawl catches were standardized for unit effort (no. ind. or biomass h⁻¹).

Table 1. Georges Bank trawl data from 2004 listed by station number. Maximum net depth was measured using a Scanmar acoustic link depth sensor attached to the headrope of the trawl

Station	Date	Starting Lat (N)/Long (W)	Solar cycle	Max net depth (m)	Length of trawl (min)
4	19 May	40°18'/68°07'	Day	670	110.23
5	19 May	40°23'/68°09'	Night	620	70.22
6	19 May	40°19'/68°07'	Night	565	30.00
10	20 May	40°14'/67°58'	Day	480	30.02
12	20 May	40°17'/67°59'	Day	550	101.27
14	20 May	40°13'/67°58'	Night	490	29.68
16	21 May	40°18'/67°56'	Day	470	105.67
19	21 May	40°19'/67°52'	Day	505	88.72
20	21 May	40°21'/67°52'	Day	450	72.10
23	22 May	40°15'/67°42'	Day	435	29.98
24	22 May	40°15'/67°41'	Day	450	29.95
25	22 May	40°18'/67°42'	Day	470	87.52
26	22 May	40°21'/67°21'	Night	470	30.00
27	23 May	40°23'/67°24'	Day	500	108.73
28	23 May	40°23'/67°25'	Day	450	29.92

Trawl samples were sorted on board immediately after trawl retrieval. All fish species were counted, measured, and weighed using a Marel motion-compensating scale, and then either fixed or frozen aboard the ship. Crustacean taxa were weighed by lot and a subsample was preserved for enumeration and taxonomic determination. All catch weights are presented as wet weight in grams (WWg). Specimens were preserved in a 10% buffered formalin:seawater mixture, and then transferred to a 70% ethanol solution. Large-volume fish samples were frozen onboard in lots by sample number, and later preserved. As for other taxa, high-speed midwater trawls do not quantitatively sample gelatinous fauna, as they are often extruded through the mesh, therefore, very little gelatinous material was recovered. Mesopelagic cephalopods were rare, and thus omitted from analysis.

Diet analysis

A subset of the total number of *Nemichthys scolopaceus* specimens was selected for dissection, with the primary selection criteria being size (equal representation across size range) and time of capture (maximum representation across the 24 h cycle), in order to assess ontogenetic effects and feeding chronology, respectively (see below). This species exhibits strong sexual and ontogenetic dimorphism. As juveniles, all individuals have non-occlusible jaws bearing small villiform teeth (Fig. 1b). Upon reaching sexual maturity, males undergo a striking transformation. They experience a complete loss of teeth, the jaws radically shorten (Smith & Nielsen 1989) and develop tubular anterior nares (Nielsen & Smith 1978, Anonymous 1979), while females remain morphologically similar to juveniles. The feeding data presented in this paper represent those of juveniles and females. No males were collected during sampling.

Prior to dissection, pre-anal length (PL), defined as the distance from the posterior edge of the eye orbit to the anus, was measured to the nearest millimeter. Total length (TL) proved unreliable as both the jaws and caudal filaments are fragile and were often broken. Each study specimen was weighed to the nearest 0.01 g using an Acculab VI-I mg balance with a readability of 0.001 g. This measure of wet weight (WW) can be considered an underestimate because each time a specimen is frozen, thawed, fixed, and/or placed in ethanol, some percentage of water and organic matter is likely lost (Wiebe et al. 1975, Sutton & Hopkins 1996). Given that all taxa were subjected to the same methodol-

ogy, predator/prey biomass comparisons should be relatively unaffected.

For gut content analysis, the entire digestive tract was removed; the stomach and intestines were separated and opened individually. All large food particles and identifiable prey parts were then placed in separate vials of 70% ethanol, whereas smaller particles were mounted on glass slides for later identification. Prey items were identified to the lowest possible taxonomic level, either from whole prey or from diagnostic hard structures. The total number of prey was estimated by counting the total number of diagnostic structures and dividing by the appropriate number of structures per animal (e.g. all eyes counted and total divided by 2 to estimate number of prey). In cases where diagnostic hard structures could not be counted, a prey number of 1 was assigned to that prey category.

Feeding chronology

In order to determine when, and how many times, eels feed relative to the diel cycle, excised stomachs were ranked on a scale of stomach fullness from 0 to 4, with 0 = empty, 1 = traces of prey present, 2 = a partially to half-filled stomach, 3 = mostly full but not stretched, and 4 = a full and stretched stomach. Additionally, every prey item recovered was ranked on a scale of 1 to 4, representing the degree of digestion. The scale was as follows: 1 = no visible sign of digestion, prey whole and complete; 2 = prey partially digested, not complete; 3 = prey highly digested, only pieces remaining; and 4 = almost completely digested, only traces remaining.

Feeding selectivity

Ivlev's electivity index (E) was calculated to indicate the density-dependence of prey selection by *Nemichthys scolopaceus*. This index has been successfully used to determine the prey selectivity of a plethora of marine and freshwater fishes (e.g. Islam et al. 2006, Ribeiro & Nuñez 2008). Ivlev's electivity index is defined as:

$$E = (r - p) / (r + p) \quad (1)$$

where r = percentage of a given prey taxon in the diet and p = percentage of that prey item in the environment. Values range from -1 to $+1$, with all values greater than zero indicating an overrepresentation of the prey, zero indicating ambient representation, and

all values less than zero indicating underrepresentation of the prey within the predator's diet (Ivlev 1961, Strauss 1979, Gras & Saint-Jean 1982, McIlwain & Jones 1997, Alwainy et al. 2003).

RESULTS

Pelagic nekton assemblage composition and abundance

Macrocrustaceans (decapod crustacea, mysids, lophogastrids, and large euphausiids) dominated the nekton assemblage (Table 2), both in terms of numbers (96.1%) and biomass (71.4%). The dominant components of the macrocrustacean assemblage were decapod crustaceans (57.3% abundance, 78.7% WWg), primarily *Sergestes arcticus*, followed by euphausiids, mainly *Meganyctiphanes norvegica*. Lophogastrids of the genus *Gnathopausia* were occasionally taken, but were much less abundant than the other 2 taxa.

A total of 85 fish species, ranging from 1 to 4904 individuals, were collected by midwater sampling. *Nemichthys scolopaceus* ranked first in total fish biomass (1628.7 WWg h⁻¹) and second in abundance (130.1 ind. h⁻¹), trailing only the glacier lanternfish *Benthoosema glaciale* (Table 3). After these 2 species,

Table 2. Micronekton/nekton assemblage abundance (total ind. for all trawls) and biomass (total wet wt for all trawls, g) collected along the southern slope of Georges Bank

	Abundance	%	Biomass	%
Fish	9865	3.9	54116.3	28.5
Decapod	138495	55.0	106649.2	56.2
Euphausiid	103094	41.0	28725.0	15.1
Mysid	304	0.1	144.2	0.1
Totals	251758		189634.7	

Table 3. Total abundance (N) and biomass (total wet wt) for the dominant deep-pelagic fish species caught along the southern slope of Georges Bank

Species	N	Species	Total wet wt (g)
<i>Benthoosema glaciale</i>	4904	<i>Nemichthys scolopaceus</i>	20 000.0
<i>Nemichthys scolopaceus</i>	1487	<i>Stomias boa</i>	11 919.0
<i>Stomias boa</i>	710	<i>Benthoosema glaciale</i>	5570.7
Myctophids (damaged)	500	<i>Chauliodus sloani</i>	3997.0
<i>Chauliodus sloani</i>	395	<i>Merluccius bilinearis</i>	2332.3
<i>Serrivomer beanii</i>	212	<i>Sigmops elongatum</i>	1992.5
<i>Arctozenus risso</i>	206	<i>Serrivomer beanii</i>	1526.3
<i>Maurollicus weitzmani</i>	144	<i>Xenodermichthys copei</i>	763.7
Scorpaenid juveniles	133	<i>Etmopterus gracilispinis</i>	70.0

fish abundance per species declined sharply with the next-most abundant fish, *Stomias boa* (Stomiidae), occurring at abundances approximately half that of *N. scolopaceus* (Table 3). The number of *N. scolopaceus* caught appeared to vary as a function of day-light (Tables 4 & 5), with 3 of the 4 highest catches occurring at night, but this difference was not significant (2 tailed *t*-test, $p > 0.29$). Additionally, standard deviation was run for day and night catches (Table 4), showing that there was as much variability within day or night samples as there was between them.

Trophic ecology of *Nemichthys scolopaceus*

A total of 164 specimens were analyzed for gut contents. Seventy percent of the stomachs dissected (115 of 164) contained prey items. In the first 37 positive stomachs, 9 prey taxa were identified, with only 4 additional taxa identified in the remaining 78 stomachs. This pattern suggested that while additional specimens may yield a few new prey taxa, the sample size for this species was adequate to describe its trophic ecology (Hurtubia 1973).

Stomachs contained 13 prey taxa (Table 6), primarily decapod crustaceans (60% occurrence, 52% frequency) and euphausiids (54% occurrence, 47% frequency). There were many organisms that were not found in the guts (fishes, cephalopods, and larger crustaceans, such as crabs), even though they were collected from the environment. Ivlev's electivity index (*E*) suggested that *Nemichthys scolopaceus* selected for macrocrustacea, defined as decapods, euphausiids, and lophogastrids (+0.020; Table 7). It should be noted that smaller potential prey (e.g. copepods, amphipods, etc.) were not sampled with the gear used, so this index underestimates total prey selectivity. Fishes were completely selected against

as prey ($E = -1$), despite the fact that the most abundant fish, *Benthoosema glaciale*, is comparable in size to the crustaceans taken and co-occurred with *N. scolopaceus*.

Our sampling could not discern diel changes in feeding activity (Fig. 3). Eels taken from the same trawls had varying levels of stomach fullness and differing degrees of prey digestion; i.e. the assemblage did not appear to feed synchronously. The averages of stomach fullness for day and night (1.34 and

Table 4. Assemblage composition of micronektonic Crustacea and fishes sampled along the southern slope of Georges Bank. Recorded values are average ind. h^{-1} , both day and night (standard deviation)

	Day	Night
Crustacea		
Decapod	10399 (9232)	19341 (26316)
Euphausiid	8491 (9777)	6720 (7499)
Mysid	6 (8)	110 (220)
Fishes		
<i>Benthoosema glaciale</i>	327 (375)	542 (535)
<i>Nemichthys scolopaceus</i>	89 (77)	244 (220)
<i>Stomias boa</i>	57 (64)	114 (130)
<i>Chauliodus sloani</i>	41 (50)	28 (46)
Other myctophids	55 (63)	135 (105)
Other fishes	130 (121)	95 (26)

Table 5. Numbers of snipe eel *Nemichthys scolopaceus* captured according to solar cycle along the southern slope of Georges Bank. Eel abundance = ind. h^{-1}

Station	Solar cycle	Eel abundance
4	Day	45.6
5	Night	163.3
6	Night	0.0
10	Day	296.0
12	Day	61.8
14	Night	520.0
16	Day	22.2
19	Day	70.7
20	Day	95.0
23	Day	60.0
24	Day	122.0
25	Day	24.0
26	Night	192.0
27	Day	56.7
28	Day	122.0

Table 6. Number of prey items identified from *Nemichthys scolopaceus* (n = 164) collected from the southern slope of Georges Bank

	Stomach	Intestine
Crustacea	213	64
Euphausiid	103	25
<i>Meganyctiphanes norvegica</i>	23	–
Decapoda	93	27
Sergestidae	10	–
<i>Sergestes arcticus</i>	3	–
<i>Sergestes</i> sp.	2	–
<i>Sergia</i> sp.	1	–
Caridean	4	–
<i>Acanthephyra purpurea</i>	1	–
<i>Parapasiphaea sulcatifrons</i>	1	–
Lophogastrida	1	–
<i>Gnathophausia</i> sp.	1	–

Table 7. Abundance and percent occurrence of prey groups in the water column and in stomach contents of *Nemichthys scolopaceus*, day and night combined, and Ivlev's electivity index values (E) for 2 main prey groups. Macrocrustacea is defined as decapods, euphausiids, and lophogastrids. N = total number of specimens caught in trawls; N_1 = total number of specimens within the gut

	Environment		Eel stomachs	
	N	%	N_1	%
Macrocrustacea	241893	96	131	100
Fishes	9865	4	0	0
Macrocrustacea	$E = 0.020$			
Fishes	$E = -1$			

1.56, respectively) were very similar, suggesting these eels do not feed at a specific time of day. The degree of digestion averages (3.36 for day and 3.76 for night) revealed that most eels collected had well-digested prey material in their stomachs no matter what time of day. Further, 12 of the 115 eels with positive stomachs contained multiple prey items exhibiting different states of digestion. These prey item combinations generally contained one 'fresh' prey item and one almost completely digested. The remaining eels contained either one fresh large prey item or a stomach containing mainly digested material.

DISCUSSION

Diet composition

Nemichthys scolopaceus apparently selects for macrocrustacea while ignoring other potential prey, either by choice or by morphological necessity (non-occlusile jaws). Of the 164 eels dissected, 135 were positive for gut contents (either stomach or intestine), all of which contained large pelagic crustaceans. Other possible prey, such as fishes, pelagic molluscs, and larger zooplankton, were absent from the specimens examined, even though they can appear in large mixed aggregations with *N. scolopaceus* (Auster et al. 1992). This agrees with prior findings that captured *N. scolopaceus* guts usually contain only crustacean prey items (Mead & Earle 1970, Gartner 1981, Appelbaum 1982, Karmovskaya 1982, Hopkins et al. 1996, Bowman et al. 2000). Indeed, the high abundances of pelagic macrocrustacea (96.9% of the total micronekton assemblage numbers) may be responsible for the high relative abundance of *N. scolopaceus* (15.1%) at this, and other shelf-break study sites.

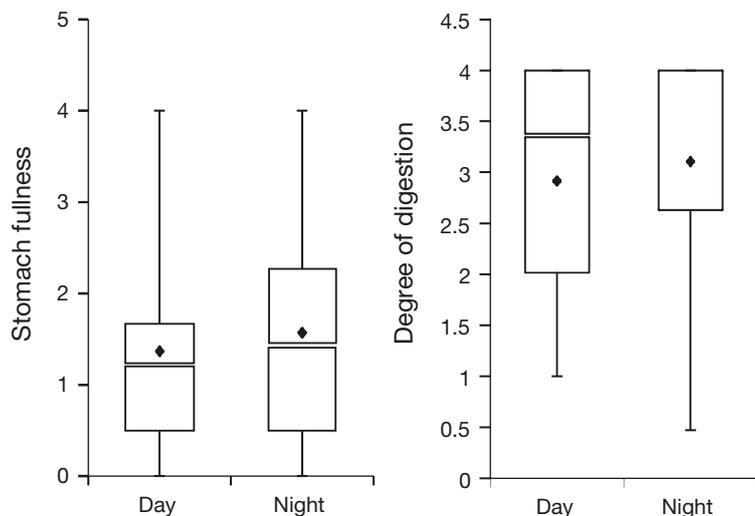


Fig. 3. Feeding chronology of *Nemichthys scolopaceus*. Stomach fullness of 0 = empty stomach, while 4 = a full and stretched stomach. Degree of digestion of 1 = recently ingested prey, while 4 = well digested prey. Average per solar cycle designated with ♦

Feeding chronology

Feeding chronology (i.e. when during the diel cycle a fish feeds most actively) represents a key element of a species' trophic ecology. Vertical migration can play a large role in the feeding patterns of many deep-sea fishes, while others exhibit no change over the diel cycle (Merrett & Roe 1974). In the case of *Nemichthys scolopaceus*, the shrimp prey are large enough that they would not necessarily clear the eel's stomach within a 24 h period (Pandian 1967a,b). Additionally, deep-sea fishes are known to have lower metabolic rates (Torres & Somero 1988a,b). Digestion rates may be impacted by the colder water temperature at depth (Childress 1995) and lower oxygen levels at the oxygen minimum zone (Torres et al. 2012); due to this, digestion rates in deep-sea fishes should be lower. Therefore, this species could be feeding at certain times of the day, but chronology would be masked by long digestion times. This bias was found in *Photostomias guernei* (Stomiiformes: Stomiidae), another fish species feeding primarily on decapod shrimps (Sutton & Hopkins 1996); these authors concluded that *P. guernei* feeds at various times of the day, and then digests prey over a period of more than one day. This long digestion time also holds for many other deep-sea predatory fishes that feed only infrequently and are often found with empty stomachs (Gartner et al. 1997). We might expect that *N. scolopaceus* feed mostly at night. Mid-water shrimps migrate upwards at night (Foxton 1970a,b, Flock & Hopkins 1992), thus concentrating

their numbers by occupying a narrower depth stratum relative to daytime distributions. Shrimp predators could hypothetically increase their encounter rate with their prey at night and eat larger numbers of shrimp in a smaller area and time, thus increasing their energetic gains per expense. Conversely, daytime feeding eels might gain an advantage in that their migratory prey are 'recovering' from the previous night's migration, and are thus less active (and less able to avoid predation). This feeding pattern contrasts with the 'sit-and-wait' predation style adopted by most piscivorous deep-sea fishes that use lures (e.g. Stomiidae) to attract prey. This feeding pattern, along with the muscular body of *Nemichthys*, suggests this eel relies on active searching rather than passive luring to encounter and capture their prey. Concurrent are the findings of Karmovskaya (1982), which suggest that *N. scolopaceus* undergo a 'very active round-the-clock migration' associated with feeding. Moreover, a high consumption rate of shrimps by eels is suggested by the fact that the percentage of eels containing prey items in their stomachs was higher (~70%) than that previously reported for other top mesopelagic predators (40%) (Sutton & Hopkins 1996, Gartner et al. 1997).

Feeding selectivity

It was originally thought deep-sea environments would force fishes to be capable of eating any potential prey encountered (Gage & Tyler 1991). At higher food densities, foragers would theoretically concentrate on the capture of more energetically valuable prey items. As prey abundance declines, the diet of most fishes would be expected to broaden (Hart 1989). However, this explanation may be overly simplistic. Some fishes may exhibit a low diversity diet simply because that prey item is the most prevalent in that particular area. Prey selection is also a function of the morphology of predator and prey. The jaw shape of *Nemichthys scolopaceus* appears specialized to catch decapod prey by means of antennal entrapment (Beebe & Crane 1937, Mead & Earle 1970, Karmovskaya 1982). Antennal entrapment, as described by Mead & Earle (1970), hypothesizes that, based on the morphologically unique structure of the nemichthyid jaws and the fact that they are covered

in multiple rows of villiform teeth, the 'hairy' antennae of passing shrimp species would become entangled, thus allowing for easy capture. This could be why *N. scolopaceus* does not consume fish species. As fish would not have these longer antennae, the eels may be morphologically unable to catch and ingest them. In comparison, the members of the eel genus *Serrivomer* have much shorter, occlusible jaws, and they have been found with shrimp, euphausiids, small crustaceans, fish, and cephalopods within their stomachs (Beebe & Crane 1936, Geidner 2008). Lacking empirical data, our data provide circumstantial evidence corroborating this antennal entrapment hypothesis. Further, given the numerical dominance of macrocrustacea as potential prey, one could also infer that the feeding of piscivorous micronekton predators (e.g. most Stomiidae) that do not consume macrocrustacea is an even higher form of feeding selectivity (Sutton & Hopkins 1996).

Post-capture ingestion ('net feeding') can potentially affect the observed diet patterns of some midwater fishes (Lancraft & Robison 1980), particularly with regard to feeding selectivity. However, in the case of *Nemichthys scolopaceus*, net feeding was deemed an unlikely source of bias. This species has a long, fragile body and jaws that upon capture become entangled in the trawl mesh prior to the codend. This was observed during this study by one author (T. T. Sutton pers. obs.) while picking specimens from the trawls; most specimens were taken from the forenet and had broken necks. Further evidence against net feeding bias included: (1) most specimens with positive guts had diet items that were either somewhat digested or compressed and covered in a slime coating, and (2) the high degree of selectivity within the eel's diet (codends are crowded with a diverse array of potential prey). Thus, while acknowledging the potential for bias, we consider the data presented herein to represent the active, *in situ* feeding of the species.

Pelagic eel and macrocrustacean linkage at the oceanic rim

In this study, we sampled a total of 85 fish species and at least 5 major groups of crustaceans. *Nemichthys scolopaceus* stomach contents revealed 13 prey types, primarily species of euphausiid and decapod crustaceans. Other potential prey, such as fishes, squids, and larger zooplankton, were absent from the diet, suggesting a fairly selective 'macrocrustaceivorous' feeding preference. Moreover, this eel is one of

only a few mesopelagic fish predators of shrimps and euphausiids in the area, the others being relatively rare. Even though crustacean predators are few, the crustacean prey are not. Decapod crustaceans represent an important part of the mesopelagic fauna, in certain areas making up over one-third of the total micronekton biomass (Foxton & Roe 1974). In the area sampled in this study, large species of euphausiids were also highly prevalent (e.g. *Meganyctiphanes norvegica*, one of the largest euphausiid species) (Greene et al. 1988). In a recent study focused on coastal and epipelagic fauna in the Gulf of Maine ecosystem, Johnson et al. (2011, p. 2) state:

Euphausiids, notably the carnivorous *Meganyctiphanes norvegica*, are important constituents in the diet of upper level carnivores in the GoMA.

These large euphausiid populations are thought to be a very important link in the food chain between plankton and pelagic fishes in the Georges Bank ecosystem (Greene et al. 1988). Euphausiids were one of the most highly consumed prey taxa identified for *N. scolopaceus* in this study.

The area studied here represents a transition zone between coastal and deep-sea environments, a region for which we know very little about carbon transport. The southern Georges Bank flank, characterized by a series of submarine canyons, is populated by abundant midwater fishes. Of that assemblage, *Nemichthys scolopaceus* ranked second in abundance and first in total fish biomass. Prior published studies of nemichthyid eels show low numbers (Hopkins et al. 1996, Sutton et al. 2008). Post & Tesch (1982) even stated that for *N. scolopaceus*, 'samples of more than 5 specimens are exceptional.' We find that that this species not only dominates fish biomass in this location, but also, within the mesopelagic zone, *Nemichthys* appears to cycle a significant portion of the macrocrustacean biomass to higher trophic levels. The daily rations (amount of prey consumed per day, expressed as a % of the predator's weight) of pelagic eels are unknown, but if their rations scale with other midwater fishes (1–4%, but probably on the higher end given their activity and muscularity), then shrimp predation by this single species could be the dominant higher trophic level interaction in this region, and possibly other outer continental shelf ecosystems.

Acknowledgements. The authors thank the invaluable contributions of M. Fogarty and J. Galbraith of the NOAA NMFS Northwest Fisheries Science Center for providing the research platform, which made this study possible, and for

providing sampling information for distributional analyses. We also thank the crew of the FSV 'Delaware II' for their excellent shiptime services and the Harbor Branch Oceanographic Institute for research and laboratory space. GoMA is a Census of Marine Life project. Funding for J.N.F.-B. was provided by the Florida Atlantic University Biology Department and for T.T.S. by a grant from the National Science Foundation Ocean Sciences Division – Biological Oceanography Program (OCE 0623551).

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Editorial responsibility: Paul Snelgrove, St. John's, Newfoundland and Labrador, Canada

*Submitted: February 6, 2013; Accepted: December 18, 2013
Proofs received from author(s): March 24, 2014*