A size-based approach to quantifying predation on longfin inshore squid *Loligo pealeii* in the northwest Atlantic

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ABSTRACT: Cephalopods are primary prey to a wide range of predators in global marine ecosystems. Despite their apparent ecological importance, little information exists on size-based predation respective to this taxon. Using long-term food habits and data from population surveys and commercial landings, we quantified size-based patterns of predation respective to 11 species of finfish, elasmobranchs, and marine mammals over ontogenetic scales. General trends of size-selective and seasonal foraging behavior are also presented for 25 species of predators from the northwest Atlantic Ocean. The functional role of squid was evaluated by contrasting patterns in size-based predation between squid and fish prey types. Measurements of predator gape morphology and prey body depths ascertained if predators were physically limited when feeding on squid. Additionally, the amount of overlap between natural predators and the commercial fishing industry for squid size resources was estimated. Predation by finfish and elasmobranchs was generally focused on juvenile and sub-adult squid, while marine mammals primarily targeted adults. Consequently, marine mammals had the highest overlap with the commercial fishing industry for squid size resources. All predators exhibited size-selective feeding behavior, and trends persisted over seasonal time periods. Predators fed on a wider range of fish prey sizes than squid and did not appear to be gape limited when feeding on squid; however, large squid were not common in predator diets. Results suggest squid behavior and availability in the environment are paramount in shaping size-based patterns of predation.

KEY WORDS: Size-based predation · Size-selection · Trophic niche breadth · Gape limitation · Longfin inshore squid · *Loligo pealeii*

INTRODUCTION

Predators are opportunistic, switching between prey species on the basis of their absolute and relative availabilities in the environment; however, to some extent all predators are selective (Bax 1998). In marine piscivores, the relationship between predator and prey body size directly influences foraging success and is one of the best indicators of the physical constraints on an individual (Peters 1983, Claessen et al. 2002). Other morphological features that change in proportion to a predator's body size, such as mouth gape, are informative and define the upper size limits of prey consumed both intra- and interspecifically (Juanes 1994, Nilsson & Bronmark 2000, Juanes et al. 2002). As predators grow, the maximum size of prey consumed generally increases, but diets are often concentrated on, or continue to include, small prey (Juanes & Conover 1995, Scharf et al. 2000). Few marine predators feed exclusively on the largest prey they possibly can because (1) it is energetically costly to pursue large prey (Scharf et al. 2003), and (2) smaller individuals are exponentially more abundant in marine food webs in comparison to larger ones (Brooks & Dodson 1965, Rice &

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Gislason 1996). Accordingly, the total range of prey sizes consumed by a predator depends largely on what it can physically manipulate, what is available in its immediate environment, and how energetically profitable it is to pursue increasingly larger prey.

The range of absolute prey sizes consumed by many marine predators will increase by orders of magnitude as their diets shift from planktivory during early life stages to piscivory as adults. For this reason, an individual's trophic position within its community is more accurately described by body size rather than species (Jennings & Reynolds 2007). Alternatively, the range of relative prey sizes consumed ontogenetically by a predator, known as its size- or ratio-based trophic niche breadth, often remains constant with predator ontogeny (Pearre 1986, Scharf et al. 2000). Size-based trophic niche breadths are useful for identifying physical limitations on a predator's feeding patterns, provide equivalent measures of resource use among species, and are appropriate for assessing competition for prey size resources (Bethea et al. 2004, Beauchamp et al. 2007).

While much attention has been given to size-based predation by piscivores (Juanes 1994, Mittelbach & Persson 1998, Manderson et al. 1999, Dorner & Wagner 2003), little to no information exists on the size-dependent relationships between cephalopods and their predators. Many top predators that are primarily piscivorous also include cephalopods in their diets over different seasonal, spatial, and ontogenetic scales (Stillwell & Kohler 1982, Clarke 1996, Dawe & Brodziak 1998, Chase 2002, Staudinger 2006). For example, while cephalopods are virtually absent from predator diets in estuarine environments, there is a transition towards cephalopods in shelf, slope, and open ocean habitats (Smale 1996). Previous studies have focused primarily on the weight contribution of cephalopods to predator diets and have neglected to detail size-based patterns in feeding and behavioral interactions. In studies of food habits in which squid body sizes have been reported, large squid are often prevalent in predator diets (Kohler 1987, Smale 1996, Gannon et al. 1997, Chase 2002, Staudinger 2006). Small squid are rarely reported in diet analyses; consequently, natural mortality rates for paralarval squid are thought to be relatively low in comparison to those of fish (Pierce & Guerra 1994). If predation pressure is concentrated during the later stages of life, this would suggest that predation may primarily act as a control on population structure and individual life history rather than recruitment success as is common in many species of fish (Claessen et al. 2002, Dorner & Wagner 2003).

Squid have been described as functionally similar to fish in many aspects of their ecology; their habitat distributions, schooling behaviors, body sizes, and shapes are analogous to those of many fishes (Packard 1972,

Hanlon & Messenger 1996, Pauly 1998). For these reasons, size-based predation on squid may be comparable to that on fish that occupy analogous trophic roles (e.g. clupeids) (Packard 1972). Conversely, squid possess traits that could make them more susceptible to predation than prey fish. Squid lack hard defensive structures such as spines and bony plates. Squid also have soft, cylindrical body forms that may make larger individuals easier to be engulfed by predators. Optimal diet theory states that predators should select prey that provides the greatest energetic return for the least amount of effort to retain (Stephens & Krebs 1986, Sih & Christensen 2001). Additionally, when a higher quality food source becomes more abundant, it should become more important in a predator's diet. The high nutritional value of cephalopods offers predators an added incentive of approximately 20% more digestible protein per unit body mass than that of fish (Lee 1994). The reward of a higher quality meal may motivate predators to pursue larger sized squid than fish. Currently, we do not know enough about size-dependent relationships between squid and their predators to predict how size, morphology, quality, and availability interact to influence predator selection for squid in comparison to prey fish resources.

Overfishing has altered the trophic structure of marine food webs by systematically removing the largest individuals and depleting predator populations to fractions of their former abundance levels (Jackson et al. 2001, Baum et al. 2003, Myers & Worm 2003, Ward & Myers 2005). To replace yields lost by the collapse of more traditional fish stocks, commercial fisheries have increasingly targeted squid and other forage fish (Pauly et al. 2002, FAO 2007). Despite the overfished status of many teuthophagous species, predatory demand on squid populations has been estimated to exceed commercial landings by orders of magnitude and to be equal to or greater than maximum sustainable yield (Buckel et al. 1999, Overholtz et al. 2000). It has been suggested that the short life cycles and high growth rates inherent to cephalopod populations have allowed them to rapidly increase productivity in response to reduced predation pressure (Caddy & Rodhouse 1998, Dawe & Brodziak 1998, Piatkowski et al. 2001); however, it is uncertain if squid populations can endure the demands imposed by a community of predators as well as a growing fishing industry. To manage both cephalopods and their predators sustainably, a holistic approach that considers multispecies trophic interactions is crucial. Natural and anthropogenic sources of mortality may inflict opposing or cumulative forces of size-selection on squid populations; therefore, it is also important to evaluate how predation is concentrated relative to fishing pressure (Duplisea 2005).

The overall objective of this paper is to provide baseline information on size-dependent relationships between one of the most ecologically and commercially valuable species of cephalopod in the northwest Atlantic ecosystem, longfin inshore squid *Loligo pealeii*, and its predators. Using data on long-term food habits, population survey data, and commercial landings information, we (1) quantify how size-based patterns of predation on squid vary among predator species, over ontogenetic scales, and during seasonal time periods; (2) contrast the functional role of squid in comparison to that of other forage fish; (3) evaluate morphological characteristics in squid and teuthophagous predators that constrain size-dependent relationships; and (4) estimate the amount of overlap between natural predators and the commercial fishing industry for squid size resources.

MATERIALS AND METHODS

Diet data. Predator and prey body size data were obtained from several sources. The largest data set was collected as part of long-term fishery-independent population surveys conducted by the Northeast Fisheries Science Center (NEFSC). Surveys were conducted during the winter, spring, and fall seasons and spanned the region from Cape Lookout, North Carolina, northward to waters off Nova Scotia, Canada. Survey details can be found in the reports by Azarovitz (1981) and the Northeast Fisheries Center Survey Working Group (NEFC 1988). Data sets on finfish and marine mammal diets, collected by several independent authors, were also included (Gannon et al. 1997, Staudinger 2006, K. Ampela unpubl. data). Predator names, sample sizes, dates of food habits collection, and geographic ranges are listed in Table 1.

The majority of squid mantle lengths (ML) were measured directly using intact specimens found in predator stomachs. If prey remains were highly digested, the chitinous gladius (or pen) was used as an equivalent for ML. In several data sets, squid beaks were recovered during diet analyses, and original body size was reconstructed using predictive equations relating the lower rostral length of the lower beak to ML (Clarke 1986, Staudinger et al. 2009). Grey seal *Halichoerus grypus* diets were collected from haul-out sites on Muskeget and Monomoy Islands. The majority of seals at these sites were sub-adults and adults of mixed sex and were estimated to range from 90 to 275 cm in total length (K. Ampela pers. comm.). Because squid remains were collected from scat, body

Table 1. Predators of longfin inshore squid *Loligo pealeii*. n = indicates sample sizes of squid lengths, bolded values indicate predators included in quantile regression analyses. a: Cape Lookout, North Carolina to Nova Scotia, Canada; b: Massachusetts; c: North Carolina to New York; d: New Jersey to Massachusetts

Common name	Scientific name	n	Yr	Region	Source
Atlantic cod	*Gadus morhua*	5	1991–2004	a	
Atlantic halibut	*Hippoglossus hippoglossus*	3	1991–2004	a	
Atlantic mackerel	*Scomber scombrus*	45	1991–2004	a	
Black sea bass	*Centropristis striata*	7	1991–2004	a	
Bluefish	*Pomatomus saltatrix*	**267**	1991–2004	a, d	Staudinger (2006)
Clearnose skate	*Raja eglanteria*	2	1991–2004	a	
Fourspot flounder	*Paralichthys oblongus*	**136**	1991–2004	a	
Goosefish	*Lophius americanus*	**96**	1991–2004	a, d	Staudinger (2006)
Grey seal	*Halichoerus grypus*	**84**	2004–2007	b	K. Ampela (unpubl. data)
Little skate	*Leucoraja erinacea*	9	1991–2004	a	
Long-finned pilot whale	*Globicephala melas*	**497**	1989–1991	c	Gannon et al. (1997)
Offshore hake	*Merluccius albidus*	2	1991–2004	a	
Pollock	*Pollachius virens*	8	1991–2004	a	
Red hake	*Urophycis chuss*	11	1991–2004	a	
Sea raven	*Hemitripterus americanus*	19	1991–2004	a	
Silver hake	*Merluccius bilinearis*	**82**	1991–2004	a, d	Staudinger (2006)
Smooth dogfish	*Mustelus canis*	**255**	1991–2004	a	
Spiny dogfish	*Squalus acanthias*	**615**	1991–2004	a	
Spotted hake	*Urophycis regia*	**58**	1991–2004	a	
Striped bass	*Morone saxatilis*	28	1991–2004	a	
Summer flounder	*Paralichthys dentatus*	**277**	1991–2004	a, d	Staudinger (2006)
Weakfish	*Cynoscion regalis*	25	1991–2004	a	
White hake	*Urophycis tenuis*	3	1991–2004	a	
Windowpane	*Scophthalmus aquosus*	5	1991–2004	a	
Winter skate	*Leucoraja ocellata*	32	1991–2004	a	

lengths could not be confirmed for individual seals; therefore, only prey length data were used for this predator species.

Size-based patterns of predation. To identify the sizes of squid most recurrent in predator diets and to determine at which stage of each squid's life cycle size-specific predation was most prevalent, absolute body size relationships between squid and their predators were evaluated using least squares and quantile regression techniques. Individual predator species were evaluated by graphing predator-prey length data as scatter-plots. Quantile regression was used to estimate the rate of change in the lower and upper bounds of predator-prey body size distributions respective to each predator species and over a wide range of predator body sizes (Scharf et al. 1998a, Cade et al. 1999, Scharf et al. 2000, Cade & Noon 2003). Estimated lower and upper bounds were represented either by 5th/95th, 10th/90th, or 25th/75th quantiles, depending on sample size restrictions as suggested by Scharf et al. (1998a). Lastly, mean predator-prey body size relationships were estimated using ordinary least-squares regression.

Relative predator-prey body size relationships were used to quantify size-based trophic niche breadths of individual predator species and evaluate interspecific competition for squid size resources. Relative body sizes were calculated by dividing the total length of each squid (length of squid mantle and arms, tentacles excluded [Staudinger et al. 2009]) by its corresponding predator length (PL). Resulting predator-prey size ratios were examined as relative and cumulative frequency distributions to determine the percentages of relatively small (<20% relative body size), medium or intermediate (20% ≥ and <50% relative body size), and large (≥50% relative body size) squid in each predator's overall diet.

Size-based trophic niche breadths were determined by graphing relative size ratios as the dependent variable against predator size (independent variable) and displayed as scatter-plots (Scharf et al. 2000, Juanes 2003). Quantile regression was then used to estimate the lower and upper bounds of these scatter-plots. The 10th and 90th quantiles were chosen to evaluate all predator species because they adequately described the shapes of relative body-size distributions while remaining conservative even when sample size restrictions (Scharf et al. 1998a) were not strictly adhered to. This methodology ensured that estimates of size-based trophic niche breadths were standardized and comparable across predator species. An F-test was used to detect differences between the lower and upper bound slopes and determine if size-based trophic niche breadths were parallel, converging, or diverging (Scharf et al. 2000, Juanes 2003). No difference

between lower and upper bound slopes indicated parallel size-based trophic niche breadths and hence a constant range of relative squid sizes consumed with predator ontogeny. Significant differences between slopes indicated either diverging and expanding, or converging and contracting size-based trophic niche breadths.

The mean size-based trophic niche breadth (TNB) respective to each predator was calculated using Eq. (1):

$$TNB = \frac{\sum_{i=1}^{i=n} [(m_{90})(PL_i)+(b_{90})] - [(m_{10})(PL_i)+(b_{10})]}{n} \quad (1)$$

where i = an observation of predator length (PL), n = the total number of observed species-specific predator-prey length combinations; m = the slope, and b = the intercept calculated for the 10th and 90th quantiles of relative predator-prey size ratios regressed on predator size in each predator data set. Size-based trophic niche breadths were then plotted as box and whisker plots and ordered from smallest to largest.

To determine if predators were feeding opportunistically or exhibiting size-selection on squid, size distributions of longfin inshore squid populations available in the environment were compared to the distributions of squid lengths recovered from predator diets. If a predator was feeding opportunistically, the distribution of squid lengths in its diet was similar to the distribution of lengths in the environment. Negative size-selection occurred if predators had greater frequencies of relatively smaller squid lengths in their diets compared to lengths available in the environment. Conversely, positive size-selection was supported if a greater proportion of a predator's diet was composed of relatively larger squid lengths than were most abundant in the environment.

Squid population data were collected as part of the NEFSC bottom-trawl survey and subset to correspond to the same time period (from 1991 to 2004) during which the majority of diet data were collected. Squid lengths were grouped into 1 cm ML increments to generate frequency distributions. All population and diet length distributions were positively skewed and in violation of normality; therefore, the Kolmogorov-Smirnov test was chosen to contrast differences (Zar 1984, Sokal & Rohlf 1995) and performed using the NPAR1WAY command in SAS (SAS 2003). When significant differences between predator diets and squid population data were detected, visual inspections of length frequency distributions were conducted to ascertain if negative or positive size-selection was occurring. Seasonal trends in size-selection were also evaluated for winter, spring, and fall; population data were not available for summer.

Functional roles of squid and forage fish. Predator diets in the northwest Atlantic contain a greater diversity of prey fish species than cephalopod species; however, this does not necessarily mean that a greater range of fish prey sizes will be consumed. Size-based trophic niche breadths respective to squid and forage fish were compared to evaluate if predators were exploiting the 2 prey types similarly. Body size data on prey fish were collected as part of the food-web dynamics program (NEFSC) and correspond to the same predators and time periods that were used for calculations of squid size-based trophic niche breadths.

To determine how squid ranked on the spectrum of potential body shapes available to predators, measurements of squid body depth (BD) and width (BW) were compared with those of several common prey fish found throughout the northwest Atlantic. Longfin squid were collected from coastal waters off Massachusetts by otter-trawl on the RV 'Gemma' between May and August in 2007. Measurements of squid BD and BW were made at the maximum points on the mantle with digital calipers to the nearest 0.01 mm. The resulting relationship between squid BD and total length was compared with butterfish *Peprilus triacanthus*, sand lance *Ammodytes americanus*, and Atlantic herring *Clupea harengus*, using previously published morphometric equations (Scharf et al. 1998b). Sand lance and butterfish were representative of the minimum and maximum BDs, respectively, of prey fish available to predators in the northwest Atlantic (Ménard et al. 2006), and Atlantic herring was assumed to most closely resemble squid in overall body form (Packard 1972).

Morphological constraints on size-dependent relationships. If predators are gape limited, prey BD may be influential in constraining foraging behavior (Nilsson & Bronmark 2000). Relationships among squid BD and BW, PL, and predator gape size were examined to determine if predators were feeding near their physical limits over ontogeny. Gape sizes were assessed from specimens of Atlantic mackerel *Scomber scombrus*, fourspot flounder *Paralichthys oblongus*, smooth dogfish *Mustelus canis*, spotted hake *Urophycis regia*, and summer flounder *Paralichthys dentatus* collected on the NEFSC 2008 spring bottom-trawl survey. All other predator gape relationships were adapted from Scharf et al. (2000). Gape height (GH) was measured as the maximum linear distance from the upper and lower jaws with the mouth stretched open. Gape width (GW) was measured as the linear distance from the corners of the stretched open mouth. Squid length data were converted to BD and BW using equations developed from the data collected above. Relationships between the limiting squid body metric and the limiting predator gape dimension were plotted as dependent variables against corresponding PLs (independent variables).

Overlap between predators and the commercial fishing industry. To evaluate whether predators were exploiting similar squid size resources as the fishing industry, squid lengths from predator diets were compared with those landed commercially. Predator diet data (Table 1) were pooled and grouped into 1 cm increments. Commercial data were obtained from the most recent stock assessment (NEFSC 2002) and subset to match the primary period during which predator diet information was collected (from 1991 to 2004). In addition to testing differences of location and distribution using a Kolmogorov-Smirnov test, the degree of overlap between predators and the fishing industry was estimated by calculating the overlapping area under the 2 distribution curves.

RESULTS

Size-based patterns of predation

Juvenile and sub-adult squid (from 2 to 10 cm ML) were most important to finfish and elasmobranch predators while adults (≥15 cm ML) dominated (>90%) the diets of marine mammals (Fig. 1). The mean size of all predators sampled was 128 cm, and the vast majority were ≤100 cm.

Of the 25 predators listed in Table 1, 10 species had sample sizes large enough to meet minimum requirements suggested for conducting quantile regression analysis (n ≥ 40). Estimations of the lower bound (from −0.01 to 0.35), mean (from −0.03 to 0.51), and upper bound (from −0.09 to 0.67) regression slopes for absolute body size relationships between squid and their predators spanned several orders of magnitude and ranged from negative to positive. With the exception of Atlantic mackerel, all predators exhibited lower bound slopes that were moderate in comparison to mean and upper bound slopes (Table 2).

Small predators (<40 cm PL) such as Atlantic mackerel, fourspot flounder, and silver and spotted hakes exhibited rapid and simultaneous increases in the minimum and maximum sizes of squid in their diets (Fig. 2). Consequently, a narrow range of squid lengths was consumed by small predators at any given size, but predation shifted across multiple squid life stages (e.g. juvenile to sub-adult) as predators grew. In contrast, large predators such as goosefish, pilot whales, and smooth and spiny dogfish maintained relatively constant and broad ranges of squid sizes in their diets at all stages of growth (Fig. 2). The 2 intermediate sized predators, bluefish and summer flounder, exhibited the greatest

variation between the minimum and maximum size of squid in their diets. Both species expanded the overall distribution of squid sizes in their diets with ontogeny, although summer flounder's upper limit (25 cm ML) was much higher than that of bluefish (15 cm ML). Similar shapes in predator-prey body size distributions were observed among closely related predators (e.g. dogfish), yet the limits of size-based predation were highly species-specific. For example, the onset of squid predation by spiny dogfish (25 cm PL) occurred at much smaller sizes in comparison to that by smooth dogfish (50 cm PL).

Most predators consumed squid that were <30% relative to their own body sizes, and diets were concentrated on squid within a relative size range (from 10 to 20%). The dominant size class in each predator's overall diet varied widely, ranging from <10% in pilot whales to 40% in fourspot flounder and spotted hake (Fig. 3). Goosefish diets contained the greatest diversity and largest (up to 84%) relative squid sizes of all predators examined. Some predators (e.g. summer flounder) displayed wide distributions of relative squid sizes in their diets, while others (e.g. Atlantic mackerel) exhibited definitive peaks, after which the frequency of larger relative body sizes declined steeply (Fig. 3).

Parallel size-based trophic niche breadths were most common among squid predators (Table 3 & Fig. 4). Spiny dogfish was the only predator evaluated to exhibit a converging size-based trophic niche breadth,

and silver hake was the only predator exhibiting a diverging size-based trophic niche breadth. Visual inspection of several scatter-plots of relative body size suggests diverging (e.g. spotted hake and summer flounder) and converging (e.g. bluefish and goosefish) size-based trophic niche breadths, although differences between the lower and upper bound slopes were not statistically significant.

Comparisons between squid length distributions from population surveys and prey lengths recovered from predator diets determined that all predators were size-selective towards squid (D statistics were ≥0.89; p-values were <0.0001). Atlantic mackerel was the only species to display negative size-selection. All other predators exhibited positive size-selection, which was most pronounced in the 2 species of marine mammals (Fig. 5). Trends of positive size-selection also persisted seasonally (D statistics were ≥0.36; p-values were ≤0.006). The largest differences were detected during spring, and secondarily during the winter.

Morphological constraints on size-dependent relationships

The relationship between squid BW and body length (BW = 0.154ML + 0.680, r^2 = 0.94, n = 61, p < 0.0001) increased at a slightly greater rate in comparison to the
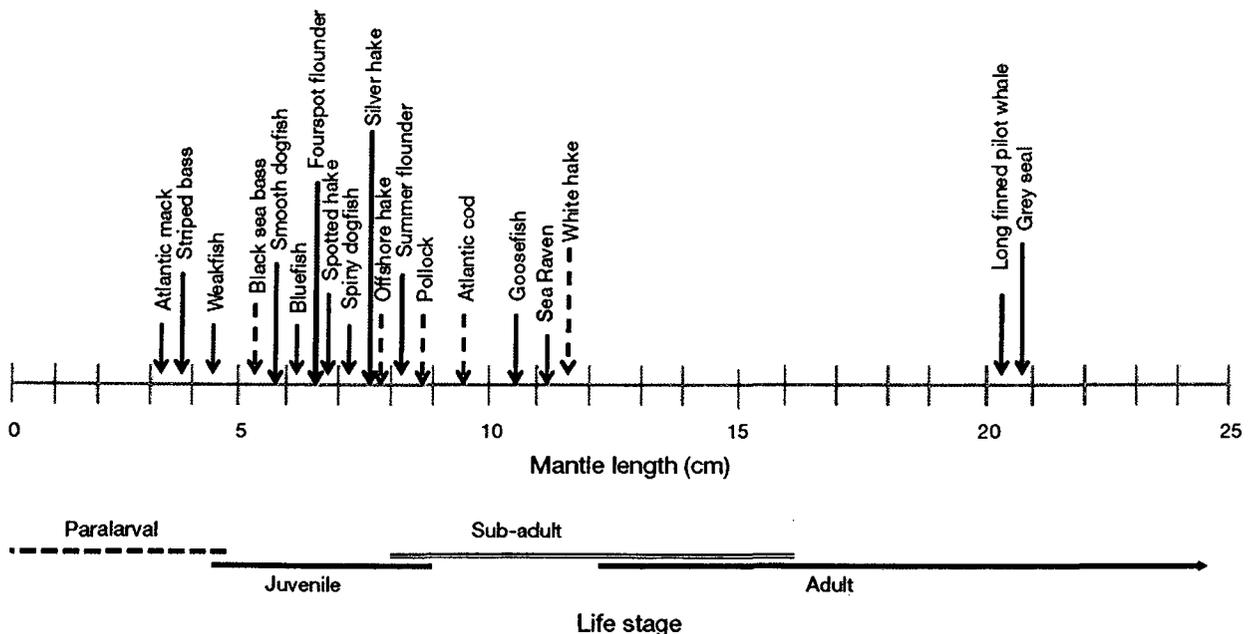

Fig. 1. *Loligo pealeii*. Community spectrum of predation over the life span of longfin inshore squid. Arrows point to the mean size of squid consumed by each predator species. Dashed lines indicate predators with sample sizes ≤10 cm. Predator scientific names are listed in Table 1. Squid life stages are approximated to mantle lengths reported by Jacobson (2005)

relationship between squid BD and body length (BD = $0.148 \times ML + 0.581$, $r^2 = 0.92$, $p < 0.0001$), but the difference between slopes was not significant.

Predator gape sizes measured in the present study (Table 4) and previously by Scharf et al. (2000) were much greater than squid BD and BW. Consequently, most predators did not appear to be gape limited when feeding on squid. Silver hake and spotted hake were the only predators found to target squid at or near their assumed physical limit and over ontogenetic scales; large silver hake even appeared to consume squid that were beyond their estimated gape (Fig. 6). At small predator body sizes, spiny dogfish consumed squid that were comparable in depth to the span of their gape. No squid size data were reported for body sizes <25 cm PL, suggesting that spiny dogfish may be gape limited below this size. After approximately 50 cm PL, spiny dogfish gapes expanded more rapidly than the squid sizes they were feeding on, and spiny dogfish no longer appeared to be gape limited.

Functional roles of squid and forage fish

Squid body shapes were intermediate in butterfish and sand lance and changed at a more moderate rate in comparison to that of Atlantic herring (Fig. 7). This suggests that squid's window of vulnerability to predation would be protracted in comparison to the majority of forage fish common throughout the northwest Atlantic. Predators consumed a smaller range of relative squid sizes in comparison to forage fish; however, mean trophic niche breadths for the 2 prey types differed only by about a 10% margin in the majority of predators (Fig. 8). Goosefish, silver hake, and dogfish were the few predators that exploited considerably larger relative size ranges of fish prey sizes (from 20 to 50% greater) in comparison to squid.

Overlap between predators and the commercial fishing industry

The commercial fishing industry harvested significantly larger squid ($D = 0.431$, $p < 0.0001$) than were targeted by predators. The total estimated overlap between harvested and consumed lengths was 23% and peaked between 9 and 16 cm ML (Fig. 9). Diet data were partitioned by the 3 major taxonomic predator groups—finfish, elasmobranchs, and marine mammals—and overlap with the fishing industry was calculated for each group. Marine mammals had the greatest amount of overlap (17%) with the commercial fishery for squid size resources (Fig. 9). Finfish and

Table 2. Equations of absolute body size relationships between longfin inshore squid and its predators. Quantile regression was used to estimate the lower and upper bound equations of scatter data; mean equations were estimated from ordinary least squares regression. ML_{min} and ML_{max} indicate the minimum and maximum squid lengths consumed by each predator, respectively. ML = mantle length, PL = predator length. n = number of prey lengths. The 25th and 75th quantiles were used for $40 \le n < 100$; 10th and 90th quantiles for $100 \le n < 200$; and 5th and 95th for $200 \le n < 1000$. NS indicates a non-significant p-value

| Predator species	n	Quantiles analyzed	ML_{min} (cm)	ML_{max} (cm)	Lower bound (cm)	Mean (cm)	Upper bound (cm)
Atlantic mackerel	45	25th/75th	1.0	5.6	$ML = 0.14PL - 1.71$	$ML = 0.12PL - 0.25$	$ML = 0.11PL + 0.51^{NS}$
Bluefish	267	5th/95th	1.2	15.0	$ML = 0.03PL + 0.90$	$ML = 0.06PL + 2.88$	$ML = 0.18PL + 1.93$
Fourspot flounder	136	10th/90th	0.5	18.5	$ML = 0.24PL - 3.40$	$ML = 0.36PL - 4.40$	$ML = 0.46PL - 4.86$
Goosefish	96	25th/75th	0.9	25.0	$ML = -0.01PL + 6.63^{NS}$	$ML = -0.03PL + 12.08^{NS}$	$ML = -0.09PL + 18.18^{NS}$
Pilot whale	497	5th/95th	4.5	36.6	$ML = -0.01PL + 12.50^{NS}$	$ML = 0.01PL + 16.73^{NS}$	$ML = 0.02PL + 24.01$
Silver hake	82	25th/75th	0.5	26.1	$ML = 0.35PL - 5.42$	$ML = 0.51PL - 7.90$	$ML = 0.67PL - 10.67$
Smooth dogfish	255	5th/95th	1.1	21.0	$ML = 0.01PL + 1.01^{NS}$	$ML = 0.01PL + 4.59^{NS}$	$ML = 0.03PL + 8.40^{NS}$
Spiny dogfish	615	5th/95th	1.3	25.0	$ML = 0.00PL + 2.50^{NS}$	$ML = 0.01PL + 6.53^{NS}$	$ML = 0.07PL + 10.27^{NS}$
Spotted hake	58	25th/75th	2.0	15.5	$ML = 0.27PL - 2.53^{NS}$	$ML = 0.43PL - 5.54$	$ML = 0.53PL - 6.48$
Summer flounder	277	5th/95th	0.9	25.0	$ML = 0.10PL - 2.00$	$ML = 0.23PL - 2.22$	$ML = 0.39PL - 3.58$
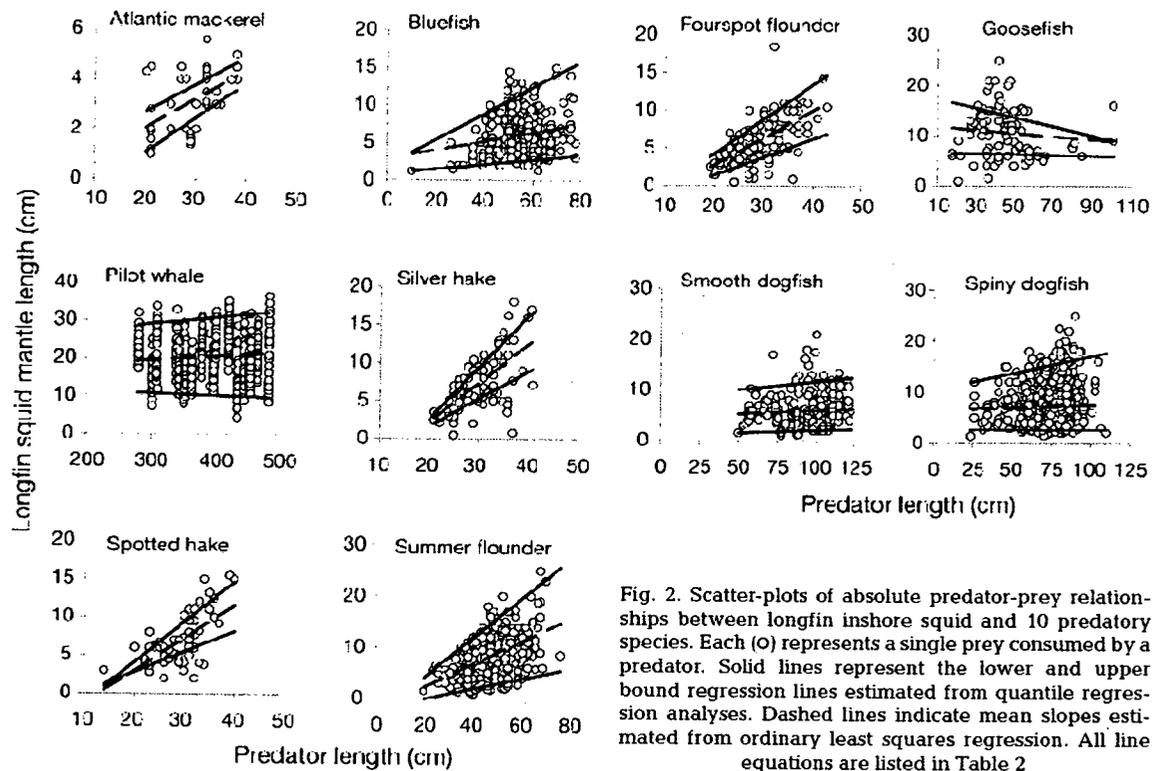
Fig. 2. Scatter-plots of absolute predator-prey relationships between longfin inshore squid and 10 predatory species. Each (O) represents a single prey consumed by a predator. Solid lines represent the lower and upper bound regression lines estimated from quantile regression analyses. Dashed lines indicate mean slopes estimated from ordinary least squares regression. All line equations are listed in Table 2
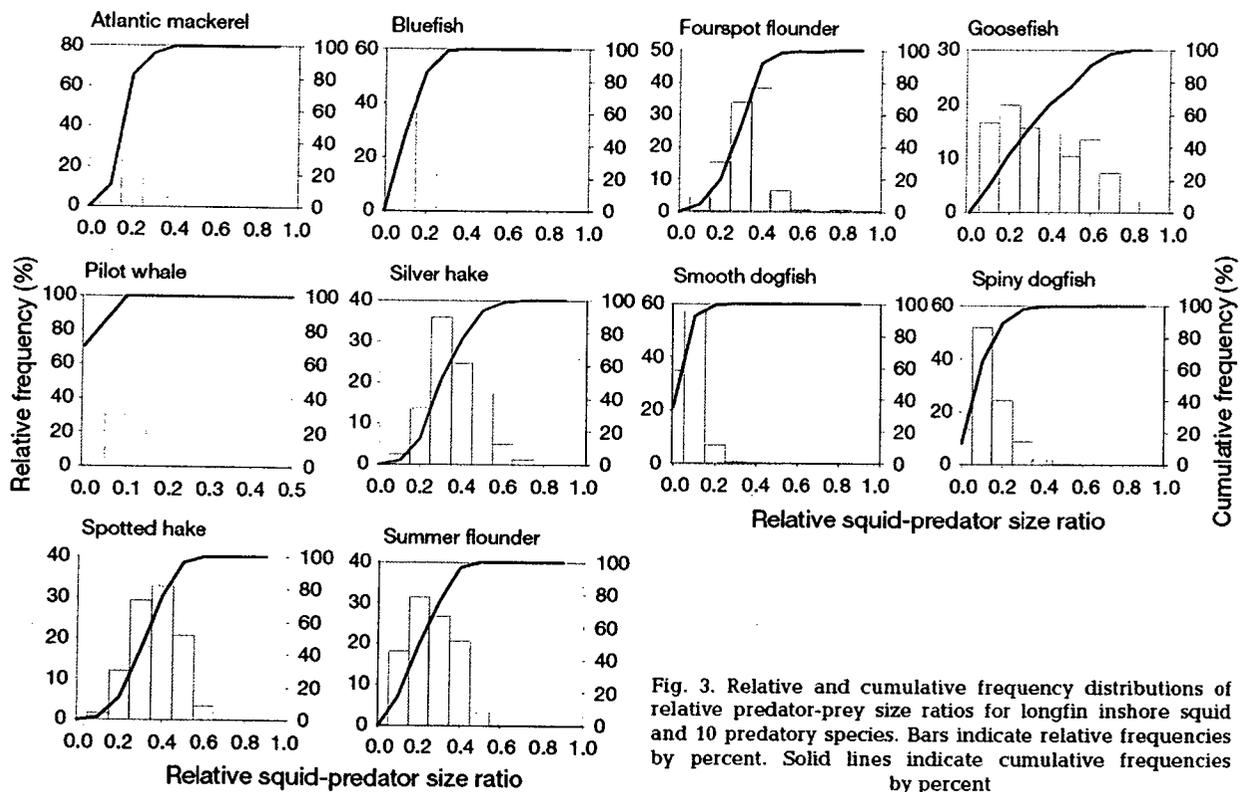

Fig. 3. Relative and cumulative frequency distributions of relative predator-prey size ratios for longfin inshore squid and 10 predatory species. Bars indicate relative frequencies by percent. Solid lines indicate cumulative frequencies by percent

elasmobranchs were nearly equal in their overlap with the fishery but progressively less than marine mammals (11% and 9%, respectively).

DISCUSSION

Although it is well known that predation is the dominant force structuring squid populations in the northwest Atlantic (Buckel et al. 1999, Overholtz et al. 2000), information on size-dependent relationships between squid and their predators has been scarce. The results provided in this study shift from the broad perspective of community down to individual species and represent the most comprehensive evaluation of size-based predation on a cephalopod species conducted to date.

Size-based feeding patterns on longfin inshore squid varied widely among teuthophagous predators. Maximum squid sizes exhibited the greatest rates of change both within predator species and interspecifically. Teuthophagous predators consumed a narrower range of squid body sizes than were previously reported when all prey types (e.g. crustaceans, fish) were included in size-based diet analyses (Scharf et al. 2000, Ménard et al. 2006). Given the fact that our analyses were limited to a single prey species, this result is not completely unexpected. However, it is noteworthy that the contracted ranges of squid sizes found in predator diets were largely shaped by ontogenetic changes in the minimum size of squid consumed. Rates of change in minimum prey sizes were also greater than have been found in piscivorous predators (Scharf et al. 2000, Ménard et al. 2006).

Small teuthophagous predators (e.g. mackerel, hakes, and flounders) increased both the minimum and maximum sizes of squid in their diets with growth and generally consumed narrow ranges of prey sizes. Consequently, size-based predation by small predators has the potential to fluctuate widely with variations in year-class strength and overall demographic structure. Larger predators such as dogfish and pilot whales targeted a comparatively wide range of squid sizes and exhibited little to no change in the overall sizes of squid in their diets. Accordingly, size-based patterns in predation by these species would remain relatively consistent on all targeted squid life stages regardless of the size-composition of predator populations.

With the exception of silver hake and spiny dogfish, size-based trophic niche breadths of teuthophagous predators did not show significant trends of expansion or contraction. This is in contrast to the findings of Scharf et al. (2000) who found an increasing tendency towards narrowing trophic niche breadths in progres-

Table 3. Equations for relative body size relationships between longfin inshore squid and its predators. The 10th and 90th quantiles were used to estimate the lower and upper bounds, respectively, for all predator species. F = the F-test statistic for differences between lower and upper bound lines; p = significance of F-test. RBS = relative predator-prey body size, and PL = predator length

| Predator species	Lower bound (cm)	Upper bound (cm)	F	p	Trophic niche breadth
Atlantic mackerel	RBS = -0.004PL + 0.29	RBS = -0.01PL + 0.58	0.84	0.36	Parallel (decreasing)
Bluefish	RBS = -0.002PL + 0.24	RBS = -0.003PL + 0.47	3.12	0.08	Parallel (decreasing)
Fourspot flounder	RBS = 0.002PL + 0.22	RBS = 0.003PL + 0.41	0.09	0.76	Parallel (constant)
Goosefish	RBS = -0.003PL + 0.32	RBS = -0.01PL + 0.98	2.41	0.12	Parallel (decreasing)
Long-finned pilot whale	RBS = -0.0002PL + 0.12	RBS = -0.0002PL + 0.20	0.001	0.98	Parallel (decreasing)
Silver hake	RBS = 0.001PL + 0.24	RBS = 0.02PL + 0.10	6.33	0.01	Diverging
Smooth dogfish	RBS = -0.001PL + 0.14	RBS = -0.001PL + 0.30	0.98	0.32	Parallel (decreasing)
Spiny dogfish	RBS = -0.002PL + 0.22	RBS = -0.004PL + 0.57	48.53	0.0001	Converging
Spotted hake	RBS = -0.01PL + 0.50	RBS = 0.004PL + 0.45	3.66	0.06	Parallel (constant)
Summer flounder	RBS = -0.002PL + 0.25	RBS = 0.0004PL + 0.43	2.41	0.12	Parallel (constant)
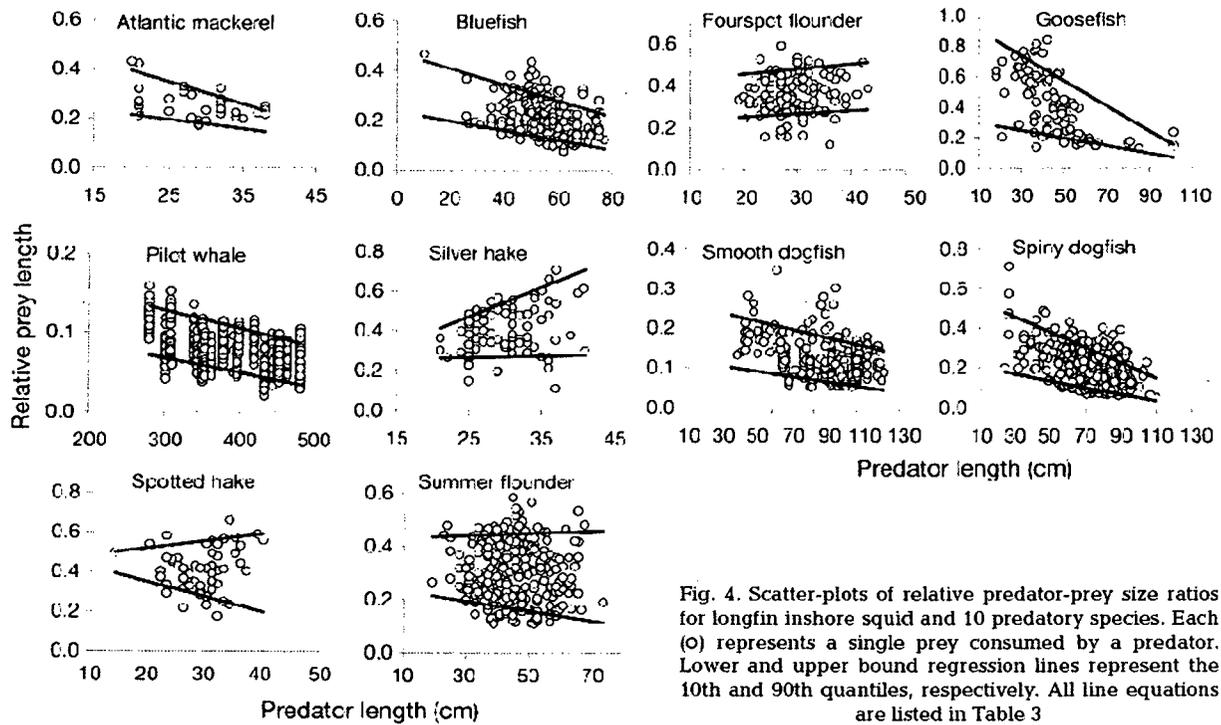
Fig. 4. Scatter-plots of relative predator-prey size ratios for longfin inshore squid and 10 predatory species. Each (o) represents a single prey consumed by a predator. Lower and upper bound regression lines represent the 10th and 90th quantiles, respectively. All line equations are listed in Table 3
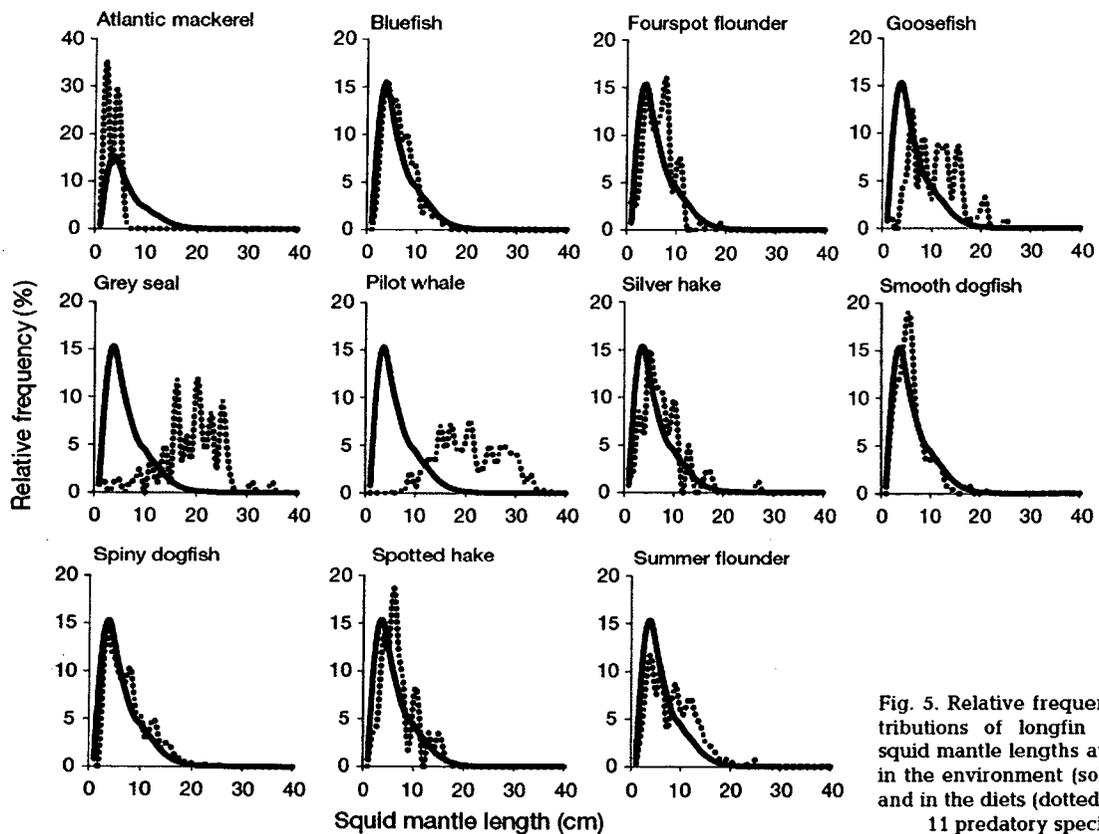

Fig. 5. Relative frequency distributions of longfin inshore squid mantle lengths available in the environment (solid line) and in the diets (dotted line) of 11 predatory species

sively larger piscivorous predators. Interspecific comparisons of mean size-based trophic niche breadths indicated high correspondence among predators for squid resources. Notable exceptions on both ends of the spectrum were goosefish and pilot whales. Species that co-occur will compete more directly; however, the high amount of overlap observed for squid size resources was probably not limiting to predators since many populations are separated temporally and spatially on the shelf (Bethea et al. 2004). Relative frequency distributions and predator-prey body size relationships determined that the relative size class of squid favored in individual predator diets was highly species specific and varied even among closely related species (e.g. fourspot and summer flounders). Differences among predators were likely shaped by morphological variations, foraging tactics (e.g. lie-and-wait, active), habitat associations, and swimming abilities (Scharf et al. 2000).

Table 4. Linear regression equations for predator length (PL) to gape width (GW) and gape height (GH) for Atlantic mackerel, fourspot flounder, smooth dogfish, spotted hake, and summer flounder. All lengths were measured in cm. All regression equations were highly significant (p < 0.0001)

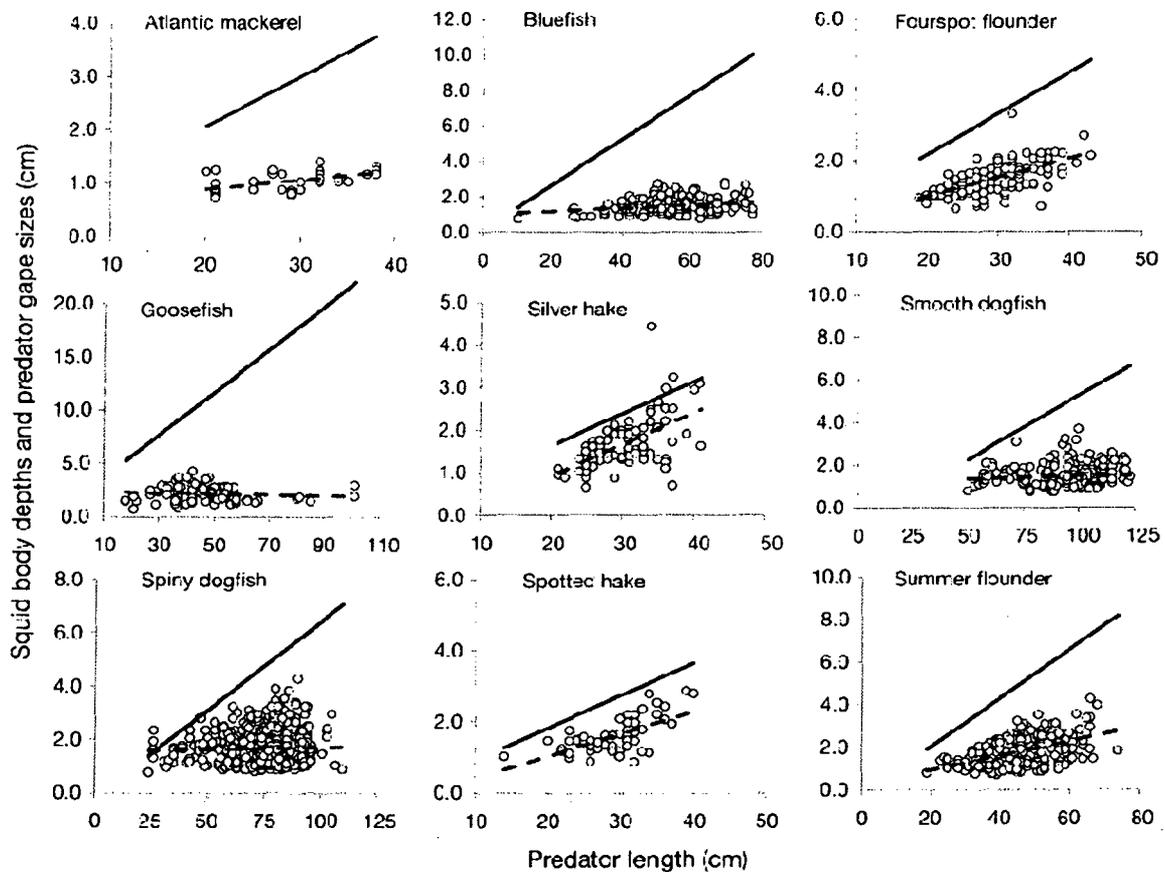| Predator	n	Equation	r^2
Atlantic mackerel	32	GH = 0.117 PL + 0.334	0.86
		GW = 0.094 PL + 0.188	0.67
Fourspot flounder	24	GH = 0.156 PL − 0.795	0.93
		GW = 0.116 PL − 0.161	0.84
Smooth dogfish	35	GH = 0.060 PL − 0.753	0.93
		GW = 0.065 PL − 0.253	0.96
Spotted hake	40	GH = 0.092 PL − 0.014	0.88
		GW = 0.118 PL − 0.403	0.96
Summer flounder	37	GH = 0.130 PL − 0.195	0.95
		GW = 0.114 PL − 0.261	0.96

Fig. 6. Scatter-plots of longfin inshore squid body depth (BD) versus length of 9 predatory species. Each (o) represents a single squid consumed by a predator. All relationships for predator gape width (GW) and height (GH) are reported in Table 4. Solid lines represent the relationship between PL and predator GW for all predators except spotted hake. GH was found to increase at a lesser rate than width in spotted hake and was therefore plotted as the limiting morphometric gape relationship. Dashed lines indicate linear regressions between PL and squid BD
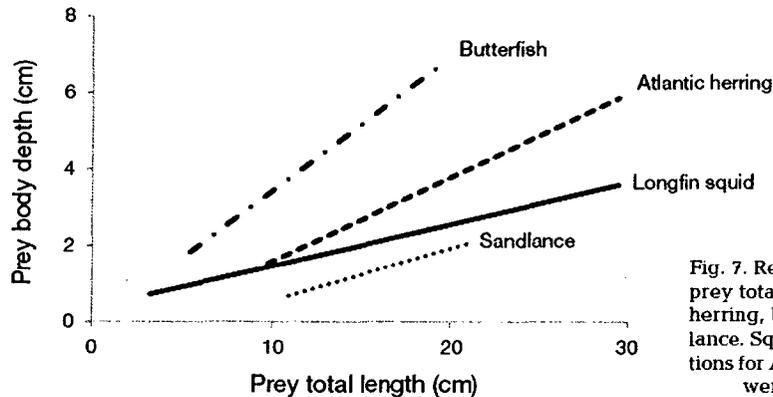
Fig. 7. Regression lines of the relationship between prey total length and prey body depth for Atlantic herring, butterfish, longfin inshore squid, and sand lance. Squid lengths were measured directly; equations for Atlantic herring, butterfish, and sand lance were adapted from Scharf et al. (1998b)
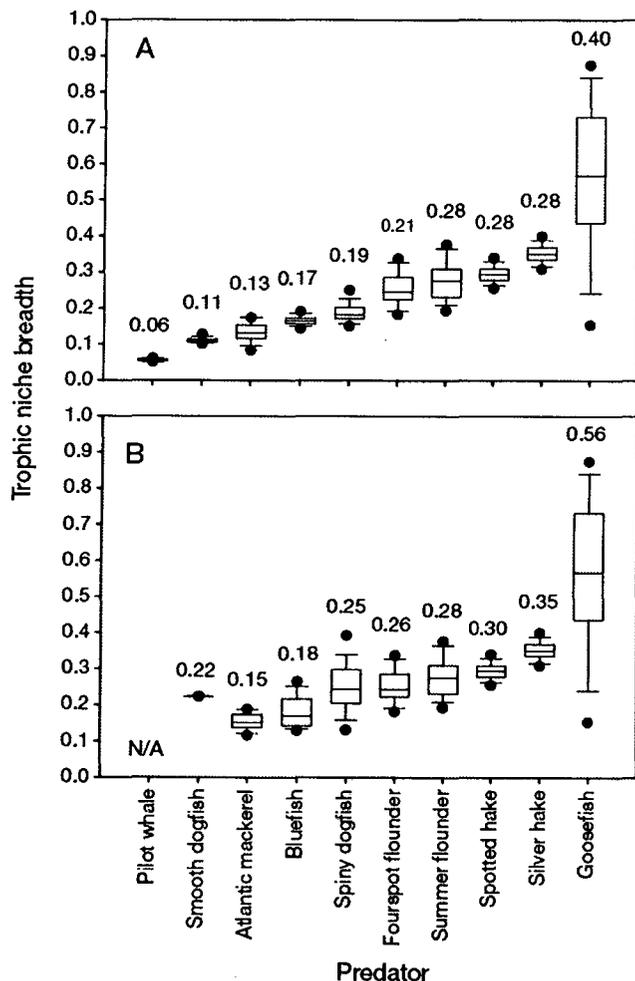

Fig. 8. Measurements of size-based trophic niche breadths for (A) longfin inshore squid and (B) prey fish. Box boundaries represent 25th and 75th percentiles; lines within boxes mark the median. Error bars indicate the 90th and 10th percentiles. Black dots show outliers in the 5th and 95th percentiles. Values indicate the mean trophic niche breadth of each predator.

Comparisons of squid and fish body shapes revealed that Atlantic herring increased BD at greater rates than were observed for squid. This signifies that clupeids outgrow gape-limited predators faster and have a smaller window of predation than squid. The same would also be true of other important prey fish such as butterfish and scup Stenotomus chrysops which are deep bodied and co-occur seasonally with squid in shelf waters (Hendrickson 2005). Squid body shapes were considerably smaller than predator GH, suggesting that predators were not gape limited when foraging on squid (Nilsson & Bronmark 2000). Despite this, large squid were not common in finfish and elasmobranch diets. Predators also possessed wider size-based trophic niche breadths for prey fish in comparison to squid, indicating they were not only capable but actually did consume relatively larger prey. Since morphological restrictions were not limiting to predators, availability and behavioral components must be influential in shaping size-based feeding strategies on squid.

Size-based encounter rates between squid and their predators are largely dictated by overall species ranges, activity levels, ontogenetic habitat utilization, and migration patterns. Encounter rates will likely be elevated during the winter and spring seasons when squid and many of their predators aggregate in southern and offshore waters (Staudinger 2006). Unfortunately, diet data were not extensive enough to evaluate seasonal trends that were also species-specific. Diel vertical migration is more pronounced in juvenile squid than in adults (Brodziak & Hendrickson 1999); accordingly, vertically migrating predators will have the highest encounter rates with juvenile squid. Although juvenile and sub-adult squid were recurrent in finfish and elasmobranch diets, paralarval and small juveniles were rare. Previous studies have also noted this deficiency (Smale 1996, Dawe & Brodziak 1998). The focus of sampling efforts on demersal predators

and environments explains to some degree why squid <5 cm were only occasionally observed in regional diets. Longfin inshore squid exhibit an ontogenetic descent from surface waters into demersal habitats at ~5 cm ML (Macy & Brodziak 2001). Not surprisingly then, Atlantic mackerel, one of the only pelagic species evaluated in this study, had a diet entirely composed of paralarval and juvenile squid. Atlantic mackerel was also the only predator observed to exhibit negative size-selection on squid.

Size distributions from population surveys suggested that squid sizes >10 cm ML were relatively scarce in the environment. Despite their scarcity, large squid were favored in the diets of pilot whales and grey seals. Marine mammal diets often reflect considerably wider ranges of cephalopod sizes and species and may be more reliable indicators of cephalopod population distributions in comparison to conventional survey gears (Clarke 2006). Previous work conducted in the northeast Atlantic found that 13 species of toothed whales and 2 species of tunas selected for larger prey than were locally abundant (MacLeod et al. 2006, Ménard et al. 2006). Mean squid lengths reported in the diets of harbor seals in the Gulf of Maine were also quite large (Williams 1999). These accounts provide mounting evidence that marine mammals and large pelagics target larger squid than are normally found in the diets of demersal shelf predators.

Sampling biases

Data on squid population and predator diet were primarily obtained from bottom-trawl surveys conducted in continental shelf waters. This method of sampling likely underrepresented large squid capable of outswimming nets, prevalent at other depths in the water column, and those that inhabit open ocean environments (Brodziak & Hendrickson 1999, Macy & Brodziak 2001, Hendrickson 2004). Sampling biases may also have influenced predator-prey size data. Data on food habits collected as part of the National Marine Fisheries Service (NMFS) bottom-trawl surveys identify squid from whole specimens and beaks, when possible, and length measurements were made only from intact specimens or pens. Species is not usually determined from pens, and the lower rostral lengths of the lower beaks were not measured as part of NMFS survey protocols. These methods decrease the total number of species-specific squid lengths in diet analyses. Perhaps most importantly, small squid degrade faster in predator stomachs in comparison to large squid; therefore, small squid will more often be recovered in a highly digested state, and the methods of collection noted above lead to underrepresentation of small body sizes (Santos et al. 2001).

Because our study compiled diet data from several sources, different methods were employed to collect prey length data. Sampling of marine mammal diets was more opportunistic than for fish predators. Pilot whale diets were derived from individuals that had been killed incidentally or stranded. It is uncertain if diets from these individuals were representative of healthy animals and the greater population (Gannon & Waples 2004). Grey seal diets were determined from scat and could not be traced back to specific individuals. In both pilot whales and grey seals, lower rostral lengths of the lower beaks were used to reconstruct original body size using the equations provided by Staudinger et al. (2009). Estimating original length from digested remains can be subject to back-calculation errors, and beaks that are highly digested may be eroded by digestion. To compensate for digestion effects, beaks recovered from grey seal scat were adjusted using a digestion coefficient (Grellier & Hammond 2006).
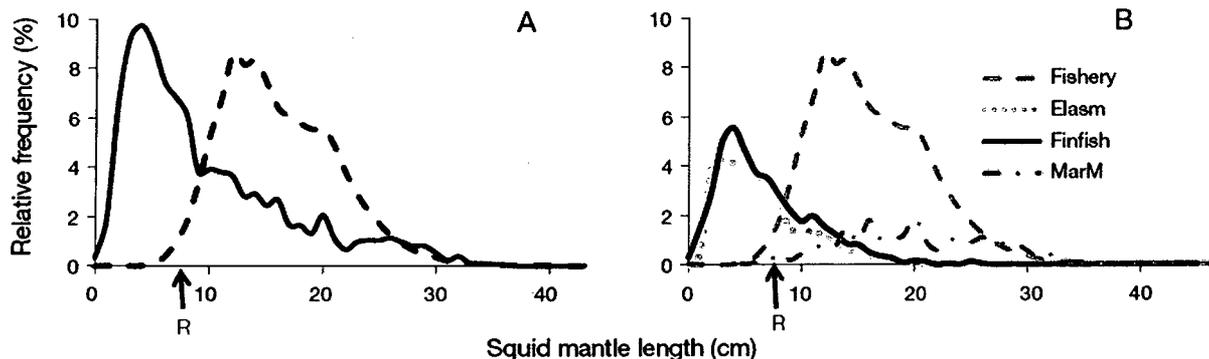

Fig. 9. Relative frequency distributions of longfin inshore squid consumed by (A) all predators (solid lines) and harvested by the commercial fishing industry (dashed lines) and (B) major predator assemblages. Groups analyzed included the commercial fishery (Fishery), elasmobranchs (Elasm), finfish (Finfish) and marine mammals (MarM). Arrows and 'R's indicate the sizes at which longfin (8 cm ML) recruit into the commercial fishery

Impacts of fishing pressure

Finfish and elasmobranch predation was focused primarily on pre-recruit squid, suggesting that overlap with the fishing industry was low. Since commercial landings data may not include biomass removed as bycatch, it is possible that size-based removals of pre-recruit squid may be higher than indicated in our analyses (Hall et al. 2000). The observed differences in size-based feeding patterns among predator taxa revealed that marine mammals had the highest overlap and therefore the greatest potential for conflict with the commercial fishing industry. Marine mammals have high energetic demands and are often specialized in their feeding ecology (MacLeod et al. 2006); however, foraging habits are also strongly associated with prey availability and seasonal changes (Andersen et al. 2007). Unfortunately, our results were limited to general depictions of size-based reliance on squid populations; to fully assess competition for squid resources between predators and the fishery, higher seasonal and spatial resolution is needed.

Fishing has eroded the predation landscape by decreasing the prevalence of larger body sizes in exploited populations (Jennings & Reynolds 2007). All of the fish and elasmobranch species examined here are harvested commercially or caught incidentally by fishing gear. Maximum body sizes of the 9 fish species evaluated using quantile regression analyses were from 20 to 50 cm smaller than their reported maximum sizes (Table 5). Information on squid-predator body-size relationships became scarcer for all species with increasing predator body size. This is almost certainly due to the low frequency of large individuals in the ecosystem rather than from diminishing predation rates on squid. Predators that were found to rapidly increase the maximum size of squid in their diets and have the potential to attain substantially larger body sizes than were common over the past several decades (e.g. bluefish, summer flounder) will likely increase their predatory demand on adult squid if population size-structure becomes less truncated. Increased abundance of large fish may also lead to heightened competition with fisheries for adult squid.

Commercial fisheries have increasingly targeted mid-trophic level species including squid to supplement or replace the yields lost from traditional fisheries, such as groundfish and large pelagics (Pauly et al. 1998, Essington et al. 2006). Squid biomass is believed to be artificially inflated due to a release from predatory demand from depressed populations of higher level predators (Caddy & Rodhouse 1998, Duplisea & Castonguay 2006). If this is true, fisheries have been taking advantage of excess biomass specifically in the adult component of squid populations that

may no longer be in surplus if predator population structure and abundance are recovered under current rebuilding efforts.

Species such as squid that serve as forage to higher level predators and form the 'waists' of marine food webs dictate the dynamic properties of the surrounding food web (Rice 1995). Key forage species have been found to be most sensitive to overfishing at high levels of predation (Collie & Gislason 2001). Because squid are known to be important mid-trophic level species, target harvest rates and long-term potential yields have been set using precautionary approaches (Brodziak 1998). However, fisheries management plans generally do not include estimates of natural mortality rates on pre-recruits in setting biological reference points (BRPs) and total mortality thresholds (Collie & Gislason 2001). Furthermore, single-species management plans fail to consider trophic interactions and do not account for changes in predator population structure (Buckel et al. 1999, Pikitch et al. 2004). Because large predators have been functionally absent from the community for several decades, it is uncertain how stock rebuilding will influence predation on squid populations. For example, harvesting adult squid could result in increased survival of pre-recruit squid due to reductions in density-dependent mortality rates. Although intraspecific predation was not included in our analyses, cannibalism within longfin squid populations can be considerable (Macy 1982, Dawe 1988). A similar scenario has been suggested for walleye pollock *Theragra chalcogramma* and its predators in the eastern Bering Sea (Livingston 1993).

CONCLUSIONS

Over the past 50 yr the northwest Atlantic has undergone profound shifts in species abundance and composition and is considered one of the most overfished marine ecosystems in the world (Link & Garrison 2002,

Table 5. Historical and sampled maximum fish lengths (L_{max}). Historical lengths were reported by Froese & Pauly (2008) and Collette & Klein-MacPhee (2002)

Species	Historical L_{Max} (cm)	Sampled L_{Max} (cm)
Atlantic mackerel	60	38
Bluefish	130	77
Fourspot flounder	45	43
Goosefish	120	101
Silver hake	76	41
Smooth dogfish	150	123
Spiny dogfish	160	110
Spotted hake	42	40
Summer flounder	94	74

Briggs 2008). Depletion of higher level predators and the prevalence of fishing down the food web are more common in the North Atlantic than in other oceans (Essington et al. 2006). This will be increasingly important as the demographic structure in predator populations is rebuilt. Even if management efforts are not successful in recovering large predators, knowledge of size-based feeding strategies will be useful in predicting the responses of existing populations to exploitation as well as seasonal, annual, and decadal shifts in environmental conditions. Taken as a whole or in parts, the information presented in this study can be used to expand single-species management plans into more holistic multispecies and ecosystem-based approaches.

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