

Size-structured patterns of piscivory of the longfin inshore squid (*Loligo pealeii*) in the mid-Atlantic continental shelf ecosystem

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Abstract: The longfin inshore squid (*Loligo pealeii*) dominates the landings in the USA mid-Atlantic continental shelf region, yet the potential ecological effects of harvesting this species are not known. Because squid feed on a wide variety of prey items, including juvenile stages of commercially important fish species, a full exploration on the predatory role of squid in this ecosystem is warranted. We examined the seasonal diet contents of *L. pealeii* and evaluated the importance of size constraints in governing patterns of piscivory. Our analyses showed that piscivory was dictated by size constraints, with larger squid demonstrating higher rates of piscivory than small squid. Squid were piscivorous at smaller sizes in the winter and spring than during the summer and autumn. Also, the frequency of piscivory was highest during the winter and spring, coincident with the time period when the number of vulnerable prey species was greatest. Our findings suggest that the frequency and intensity of piscivory are likely to be related to the duration of time that prey are vulnerable to predation, which in turn is dictated by the relative body sizes of *L. pealeii* and juvenile fishes.

Résumé : Le calmar totam (*Loligo pealeii*) prédomine dans les débarquements dans la région de la plate-forme continentale de l'Atlantique moyen aux É.-U.; cependant, les effets écologiques potentiels de la récolte de cette espèce sont inconnus. Il est nécessaire d'explorer à fond le rôle de prédateur des calmars dans cet écosystème, parce que ceux-ci utilisent une gamme étendue de proies, y compris les jeunes stades de poissons d'importance commerciale. Nous avons analysé la composition du régime alimentaire de *L. pealeii* en fonction des saisons et évalué l'importance des contraintes reliées à la taille dans l'établissement des patrons d'ichtyophagie. Nos analyses montrent que l'ichtyophagie est contrôlée par des contraintes reliées à la taille et que les calmars de plus grande taille ont des taux d'ichtyophagie plus importants que les petits calmars. Les calmars deviennent ichtyophages à des tailles plus faibles en hiver et au printemps qu'en été et en automne. De plus, la fréquence de l'ichtyophagie est plus élevée en hiver et au printemps, ce qui coïncide avec la période pendant laquelle le nombre d'espèces de proies vulnérables est le plus grand. Dans leur ensemble, nos résultats indiquent que la fréquence et l'intensité de l'ichtyophagie sont susceptibles d'être reliées à la durée de la période de vulnérabilité des proies à la prédation, elle-même déterminée par les tailles corporelles relatives de *L. pealeii* et des jeunes poissons.

[Traduit par la Rédaction]

Introduction

It is widely acknowledged that squid are a key component in marine food webs, as evidenced by their importance as prey items (Clarke 1996; Klages 1996; Piatkowski et al. 2001) and as predators (Sauer and Lipinski 1991; Rodhouse and Nigmatullin 1996; Santos and Haimovici 1998). Squid play a central role in the transfer of energy from lower to higher trophic levels (Vovk 1974; Nixon 1987; O'Dor and

Wells 1987), and their trophic relationships can be quite complex, as squid are consumed by fishes when they are young and then consume those same predators as they grow older (Vovk 1974; Hanlon and Messenger 1996). Squid predation has been suggested as a significant source of pre-recruit mortality in fish (Maurer and Bowman 1985) and may serve as a potential constraint on the recruitment success of commercially targeted fish, especially during years of high squid abundance (Dawe 1988; Rodhouse and Nigmatullin 1996).

Time series of fishery landings data show that in recent years cephalopod landings, of which squid are the majority, have dramatically increased, while groundfish landings have remained stable or declined (Caddy and Rodhouse 1998). The commercial fishery in the USA mid-Atlantic continental shelf region is an example of this trend. Landing approximately 100 000 t·year⁻¹ (National Oceanographic and Atmospheric Administration (NOAA) Fisheries 2002), this fishery is composed of a diverse assemblage of groundfish, small pelagics, and squids. The domestic fishery for longfin inshore squid, *Loligo pealeii*, developed within the last

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25 years and constitutes a dominant percentage (15%, NOAA Fisheries 2002) of the total commercial landings of nektonic species in the mid-Atlantic region. Notably, in New York, the landings of *L. pealeii* nearly doubled over the 1990s from 2890 to 5641 t and have dominated the total landings since 1999 (20%, NOAA Fisheries 2002), an indication of the increasing importance of their role in this fishery.

The ecological effects of squid harvesting are not known. Past studies provide some suggestion that *L. pealeii* play a pivotal role in the mid-Atlantic food web. Predators of *L. pealeii* include *Pomatomus saltatrix*, *Scomber scombrus*, *Melanogrammus aeglefinus*, *Pollachius virens*, *Merluccius bilinearis*, *Urophycis* sp., and *Paralichthys dentatus* (Langton and Bowman 1977; Lange 1980; Bowman et al. 2000). Thus, fisheries targeting *L. pealeii* might have an unintended negative impact on the productivity of other commercially valuable stocks. However, diet analyses have also found that *L. pealeii* prey upon juvenile gadids, merluccids, clupeids, and scombrids (Vovk 1972, 1985; Macy 1982), suggesting the possibility of positive effects of squid fishing on finfish production. Thus, not only the magnitude but also the direction of the effect of squid fisheries on other fisheries in this region is difficult to predict without detailed information on the interactions between squid and fishes in the food web.

Any attempt to explore food web interactions involving squid needs to explicitly account for the size structure of these interactions. Size-structured interactions can have substantial effects on predator-prey dynamics (Persson et al. 1996), and many predators exhibit ontogenetic, size-dependent patterns in predation (Polis et al. 1996; Scharf et al. 2000; Juanes et al. 2002). Squid are no exception to this rule, as several studies on squid feeding habits have convincingly documented the influence of body size on diet composition (Maurer and Bowman 1985; Collins et al. 1994; Lordan et al. 1998). These shifts are possibly related to size constraints on capturing and handling prey, as indicated by the relation between the ranges of prey sizes consumed with squid body size (Rocha et al. 1994; Collins and Pierce 1996; Phillips et al. 2003). Given that squid are likely to prey upon rapidly growing larval or juvenile stages of fish, we should expect that the frequency and intensity of piscivory would be limited by the duration of time that these fish are within a size range in which they are vulnerable to squid. Moreover, we should also expect that the magnitude of predation would be dictated by the size structure of the squid population. If these hypotheses are true, then fishing might have profound effects on squid-fish interactions by inducing shifts in the size structure of squid populations. Thus, there may be more substantial effects of fishing on trophic interactions mediated by size-selective fishing and predation that might not be apparent through modeling exercises that treat predators and prey as homogeneous pools (Jennings et al. 2002).

In this study, we examined the seasonal stomach contents of *L. pealeii* and estimated the sizes of fish and squid prey to provide answers to the following questions: How is predation on fish by squid governed by size constraints? How does the ontogeny of piscivory change seasonally? Can size-constrained predation explain the patterns of piscivory? Insights derived from this study can be used in future research to construct size-structured food web models, quantify the

predatory impact of squid on fish populations, and evaluate the effects of squid predation under alternative management strategies.

Materials and methods

Collection of *L. pealeii* stomach samples

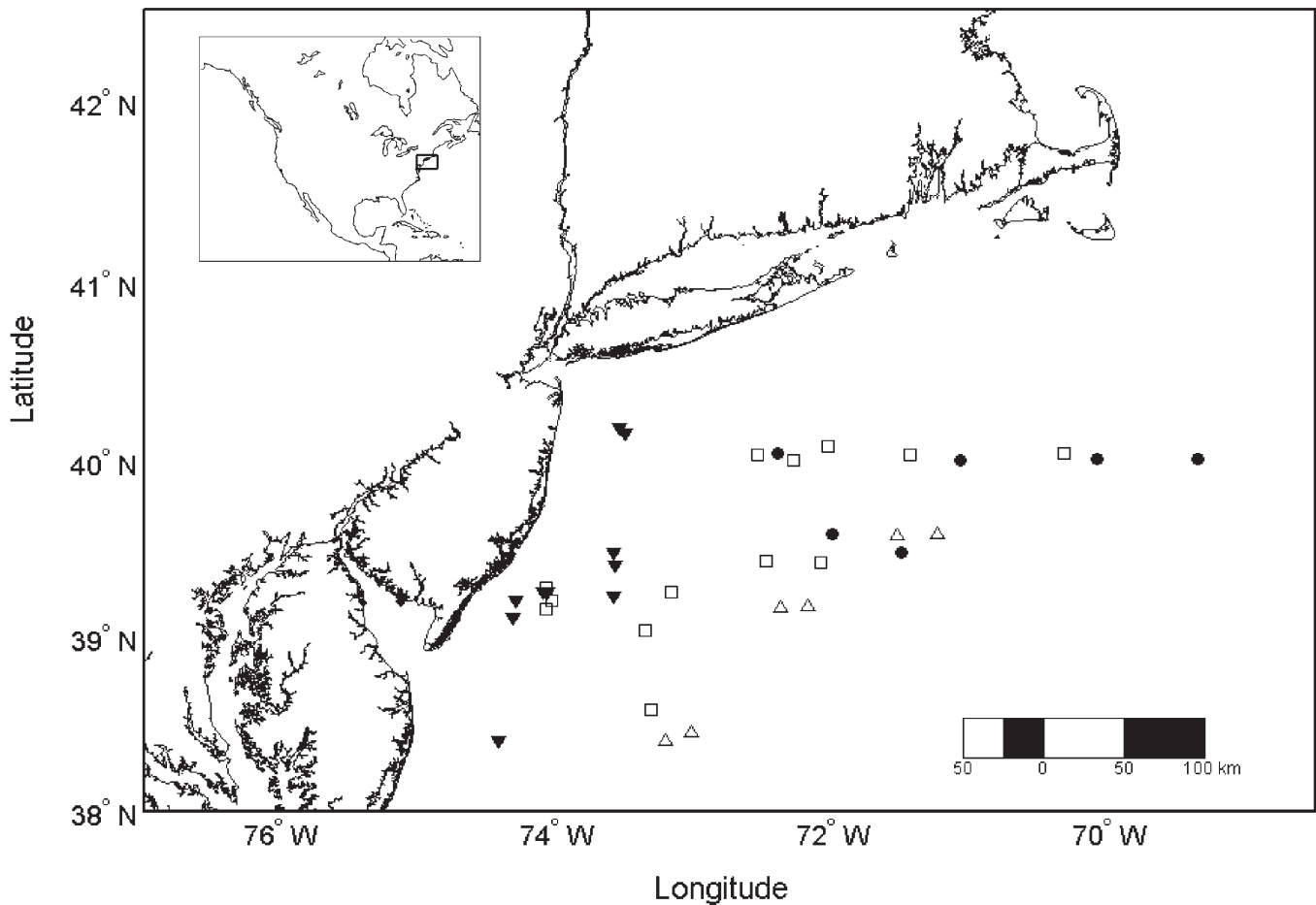
Approximately 3000 squid were collected from the mid-Atlantic continental shelf waters from April 2002 to May 2003 (Fig. 1). Squid were collected from waters offshore (>8 km) of New York and New Jersey on a monthly basis, with the exception of July, October, and November. Squid samples were obtained from bottom trawl surveys conducted by the NOAA National Marine Fisheries Service (September 2002, February and March 2003), New Jersey Department of Environmental Protection (June 2002), and from regional commercial fishing vessels (April, August, December 2002 and January–April 2003). Squid collected from bottom trawl surveys (0.5 inch mesh cod-liner; 1 in = 25.4 mm) were sampled across a wide area of the study region and were collected farthest from shore during the winter (depth: 59–217 m) and early spring (depth: 81–247 m) and closer to shore during summer (depth: 14–26 m) and autumn (depth: 11–125 m). Squid sampled from fishing vessels (min. 1.875 inch diamond mesh) during the winter and early spring were captured within the Hudson Canyon region (depth: 146–274 m), while the late spring and summer samples were captured in shallower waters south of Long Island (depth: ~30 m). These sample locations follow the natural inshore and offshore migration patterns of *L. pealeii*.

Squid were sampled from commercial vessels with the intention of collecting a wide size range of squid throughout each season to account for seasonal and ontogenetic shifts in diet compositions. In research cruises, squid were haphazardly subsampled from tows. For all squid sampled, body mass was weighed to the nearest 0.01 g, dorsal mantle length was measured to the nearest millimetre, and stomach contents were frozen until ready for identification by microscopy. Hard parts of prey, such as otoliths, scales, bones, statoliths, and beaks that remained in the stomachs, were used to identify prey of the collected squid (Vinogradov and Noskov 1979; Santos and Haimovici 1998). Crustaceans were also identified by eyes, appendages, mandibles, and exoskeletons (Karpov and Cailliet 1978; Santos and Haimovici 1998). Prey items were initially grouped by visual identification of hard parts and soft tissues as fish, squid, crustaceans, or unknown and categorized as fresh, partially digested, or well digested. Once identified, wet weights and lengths (when applicable) of each prey item were recorded, and the hard parts were stored in 90% ethanol for subsequent taxonomic classification.

General diet analyses

We quantified the diet composition of *L. pealeii* by calculating the percent frequency of occurrence of each prey item in the squid stomach contents. Other measures (e.g., percent by number or mass) are essentially impossible because squid masticate their food. To identify the order (or lowest taxon) of prey consumed by *L. pealeii*, the morphological features and size ratios of the digested otoliths were compared with those presented in guidebooks (Brodeur 1979; Härkönen

Fig. 1. Location of sampling sites for *Loligo pealeii* collected from National Marine Fisheries Service (NMFS) and New Jersey Department of Environmental Protection (NJDEP) bottom trawls surveys during the winter (solid circles), spring (open triangles), summer (solid, upsidedown triangles), and autumn (open squares). Inset of North America show the sampling area off the coast of New York and New Jersey, USA.



1986) as well as with lab reference collections. No attempt was made to match otolith pairs and each otolith was treated as a single prey item. Otoliths were classified to order or family only if the otoliths were indistinguishable from the references. Otoliths that were well digested and lacked distinctive features required for classification were categorized as unknown. To further support our classifications, we compared our findings with the expert opinions and extensive reference collection at the Fishery Biology Investigation Laboratory (Woods Hole, Massachusetts). Squid species consumed by *L. pealeii* were also identified by comparing the features of the lower squid beaks found in the stomach contents with guidebooks (Clarke 1986) and lab reference collections. *Loligo* sp. and *Illex* sp. are the only species of squid that inhabit the study region, and their lower beak features are quite distinct.

Determination of prey sizes

To determine the prey sizes of the ingested fish, the lengths of the digested otoliths were measured to the nearest 0.1 mm. Prey sizes were calculated using otolith length to body length relationships for each genus (Table 1). When otoliths could not be classified to genus, we determined prey

sizes by averaging the estimated body sizes of all species within that order or family for which regressions were available. This was only possible when regression equations of the different species were similar. The sizes of ingested squid were also determined using the lower beak rostral length and dorsal mantle length relationship for *L. pealeii* (Gannon et al. 1997) (Table 1). When only upper beaks remained in the stomach contents, the upper beak rostral lengths were used to estimate prey sizes as done by previous authors (Dawe et al. 1998). The rostral lengths of squid upper and lower beaks were measured to the nearest 0.1 mm.

We analyzed the relationship between squid and prey sizes using quantile regression (version 8.2, StataCorp Statistical Software, College Station, Texas). This technique allowed us to estimate the relationship between predator length and minimum or maximum prey sizes by analyzing the edges of scatter diagrams (Scharf et al. 1998, 2000). This regression procedure differs from the least squares technique, as the regression quantiles are determined by minimizing the sums of the absolute values of residuals rather than by minimizing the sums of squares. The 90th and 10th quantiles were used as upper and lower bound regression quantiles in this analysis and were chosen based on sample size (Rogers 1992;

Table 1. Parameters of the otolith size – fish size (mm) regression used to estimate sizes of fish ingested by *Loligo pealeii*.

Prey	<i>a</i>	<i>b</i>	Transform	Reference
<i>Loligo pealeii</i>	1.767	1.4	logL	Gannon et al. 1997
<i>Benthoosema</i> sp.	-3.3272	25.0114	TL	Markaida and Sosa-Nishizaki 2003
<i>Ammodytes americanus</i>	-4.377	9.024	FL	Bowen and Harrison 1994
<i>Sebastes</i> sp.	3.1273	1.436	lnFL	Hunt 1992
<i>Mauroliticus muelleri</i>	9.82	28.75	FL	Härkönen 1986
<i>Melanogrammus aeglefinus</i>	0.94834	1.38	logFL	Härkönen 1986
<i>Merlangius merlangus</i>	-11.936	19.7	FL	Härkönen 1986
<i>Urophycis tenuis</i>	0.18327	1.1456	logFL	Clay and Clay 1991
<i>Pollachius virens</i>	1.8117	1.6251	lnFL	Hunt 1992
<i>Merluccius bilinearis</i>	2.9475	1.0276	lnFL	Hunt 1992

Note: The general form of the model was $L' = a + bOL'$, where L' and OL' are the actual lengths or log-transformed lengths, respectively. A lower beak rostral length – dorsal mantle length (mm) regression equation was used to estimate the sizes of squid consumed by *L. pealeii*.

Scharf et al. 1998). Additionally, we used the Student's *t* test to compare the slopes of the upper bound regression quantiles to determine whether maximum prey size differed between fish and cannibal prey (Scharf et al. 2000; Juanes 2003).

Ontogenetic shifts in diet compositions

To detect ontogenetic shifts in the diet composition of *L. pealeii*, we employed logistic regression analyses. We categorized *L. pealeii* diet into fish and squid and assigned a zero or one to each category depending on whether each respective prey item was absent or present in each stomach sample. Logistic regression was used to relate the probability of occurrence of a specific prey item (fish or squid) to squid mantle length (*L*) (20–280 mm), but we introduced more biologically meaningful parameters to replace the standard logistic regression parameters. Specifically, we define F_{\max} as the maximum probability of piscivory, L_{50} is length at which the predicted rate of piscivory is 50% of the maximum (generally reflects size at onset of piscivory), and δL as the difference between L_{50} and L_5 (the length at which the predicted rate of piscivory is 5%). The δL value gives an indication as to the abruptness of the onset of piscivory. Small values indicate very abrupt ontogenetic shifts and large values indicate gradual shifts. Given these parameters, the probability of piscivory (*P*) equals

$$(1) \quad P = \frac{F_{\max} \exp[Z(-L_{50} + L)]}{1 + \exp[Z(-L_{50} + L)]}$$

$$Z = \frac{2.94}{\delta L}$$

Maximum likelihood estimates of F_{\max} , L_{50} , and δL were estimated numerically using Solver in Microsoft Excel® (Microsoft Corporation, Redmond, Washington).

Loligo pealeii reside in offshore water during the winter–spring and nearshore during the summer–autumn. We compared ontogenetic shifts in piscivory between these periods by calculating the 90% prediction intervals for the probability of piscivory through parameterization of eq. 1 using data collected during these two periods. Prediction intervals were calculated using a grid-based description of the likelihood

surface with respect to F_{\max} and L_{50} , using the best-fitting value of δL for each point along the grid. Based on these likelihoods, we calculated the expected probability of piscivory for each element of the grid and generated the 5th, 50th, and 95th percentiles of *P* based on the cumulative likelihood function. This is equivalent to a Bayesian credibility interval under the special condition of a uniform (non-informative) prior on F_{\max} , L_{50} , and δL .

Further, to evaluate whether seasonal patterns of piscivory were linked to prey size constraints, we estimated the number of species of juvenile fish that were within the prey size spectra of the squid population during each season. This analysis proceeded in four steps. First, squid length-frequency distributions were calculated from the squid sampled by bottom trawl surveys during this study. Second, we calculated the prey size spectrum for each squid length using the upper and lower bound quantile regression equations determined in this study. Third, we estimated the sizes of each potential age-0 fish prey in each season based on published literature (Sherman et al. 1984; Quinonez-Velazquez 1999; Clay et al. 1989; Able et al. 1990; Comyns and Grant 1993; Morse and Able 1995; Able and Fahay 1998; Cargnelli et al. 1999a, 1999b; Chang et al. 1999a, 1999b; Packer et al. 1999; Steimle et al. 1999; Steves et al. 1999; Steves and Cowen 2000; Lock and Packer 2004). We constrained this question to juvenile fish that are known to spatially and temporally overlap with *L. pealeii*. Lastly, based on the predator and prey sizes, we estimated the number of species of juvenile fish vulnerable to predation by squid of each length category.

Results

Description of *L. pealeii* samples

Approximately 3000 squid were sampled from both commercial and research vessels throughout the spring ($n = 911$), summer ($n = 868$), and winter ($n = 503$). In the autumn ($n = 744$), squid were collected only by research vessels because the regional squid fishery was closed owing to an enforced quota limit. Squid sizes ranged from 20 to 360 mm, with an average size of 115 ± 58 mm. The squid samples collected by bottom trawl surveys were dominated by smaller sized

squid in June and September and by larger size squid during the month of February. In March, the size distribution of *L. pealeii* was more homogeneous. The seasonal length distributions of squid collected in this study were similar to those described in some past studies that analyzed the population structure of *L. pealeii* (Macy 1982; Brodziak and Macy 1996; Hatfield and Cadrin 2002).

General diet analyses

Identifiable prey items were found in 45.7% of the squid stomachs, while the unidentifiable prey constituted 28.2% of the stomach samples. The remaining squid stomachs (26.1%) were empty. The high percentage of unknown prey is a result of the large number of unknown diet items found in the stomachs of small squid (<80 mm). Approximately 60% of the total unknown prey items were found in the stomachs of small squid. The diet contents of the smaller squid were often well digested and difficult to identify, possibly an effect of their high digestion rates and (or) feeding behavior. Of the total portion of identifiable prey, squid comprised the highest percentage of diet items followed by crustaceans and fish (Table 2). We also found a higher percentage of single prey items in comparison with multiple prey items in *L. pealeii* stomach contents (Table 2).

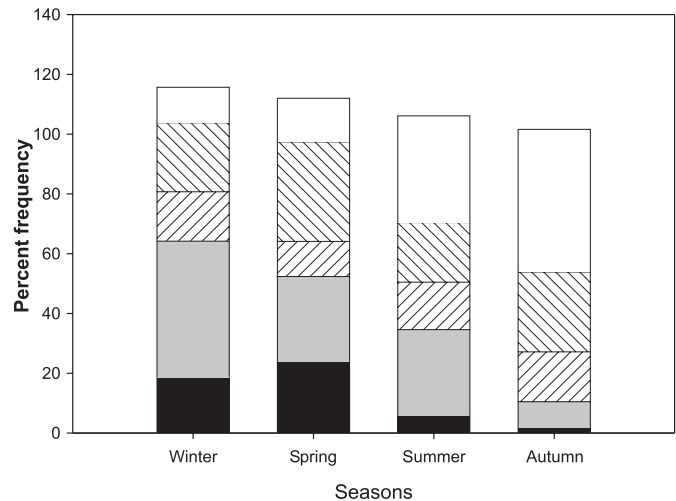
There were seasonal shifts in diet composition (Fig. 2). The highest percent occurrence of fish prey was found in the winter (16%) and spring (21%); the lowest occurrence was found during the summer (5%) and autumn (2%). The occurrence of cannibalism was high during the winter, spring, and summer (25%–39%), but decreased during the autumn (9%). The occurrence of crustaceans (10%–16%) and empty stomachs (19%–29%) were similar among all seasons. The highest occurrence of unknown prey was found in the summer (34%) and autumn (47%) samples in contrast with the low occurrence found in the spring (13%) and winter (10%). Again, the high frequency of unknown prey during summer and autumn is likely a reflection of the high number of small squid that comprised the population during these seasons and the difficulty associated with identifying their stomach contents.

Otoliths were found in ~35% of squid stomachs containing fish remains (Table 3). Overall, Myctophidae (lanternfish) were most common and constituted 30.1% of all otoliths. Although myctophids were found in squid stomachs collected during the winter and spring seasons, 87% of these were found in the spring samples. Osmeriformes (smelts–argentinies) and Sternoptychidae (pearlsides) represented 18% and 8.4% of the identified otoliths, respectively, and were also consumed during the winter and spring seasons. Gadidae and Pleuronectidae together represented approximately 10% of all the otoliths. Gadids were found in stomach samples collected throughout all seasons, and pleuronectids were identified in stomach samples from every season except winter. Ammodytidae (sand lance) represented 4.2% of all otoliths collected and were identified in summer and autumn samples. Identifying fish by their otoliths is difficult at times because the size and shape may be altered during digestion. The small otoliths of juvenile fishes may also lack the distinguishing features of adult otoliths. As a result, 18.4% of otoliths were categorized as unknown. Note, however, that an unusually high number of unknown otoliths were found

Table 2. Percent frequency of *Loligo pealeii* diet items and occurrence of stomachs containing single or multiple prey items.

Prey type	Frequency of occurrence
Squid, crustacean, or fish	82.56
Squid and fish	8.03
Squid and crustacean	5.14
Crustacean and fish	3.26
Squid, crustacean, and fish	1.01
Total squid	49.45
Total crustacean	27.73
Total fish	22.82

Fig. 2. Seasonal diet compositions of *Loligo pealeii* measured by percent frequency (%) of occurrence. The diet contents included fish (solid), squid (shaded), crustacean (right diagonal), empty (left diagonal), and unknown (open).



in the winter samples (12%). It is probable that during this season squid are consuming a group of fish for which we do not have a reference. Additionally, we collected 28 intact lower squid beaks from the diet remains; 26 were identified as *Loligo pealeii* and two were identified as *Illex illecebrosus*. We did not identify crustaceans to a lower taxonomic level; however euphausiids, and to a lesser extent hyperiid amphipods, were found in the squid stomach contents.

Sizes of the fish consumed by *L. pealeii* were estimated using regression equations for otolith length to total length or fork length. Regression equations were available for sand lance, *Sebastes* sp. (redfish), pearlsides, and myctophids (*Benthoosema* sp.), but were not available for butterfish and cusk eel (Table 1). We were unable to identify the gadiformes to the genus or species level, but we determined the prey sizes by averaging the estimated prey body sizes calculated from regression for haddock (*Melanogrammus aeglefinus*), pollock (*Pollachius virens*), whiting (*Merlangius merlangus*), silver hake (*Merluccius bilinearis*), and *Urophycis tenuis* (white hake) (Table 1). These species are a good representation of the Gadiformes previously reported

Table 3. Otoliths found in *Loligo pealeii* stomach contents identified to order or family.

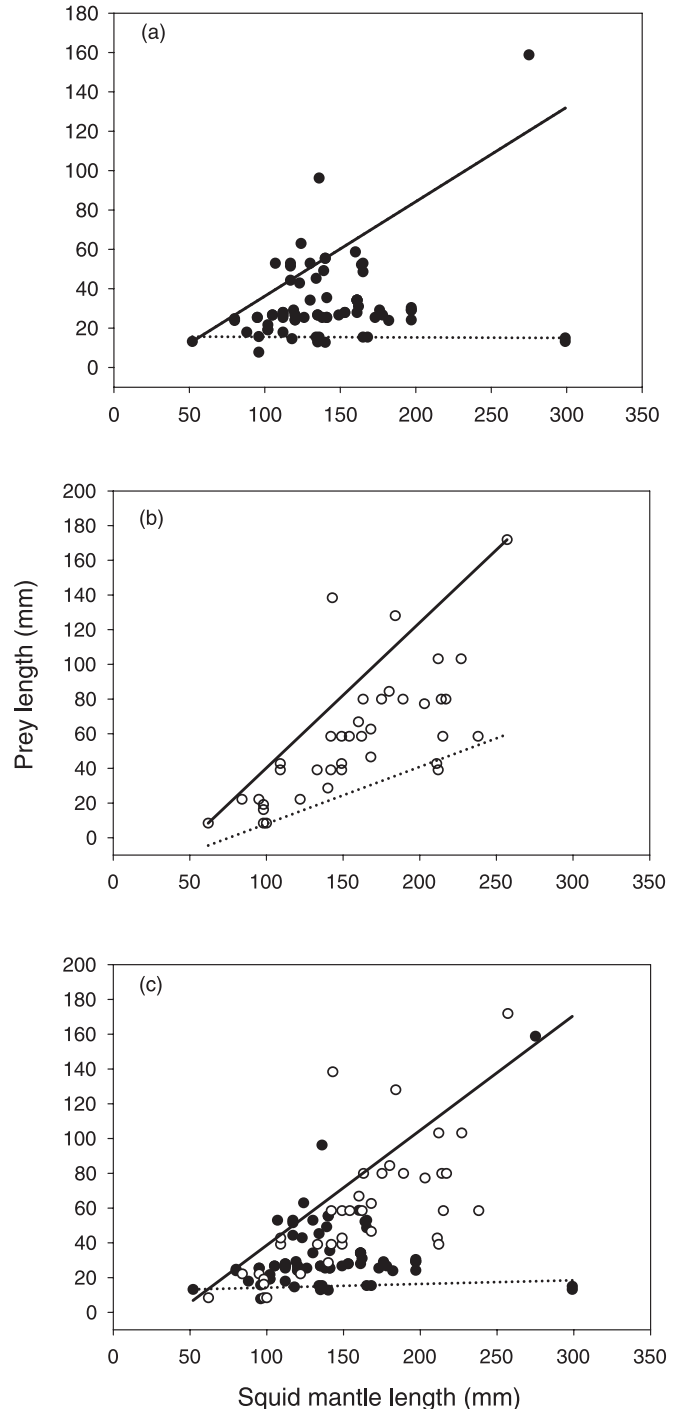
Order-Family	Winter	Spring	Summer	Autumn	Total
Myctophidae	9	61	—	—	70
Osmeriformes	3	41	—	—	44
Sternoptychidae	9	11	—	—	20
Gadiformes	6	5	2	2	15
Ammodytidae	—	—	9	1	10
Pleuronectiformes	—	4	3	2	9
Ophidiidae	—	4	2	—	6
Carangidae	—	4	—	—	4
Stromateidae	—	—	2	1	3
Sebastidae	—	2	—	—	2
Unknown	30	11	0	3	44
Broken	3	7	1	—	11
Total	60	150	19	9	238

as squid prey and (or) inhabitants of our study region during some time of the year. Additionally, the regression equations for these species were similar, providing similar estimates of prey sizes. We did not estimate the prey sizes of fish classified as Pleuronectiformes, Osmeridae, or Caraginidae because regression equations do not exist for species that well represent the order and families in our study region.

The sizes of the ingested fish ranged from 8 to 158 mm, with an average size (\pm standard deviation) of 32 ± 21 mm. The sizes of ingested squid ranged from 8 to 172 mm, with an average length of 58 ± 36 mm. The upper bound (90th quantile) regression of fish prey length and squid mantle length showed an increasing trend in upper prey size with predator length, although the slope was marginally non-significant ($p = 0.066$) (Fig. 3a). The lower bound (10th quantile) indicates that the lower fish prey size remained relatively constant ($p = 0.978$) (Fig. 3a). The quantile regression lines of the lengths of cannibalized squid indicate that maximum prey size increased with predator length ($p < 0.001$); however, in contrast with fish prey, the minimum prey size increased with predator length as well ($p = 0.002$) (Fig. 3b). Combining all ingested fish and squid prey, the regression lines demonstrate an increasing, though marginally non-significant, trend in upper prey size with increasing predator length ($p = 0.089$) and the lower prey size remained constant ($p = 0.792$) (Fig. 3c). Further, when we compared the upper bound regression lines of fish and squid to determine if the maximum prey size was dependent on prey type, we found no significant difference between the slopes ($p > 0.05$).

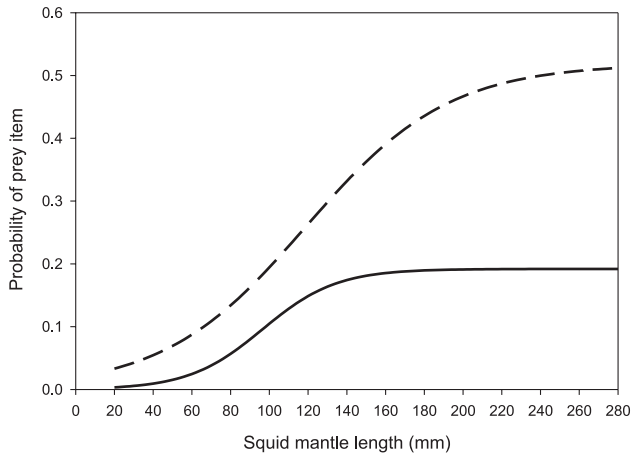
Logistic regression analyses of the stomach samples indicated a statistically significant ontogenetic shift in the diet composition of *L. pealeii* (Fig. 4). The probability of piscivory was low in small squid (<60 mm) and increased with squid size from 0.03 to 0.15 at mantle lengths between 70 and 120 mm (slope parameter $\neq 0$, likelihood ratio test, 90% confidence level = 0.04, 0.07). The probability of piscivory reached approximately 0.20 in squid larger than 160 mm in length. *Loligo pealeii* were cannibalistic at all sample lengths, although there was an overall increase in cannibalism with increasing squid size. The probability of cannibalism ranged from 0.04 to 0.51, and squid were the dominant prey item

Fig. 3. Quantile regression analyses of the relationships between prey lengths (mm) and *Loligo pealeii* mantle length (mm). Solid and dotted lines represent the 90th and 10th quantiles, respectively. (a) Fish (solid circle); (b) squid (open circle); (c) squid and fish.



of *L. pealeii* larger than 90 mm. The probability of crustaceans being consumed by *L. pealeii* initially increased with size for small size squid (30–80 mm) and then decreased over larger squid sizes. Therefore, the logistic regression model was deemed insufficient to assess this non-monotypic trend.

Fig. 4. Relationship between *Loligo pealeii* mantle length (mm) and the probability of piscivory (broken line) and cannibalism (solid line). Lines were estimated using logistic regression.

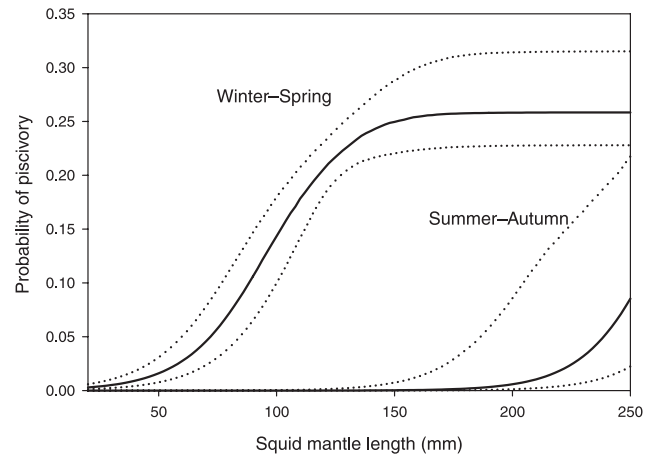


The logistic regression parameters for piscivory were significantly different between winter–spring (offshore residents) and summer–autumn (onshore residents) (Fig. 5; likelihood ratio test, $p < 0.01$). In general, squid were piscivorous at a smaller size during winter–spring. For example, the probability of piscivory of a 100 mm squid during this period was predicted to be 0.14, and 90% of the likelihood density was between 0.1 and 0.14, while during summer–autumn, the probability of piscivory was essentially 0 (Fig. 5). These contrasts in the rate of piscivory extended to the largest size classes, with 90% prediction intervals equal to 0.23–0.32 during winter–spring and 0.02–0.22 during summer–autumn (Fig. 5).

To evaluate whether the seasonal patterns of piscivory may be explained by prey size constraints, we coupled the size distributions of our squid samples with our quantile regression results and published estimates of juvenile fish body sizes. Our analyses only included juvenile fish that are known to spatially overlap with *L. pealeii* as evidenced by squid sampling locations (Fig. 1) and previous literature documenting seasonal spatial distributions of mid-Atlantic fish species. *Loligo pealeii* shared similar habitats with various commercial fish species throughout the year (Table 4), as well as with cusk eels and mesopleagic fish, including myctophids and sternoptychids (Bigelow et al. 1964; Sherman et al. 1984; Able and Fahay 1998).

The results of our analyses showed that in February the squid population was composed of larger individuals, and a high number of juvenile fish species fell within the prey size spectra of the *L. pealeii* population (Fig. 6a). The length distribution of the squid population in March was fairly homogeneous, and again, there were a high number of juvenile fish species vulnerable to predation by squid of all sizes (Fig. 6b). In June, the squid population was dominated by smaller squid, and a high number age-0 fish were of appropriate prey sizes for almost all lengths of *L. pealeii* (Fig. 6c). In September, the squid population was again dominated by small individuals; however, the availability of juvenile fish of suitable prey sizes was low for the majority of the population (Fig. 6d). Only large squid (>200 mm) were capable of

Fig. 5. Median predicted (90% prediction interval) probability of piscivory vs. body size for winter–spring samples and summer–autumn samples. The solid lines represent the medians of the likelihood distributions; dotted lines depict the 5th and 95th percentiles.



consuming high numbers of juvenile fish species during this period.

Discussion

Our analyses produced three main findings. First, predation on fish and squid by *L. pealeii* were dictated by size-related constraints, such that the prey size spectrum was a function of increasing predator size. Second, there were pronounced seasonal shifts in the frequency of piscivory among *L. pealeii*. The incidence of piscivory was higher in winter–spring than during summer–autumn. Third, there were seasonal shifts in the ontogenetic onset of piscivory, evidenced by small size-at-piscivory during winter–spring compared with summer–autumn. These findings suggest that variation in the frequency and intensity of piscivory are related to shifts in the size structures of both *L. pealeii* and prey populations. We describe the potential mechanistic linkages among our three main findings in detail below.

Estimates of *L. pealeii* prey sizes showed an increasing trend in the prey size spectra over increasing squid mantle lengths, consistent with previous studies documenting the prey sizes of squid (Rocha et al. 1994; Collins and Pierce 1996; Phillips et al. 2003). The increased range of the prey size spectrum with body size was largely governed by an increase in the upper bound of the spectrum (i.e., the maximum-sized prey increased with increasing squid size and lowest-sized prey remained fairly constant). This increase in prey size with predator size is consistent with the observation of more diverse food habits as squid become larger (Vovk 1985; Collins et al. 1994; Pierce et al. 1994). In general, diets of small squid are dominated by crustaceans, while diets of larger squid consist of many species of fish, squid, and crustacean.

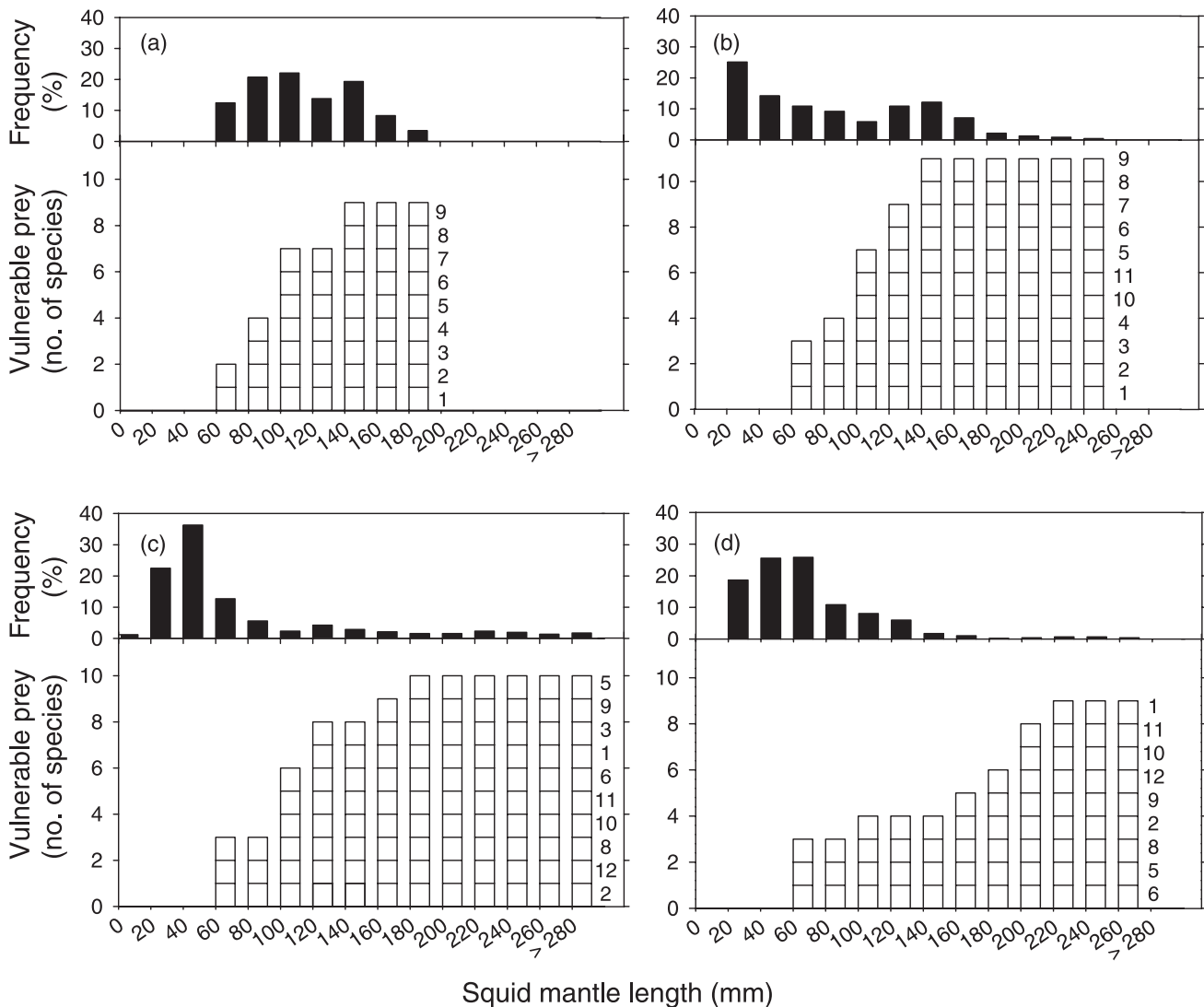
Size constraints on feeding can explain our observation that the frequency of piscivory was greatest during the winter and spring. We hypothesize that the high incidence of piscivory in winter–spring was due to the joint effects of large *L. pealeii* body sizes and the availability of many suit-

Table 4. Seasons of potential spatial overlap between *Loligo pealeii* collected on National Marine Fisheries Service (NMFS) seasonal trawl surveys and larval–juvenile commercial fish.

Fish species	Seasons	Reference
Gadiformes		
<i>Merluccius bilinearis</i>	W, Sp, S, A	Vovk 1974; Sherman et al. 1984; Lock and Packer 2004
<i>Melanogrammus aeglefinus</i>	Sp, S, A	Sherman et al. 1984; Cargnelli et al. 1999a
<i>Pollachius virens</i>	W, Sp, S, A	Able and Fahay 1998; Cargnelli et al. 1999b
<i>Urophycis</i> sp.	W, Sp, S, A	Able and Fahay 1998; Chang et al. 1999a; Steimle et al. 1999
Pleuronectiformes		
<i>Paralichthys dentatus</i>	W, Sp, S, A	Able et al. 1989; Able and Fahay 1998; Packer et al. 1999
<i>Scophthalmus aquosus</i>	Sp, S, A	Sherman et al. 1984; Morse and Able 1995; Chang et al. 1999b
<i>Peprilus tricanthus</i>	W, Sp, S, A	Sherman et al. 1984; Able and Fahay 1998; Cross et al. 1999

Note: W, winter; Sp, spring; S, summer; A, autumn.

Fig. 6. Size distributions of *Loligo pealeii* (top panels) and the number of juvenile fish species vulnerable to predation by squid based on size constraints (bottom panels), calculated for (a) February, (b) March, (c) June, and (d) September. Juvenile fish (with number codes in parentheses) include pollock (*Pollachius virens*) (1); summer flounder (*Paralichthys dentatus*) (2); spotted hake (*Urophycis regia*) (3); Myctophids (*Benthoosema* sp.) (4); silver hake (*Merluccius bilinearis*) (5); red hake (*Urophycis chuss*) (6); sternoptychids (Sternoptychidae) (7); butterfish (*Peprilus tricanthus*) (8); cusk eel (Ophidiidae) (9); white hake (*Urophycis tenuis*) (10); windowpane (*Scophthalmus aquosus*) (11); and haddock (*Melanogrammus aeglefinus*) (12).



ably sized fish. Squid larger than 120 mm were relatively common during this time period, but were rare during summer–autumn. These shifts were likely due to the seasonal pattern of growth and reproduction that produces large numbers of juveniles in the summer and early autumn, which then grow rapidly until they reach maturity and die (<1 year; Brodziak and Macy 1996; Macy and Brodziak 2001). The availability of fish prey was partly enhanced by the offshore movement of squid during the winter and early spring (Summers 1969; Serchuk and Rathjen 1974), which exposed them to small mesopelagic fish, such as myctophids and sternopythchids (Rodhouse and Nigmatullin 1996). In addition, numerous neritic fish species spawn and produce small-sized larvae and juveniles during this time period (Sherman et al. 1984).

Size constraints on feeding were also consistent with our observation that the onset of piscivory shifted throughout the year. In general, squid were piscivorous at much smaller body sizes during the winter–spring than during summer–autumn. For instance, 20% of the 125 mm squid in the winter–spring were predicted to be piscivorous, but essentially none of the same-sized squid in the summer–autumn were piscivorous. Based on our estimates of juvenile fish growth rates, we identified 9 species whose adult or juvenile body sizes would be vulnerable to a 125 mm squid during spring. In contrast, only four species had juveniles that were within the prey size spectrum of a 125 mm squid during autumn. These contrasts were partly due to juveniles outgrowing the prey size spectrum of *L. pealeii*, but also due to seasonal shifts in the spatial overlap of squid with smaller-bodied prey such as myctophids. Thus, we concluded that the estimated prey size spectrum of *L. pealeii* and available prey body sizes are consistent with the hypothesis that size constraints governed the seasonal variation in the onset of piscivory.

Size-structured interactions between squid and their prey may impact the recruitment success of larval and juvenile fish. The extent of this impact depends on the variability of the factors dictating size-based interactions, including predator and prey growth rates and size distributions and the strength of spatiotemporal overlaps between predators and prey (Rice et al. 1997). For example, at some point during the summer, the squid population shifts from being heterogeneous to being largely composed of small individuals. This shift is likely a result of the recruitment of larval–juvenile squid from the spring–summer spawning period and the loss of many adults to post-spawning mortality. Importantly, the timing of this shift in size structure may govern the intensity of piscivory during the summer and potentially the recruitment success of larval and juvenile fish. If squid spawn early in the season, the population will be composed of mostly small squid, and predation rates will be low, since juvenile fish will be too large to be consumed by the majority of the population. However, if peak spawning occurs later in the season, the squid population may be more heterogeneous in size, and the predatory impact on juvenile fish may be much greater. The degree of spatial overlap between *L. pealeii* and juvenile fish will also determine the impact of these size-structured interactions. Comparisons among our sampling sites and previously documented fish distributions revealed the potential for strong spatial overlaps between *L. pealeii*

and multiple fish species, including commercially valuable fish such as gadiformes and pleuronectiformes. The strength of these overlaps may have the most impact on fish populations during the winter–spring months when the occurrence of piscivory appears to be highest. Determining the degree and variability of these spatiotemporal overlaps is beyond the scope of our study; however, these factors will affect the strength of predator–prey interactions and should be a focus of future studies.

Understanding size-structured interactions and the factors governing these interactions is critical for determining the predatory impact of squid on fish populations. This knowledge is especially valuable for quantifying squid predation on over-harvested fish populations. Increased periods of predation on larval–juvenile stages of these populations may impede recruitment success, potentially leading to depensatory effects. To evaluate the potential for recruitment limitations, better estimates of squid predation on fish, and in particular on over-harvested fish species, are needed. Our estimates of piscivory are low in comparison with past studies (Vinogradov and Noskov 1979; Maurer and Bowman 1985; Vovk 1985), which may be attributed to the limitations of gut content analyses. First, squid macerate their prey and tend to discard the heads and hard parts of fish during feeding (Nixon 1987; Dawe et al. 1997). In particular, squid are more likely to discard the heads of larger fish (Rodhouse et al. 1992; Pierce et al. 1994; Dawe et al. 1997). Second, squid have high digestion rates (Bidder 1950), thus prey that have been consumed may not be detected in the stomach contents. As a consequence, it is difficult to quantify the percent diet composition of squid (by mass or number), and estimates of percent frequency of occurrence are likely to be underestimated. However, size relations are more robust to the limitations of gut content analyses because only observed prey sizes are used to draw conclusions regarding prey size constraints. Studies aiming to quantify the percent diet composition of squid may benefit from coupling gut content analyses with stable isotope or fatty acid analyses.

Few otoliths were collected from the diets of larger squid (>200 mm) in this study, which was most likely a result of squid feeding behavior. Although, the absence of otoliths may also be due to the overall low sample size of large squid (>200 mm), comprising only 12% of the total sample set. Our estimates of maximum prey sizes for *L. pealeii* were somewhat imprecise because of the low number of prey sizes identified for larger squid, which may further explain the marginally nonsignificant slope of upper prey sizes for fish and combined prey.

In summary, analyses of *L. pealeii* prey size spectra and the size distributions of squid and their potential prey provide support for the notion that size constraints dictate the patterns of piscivory. The squid population was composed of large, summer-spawned individuals during the winter–spring, and there were a high number of juvenile fish species that fell within the prey size spectrum of the squid population. In contrast, the summer – early autumn squid population was dominated by larval–juvenile squid, and the number of vulnerable prey species available to *L. pealeii* decreased within this period. Consequently, the ecological interactions between squid and fish may vary critically throughout the year, where *L. pealeii* acts as an important predator during winter

and spring, but acts largely as a prey species for fish in the summer and early autumn.

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