Abstract—Longfin inshore (*Loligo pealeii*) and northern shortfin (*Illex illecebrosus*) squids are considered important prey species in the Northwest Atlantic shelf ecosystem. The diets of four major squid predators, bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*), were examined for seasonal and size-based changes in feeding habits. Summer and winter, two time periods largely absent from previous evaluations, were found to be the most important seasons for predation on squid, and are also the periods when the majority of squid are landed by the regional fishery. Bluefish >450 mm, silver hake >300 mm, and summer flounder >400 mm were all found to be significant predators of squid. These same size fish correspond to age classes currently targeted for biomass expansion by management committees. This study highlights the importance of understanding how squid and predator interactions vary temporally and with changes in community structure and stresses the need for multispecies management in the Northwest Atlantic.

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Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf

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Global depletion of marine predators has had dramatic effects on ecosystem structure and function (May et al., 1979; Jackson et al., 2001; Pauly et al., 2002). In many systems, the ramifications of such changes may not be fully realized. Groundfish declines have been linked to simultaneous increases in cephalopod landings in fifteen key Food and Agriculture Organization of the United Nations (FAO) areas (Caddy and Rodhouse, 1998). It is uncertain whether cephalopod populations are experiencing increased growth due to a release from predation (Piatkowski et al., 2001), or whether increased harvests are representative of the trend toward fishing species at lower trophic levels (Pauly et al., 1998). In the Northwest Atlantic, while gadids, flatfish, and other demersal species have been reduced because of overfishing (Link and Garrison, 2002), squid have risen in status from a mere bait fishery to one of the most economically important stocks in the region (Cadrin and Hatfield[1]).

Cephalopods have been documented as principal prey for numerous species of finfish, elasmobranchs, and marine mammals (Smale, 1996); however, in comparison to the ecological relationships between fish and their predators, less is known about the ecological interactions between squid and their predators. In a comprehensive evaluation of the Northwest Atlantic food web, bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) were ranked among the most significant predators of squid (Bowman et al., 2000). Squid represented between 17% and 95% of the total mass consumed by these four finfish regionally. Dramatic changes in stock abundance and population structure have occurred since specimens for Bowman et al.'s study were collected 25–45 years ago. Exploitation of squid has risen substantially, and the four noted predators have experienced severe depletions; stock biomass levels have fallen as low as 20–50% of their respective maximum sustainable yield (B_{MSY}) limits (NOAA[2]). Additionally, the size structure of predator populations within the community has become skewed because of age-truncation. Recent evaluations of bluefish (Buckel et al., 1999a), goosefish (Armstrong et al., 1996), silver hake (Bowman, 1984), and summer flounder (Link et al., 2002) foraging habits have been conducted; however, sampling has been restricted to one or two seasons, primarily spring and fall. Analyses that base their results on feeding habits collected during a single season (Buckel et al., 1999b), or where results are based on data that have been pooled under the as-

[1] Cadrin, S. X., and E. M. C. Hatfield. 1999. Stock assessment of inshore longfin squid *Loligo pealeii*. Northeast Fish. Sci. Cent. Ref. Doc. 99-12, 107 p.

[2] NOAA (National Oceanic and Atmospheric Administration). 2001. Northeast Fisheries Science Center (NEFSC). Status of fishery resources off the northeastern United States. Website: http://www.nefsc.noaa.gov/sos/spsyn/species.html [accessed on 8 March 2006].

sumption that the diets collected in one season are a proxy for another (Overholtz et al., 2000) could overlook key periods of predation and lead to an underestimation of the total predatory demand imposed on principal prey resources, such as squid.

The two primary squid species found in Northwest Atlantic waters, longfin inshore (*Loligo pealeii*) and northern shortfin (*Illex illecebrosus*), are both highly migratory, and their distribution on the shelf is temporally variable. Squid move between inshore (spring and summer) and offshore (fall and winter) environments seasonally (Macy and Brodziak, 2001). On a diurnal basis they move from demersal waters during the day to surface waters at night (Lange and Sissenwine, 1983). The degree of vertical movement made by squid is also known to vary seasonally. Activity is more pronounced during warmer months when the water column is stratified and is diminished during winter and spring when shelf waters are well mixed (Hatfield and Cadrin, 2002). Prey availability and distribution in the water column, water temperature, and other environmental factors are believed to influence diel migration patterns (Cargnelli et al., 1999). Seasonal changes in squid behavior and habitat use will also affect encounter rates with different predators in the demersal environment.

Knowledge of species interactions is imperative to understand population dynamics and to manage stock recovery (Murawski, 1991). The present study provides a current assessment of the reliance on squid populations in the Northwest Atlantic region by four major squid predators; bluefish, goosefish, silver hake, and summer flounder. For each predator, ontogenetic and seasonal variations in feeding patterns were evaluated. Additionally, squid abundance in the demersal environment was related to predator diets as a mechanism for diurnal and seasonal changes in predation.

Materials and methods

Estimating changes in the abundance of longfin inshore squid

Longfin and shortfin squid are regularly caught in National Marine Fisheries Service (NMFS) bottom trawl surveys. However, catches of shortfin squid were exceptionally low over 2002 and 2003 (the time period evaluated during the present study), possibly because of poor recruitment. Catch data used in subsequent calculations were provided by NMFS bottom-trawl surveys (NMFS[3,4,5,6,7,8]). Sufficient information was available for longfin squid only; consequently abundance estimates were limited to this species. Furthermore, abundance surveys were not conducted during the summer; therefore adequate information was not available to evaluate this season.

To compare changes in longfin squid abundance in the demersal environment at different times of day and between seasons, the relative masses of prerecruits (W_p) and recruits (W_R) present were estimated by using the equations

$$W_{P(year,\, season,\, time\ of\ day)} = \sum_t \frac{W_t P_{t(year,\, s\ ason,\, time\ of\ day)}}{f_{t(season,\, time\ of\ day)}} \quad (1)$$

$$W_{R(year,\, season,\, time\ of\ day)} = \sum_t \frac{W_t \quad {}_{t(year,\, s\ ason,\, time\ of\ day)}}{f_{t(season,\, time\ of\ day)}} \quad (2)$$

where t = the index of tows made at NMFS stations in New York, New Jersey, Connecticut, Rhode Island, and Massachusetts respective to each year (2002, 2003), season (winter, spring, fall), and time of day (day, night, dawn and dusk);

W_t = the total mass of longfin squid caught in each tow; and

P and R = $(1 - P)$ estimate the proportion of biomass in each of two size classes, prerecruits (≤80 mm) and recruits (>80 mm), of longfin squid during each season.

f_t = the diel correction coefficient representing relative catch rates of longfin squid for each size class, season, and time of day as determined by Hatfield and Cadrin (2002) and was standardized to 1.0 during daytime for all seasons.

[3] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–SE Georges Bank: February 5–March 2, 2002, FRV *Albatross IV*, 24 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[4] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–Gulf of Maine: March 5–April 25, 2002, FRV *Albatross IV*, 34 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[5] NMFS (National Marine Fisheries Service). 2002. Fishermen's report: bottom trawl survey, Cape Hatteras–Gulf of Maine: September 4–October 25, 2002, FRV *Albatross IV*, 31 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[6] NMFS (National Marine Fisheries Service). 2003. Resource survey report: bottom trawl survey, Cape Hatteras–Southern New England: February 4–March 1, 2003, FRV *Delaware II*, 19 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[7] NMFS (National Marine Fisheries Service). 2003. Resource survey report, bottom trawl survey, Cape Hatteras–Gulf of Maine: March 5, 2003–April 27, 2003, FRV *Delaware II*, 34 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

[8] NMFS (National Marine Fisheries Service). 2003. Resource survey report: bottom trawl survey, Cape Hatteras–Gulf of Maine: September 7–November 1, 2003, FRV *Albatross IV*, 35 p. NMFS, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA, 02543.

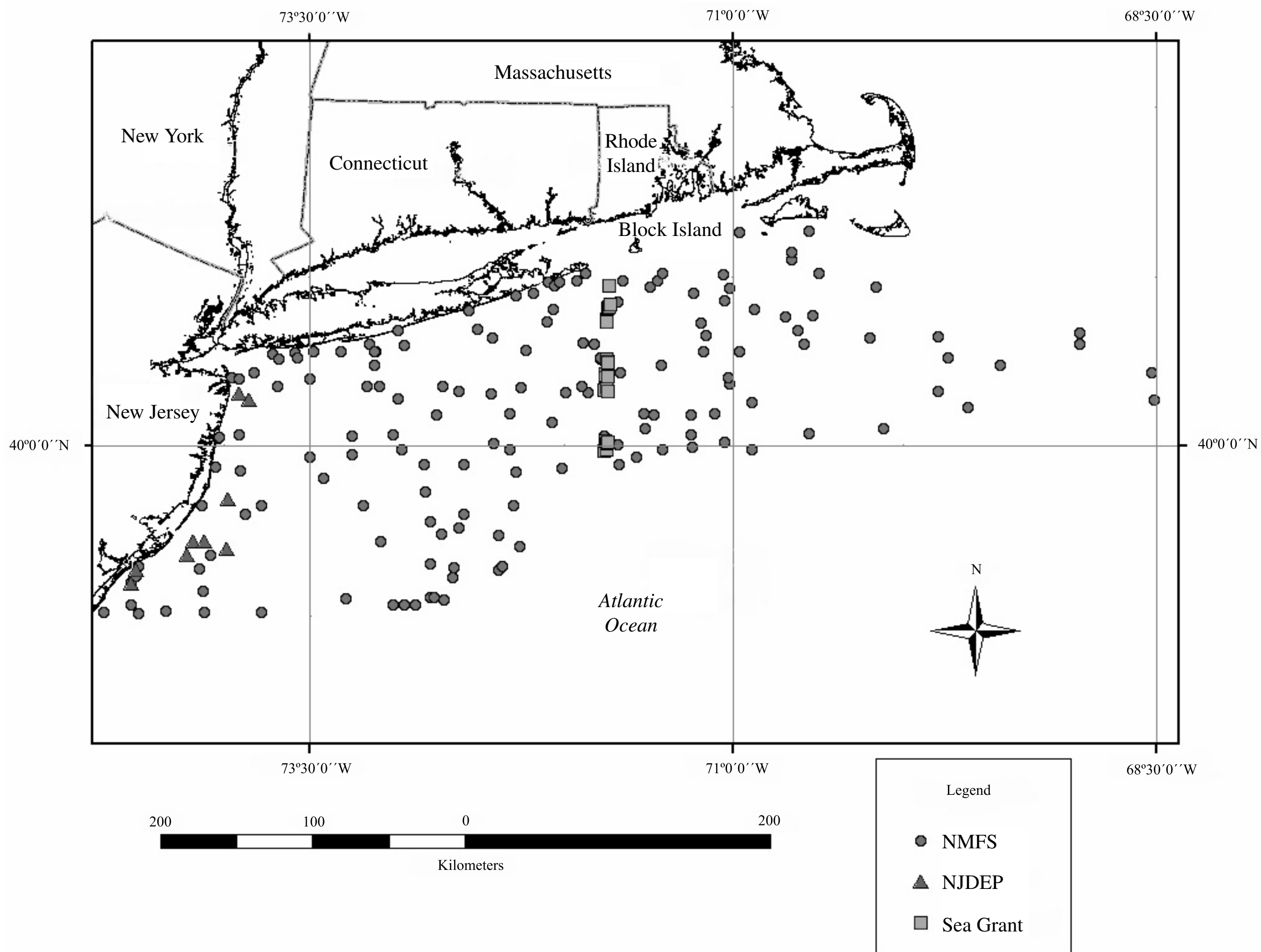

Figure 1

Map of fishery-independent sampling locations. Circles (●) are locations sampled during the National Marine Fisheries Service annual bottom-trawl survey cruise, triangles (▲) are locations sampled by the New Jersey Department of Environmental Protection, squares (■) are locations sampled during a Sea Grant sponsored cruise transecting the continental shelf along Block Island Sound Canyon.

To obtain an index of relative abundance, final mass values were divided by the number of tows made during each time of day, year, and seasonal period.

For Equations 1 and 2, values for P and R were estimated from longfin squid collected regionally during the winter, spring, and fall. Mantle lengths (mm) and the corresponding body weights (g) of individual squid measured in Hunsicker (2004) were used to calculate the percent distribution of biomass in each of the two size classes during each seasonal period. These estimated proportions were then used to partition the total catches reported at each NMFS station into prerecruit and recruit biomass. For each seasonal and diurnal period, catches were averaged between years and used to contrast relative concentrations of longfin squid in the demersal environment. Gear biases may affect the catchability of prerecruits more than recruits; therefore relative catch rates were compared among seasons only within each size class.

Sampling

Bluefish, goosefish, silver hake, and summer flounder were collected from continental shelf waters off the coasts of New York, New Jersey, Connecticut, Rhode Island, and Massachusetts from February 2002 to July 2003. Samples were obtained from two main sources: from fish landed by commercial fishing boats and from scientific survey cruises. Fishery-independent collections were made in conjunction with bottom trawl surveys conducted bimonthly by the New Jersey Department of Environmental Protection (NJDEP) and seasonally (except summer) by the National Marine Fisheries Service, Northeast Fisheries Science Center (NMFS-NEFSC) (Fig. 1). Samples were also collected aboard the RV *SeaWolf* (Sea Grant) during an independent survey that transected the continental shelf along the Block Island Sound Canyon (Fig. 1). The proportion of samples collected from fishery-independent sources is shown in

Figure 2 and the number of samples collected from all sources during all seasons is shown in Figure 3.

In addition to the stomach contents collected and analyzed for the present study, diet data collected regionally were drawn from the NMFS-NEFSC bottom trawl survey database. A full description of the survey design and collection methods used by the NEFSC can be found in Azarovitz et al.[9]

Diet analysis

The majority of samples obtained from fishery-independent sources were processed onboard research vessels. However, only cursory assessments of prey type and mass could be made at sea; therefore samples were frozen and transported to the laboratory for a more thorough examination. Each fish was weighed and measured (fork length for bluefish, total length for goosefish, silver hake, and summer flounder), stomachs were removed, prey items were weighed to the nearest 0.01 gram and identified to the level of species whenever possible. With the aid of a dissecting microscope, otoliths, beaks, and other hard parts were recovered in order to classify species. When stomach contents could not be identified because of advanced stages of digestion, they were recorded as "unidentified animal remains." As with all diet studies, there is always a chance that a portion of samples are biased because fish may feed while in the net. This problem was addressed by excluding fish where prey was found (undigested) in the mouth and esophagus or where there was a clear difference in digestion stage among prey items found in the stomachs.

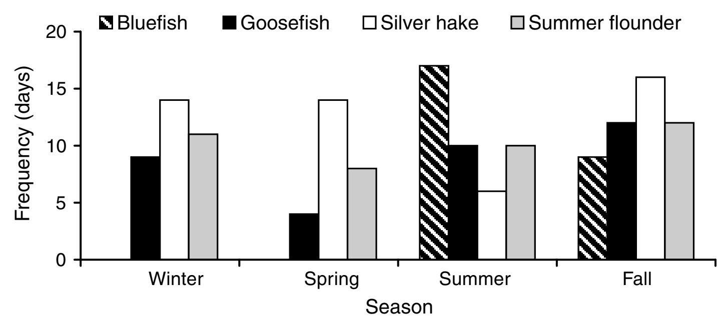

Figure 3

Frequencies (in days) of samples of bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) collected from fishery-dependent and fishery-independent sources. No samples were collected for bluefish (*Pomatomus saltatrix*) during the winter and spring seasons.

Three size classes, covering the total range of lengths of fish collected, were chosen for each species as follows: bluefish—small (200 to 450 mm fork length), medium (451 to 550 mm), and large (>551 mm); goosefish—small (50 to 250 mm total length), medium (251 to 450 mm), and large (>451 mm); silver hake—small (50 to 199 mm total length), medium (200 to 299 mm), and large (>300 mm); and summer flounder—small (250 to 399 mm total length), medium (400 to 549 mm), and large (>550 mm). Seasonal time periods were defined as winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

[9] Azarovitz, T., S. Clark, L. Despres, and C. Byrne. 1997. The Northeast Fisheries Science Center bottom trawl survey program, 22 p. ICES Council Meeting 1997/Y:33.

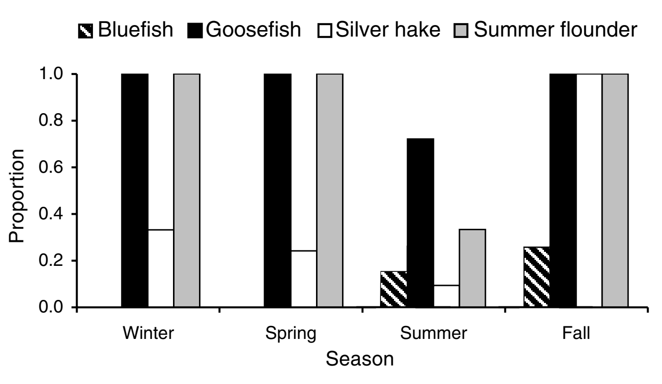

Figure 2

The proportion of samples of bluefish (*Pomatomus saltatrix*), goosefish (*Lophius americanus*), silver hake (*Merluccius bilinearis*), and summer flounder (*Paralichthys dentatus*) specimens collected from fishery-independent sources. No samples were collected for bluefish during the winter and spring seasons.

Statistical analyses

The Kruskal-Wallis test was used to test seasonal and size-based differences in predation on squid. A nonparametric test was chosen because of its robustness to assumptions of normality and skewness (Quinn and Keough, 2003). Preliminary analyses indicated that none of the data sets fitted the normal distribution and, owing to large numbers of zero values (representing the absence of squid in the diet), could not be transformed. Two sets of tests were performed on the data: first an "aggressive" set of tests were run by using individual fish as the sampling unit to give the maximum number of degrees of freedom; second, a "conservative" set of tests were run by using either stations (for data collected from fishery-independent sources) or cruises (for data collected from commercial fishery sources) as the sampling unit. The percent mass of squid in the diet of each fish (aggressive test) or pooled fish per station or cruise (conservative test) was determined and expressed as a propor-

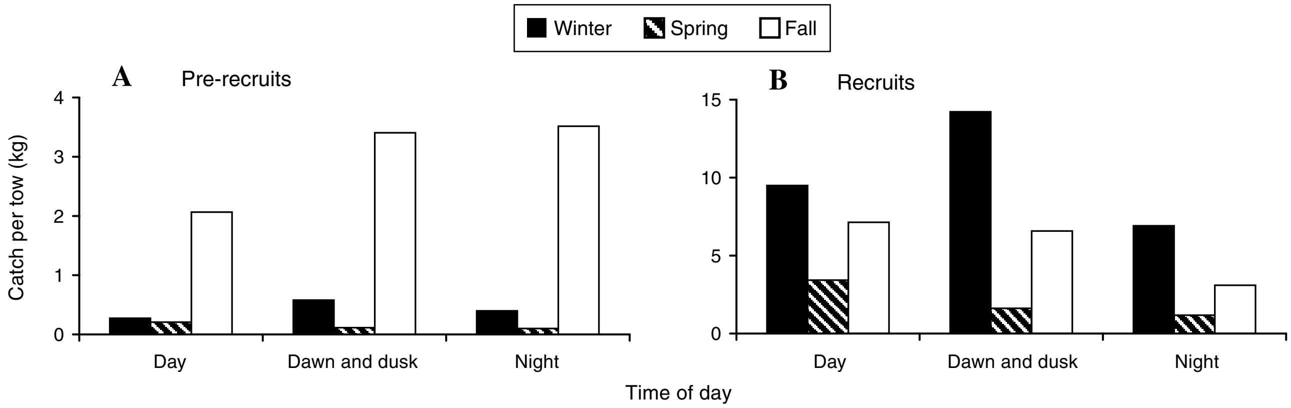

Figure 4

Relative catches of longfin inshore squid (*Loligo pealeii*) (**A**) prerecruits (≤80 mm mantle length) and (**B**) recruits (>80 mm mantle length) predicted in demersal waters during winter, spring, and fall of 2002 and 2003 (summer sampling was not conducted). Abundances of longfin inshore squid were measured as catch per tow (kg) and adjusted by seasonal diel correction coefficients specified in Hatfield and Cadrin (2002).

tion of the total mass consumed. To account for large numbers of tied rank values, an adjusted H test statistic was used to test the null hypothesis (Sokal and Rohlf, 1995). The two approaches produced similar results for the majority of tests. Therefore, only conservative test results are reported.

Results

Seasonal and diurnal differences in longfin inshore squid abundance

Predicted catches of longfin prerecruits during 2002 and 2003 indicated that the highest catch levels occured during the fall, intermediate levels during the winter, and minimum levels during the spring (Fig. 4A). These calculated values are similar to the historical abundance trends previously reported in Northwest Atlantic waters. Fall catches of prerecruits over all times of day were an order of magnitude higher in comparison to winter and spring values. The greatest variation in diurnal catches of prerecruits was predicted during the fall season (Fig. 4A). Conversely, catches of longfin recruits were estimated to be at their maximum during the winter, at intermediate levels during the fall, and at minimum levels during the spring (Fig. 4B). Maximum catch rates of longfin recruits were predicted during crepuscular and daytime periods of winter (Fig. 4B). Moreover, nighttime catches of recruits were two to three times higher during winter than during all other seasons.

Diet analysis

Bluefish Bluefish are present in Northern Atlantic waters only during the warmer months of the year; therefore sampling was restricted to the summer and fall seasons. A total of 299 bluefish from 26 sampling dates were analyzed. Fish ranged in size from 90 to 780 mm FL (average=469.6 mm). Overall, 53% of all bluefish sampled had food items present in their stomachs, and diets were split nearly equally between squid and fish. Perciforms were the dominant piscine prey; small amounts of amphipods and other pelagic crustaceans made up the remainder of the diet. A complete list of prey species recovered from all predator diets and their designated taxonomic groups can be found in Staudinger (2004).

Longfin squid was the primary squid species consumed by bluefish. A substantial amount of shortfin squid was also found in the stomachs of large fish (Table 1). Total predation on squid was greater during the summer than in the fall (Table 2); however, seasonal differences were not statistically significant possibly because of the high frequency of zero values in the dataset ($H_{adjusted}$=2.40, P=0.121, n=25). Medium and large fish were the primary consumers of squid, and small bluefish fed almost exclusively on fish (Table 1). Significant differences were found in the amount of squid consumed among all size classes of bluefish ($H_{adjusted}$= 6.62, P=0.037, n=75).

Goosefish A total of 536 goosefish stomachs were analyzed of which 269 (50%) contained prey. Goosefish ranged in size from 75 to 818 mm TL (average=341.1 mm). Goosefish were almost exclusively piscivorous; 93% of the total diet consisted of a mixture of gadiforms, clupeiforms, perciforms, and several other fish groups. Goosefish were the only species in the present study to prey on rajiforms.

Occurrence of squid in the goosefish diet was restricted to the winter and fall (Table 2) and differences among all seasons were significant ($H_{adjusted}$=15.27, P=0.002, n=46). Although medium size goosefish were

Table 1

Size-based stomach contents of fish collected in shelf waters of the Northwest Atlantic. Values presented are percentages of mass consumed (in grams). Fish lengths (small, medium, and large) are measured in millimeters. "Percent feeding" means the percentage of stomachs analyzed that contained prey. Bluefish were measured in fork length; goosefish, silverhake, and summer flounder were measured in total length.

	Bluefish			Goosefish		
Prey type	Small 200–450	Medium 451–550	Large 551+	Small 50–250	Medium 251–450	Large 451+
Squid	1.3	75.4	42.2	—	4.9	0.5
Longfin inshore squid	1.2	44.9	18.1	—	4.9	0.5
Northern shortfin squid	—	1.7	15.0	—	—	—
Unidentified squid	0.1	28.8	9.1	—	—	—
Fish	98.4	23.0	53.5	99.4	94.8	91.9
All other prey	0.3	1.6	4.3	0.56	0.24	7.68
Number of stomachs analyzed	103	99	113	148	153	235
Number containing prey (percent feeding)	76 (74)	51 (52)	49 (43)	96 (65)	75 (49)	98 (42)
Mean length (mm, SE)	316.6 (9.9)	509.8 (3.3)	628.6 (7.7)	124.8 (3.0)	358.2 (6.9)	540.0 (7.1)
Length range (mm)	200–438	460–547	555–780	75–241	255–450	460–818
	Silver hake			**Summer flounder**		
Prey type	Small 50–199	Medium 200–299	Large 300+	Small 250–399	Medium 400–549	Large 550+
Squid	0.0	2.7	18.6	16.7	33.5	20.6
Longfin inshore squid	0.0	2.7	12.3	15.3	25.4	14.7
Northern shortfin squid	—	—	0.2	—	—	5.3
Unidentified squid	—	0.1	6.1	1.4	8.1	0.6
Fish	34.7	17.6	62.0	67.2	55.1	76.0
All other prey	65.33	79.63	19.33	16.13	11.40	3.44
Number of stomachs analyzed	174	566	240	316	360	154
Number containing prey (percent feeding)	132 (76)	298 (53)	108 (45)	85 (27)	91 (25)	54 (35)
Mean length (mm, SE)	150.5 (3.1)	260.4 (1.5)	334.6 (3.9)	346.1 (4.4)	454.9 (4.1)	608.2 (6.4)
Length range (mm)	60–199	200–298	300–484	250–399	400–530	550–750

the only size class found to consume squid in notable amounts (Table 1), differences in the proportions of squid consumed among all size classes were not significant ($H_{adjusted}$=3.11, P=0.211, n=138). All squid found in the goosefish diet were classified as longfin squid.

Silver hake Of the 980 silver hake stomachs examined, over half (55%) contained prey. Silver hake ranged in size from 60 to 484 mm TL (average=248.3 mm). Feeding rates for silver hake were highest during the summer months and lowest during the spring and fall. Overall, silver hake fed primarily on fish and crustaceans, and lesser amounts of squid and other invertebrates. Amphipods and euphausiids were the dominant crustacean prey. Consumption of gadiforms, including conspecifics and unclassified osteichthyans, made up the majority of piscine prey.

Predation on squid differed significantly among seasons ($H_{adjusted}$=10.03, P=0.018, n=55) and was at its maximum during winter (Table 2). Silver hake diets exhibited a pronounced shift towards squid with increasing size (Table 1). Small and medium hake ate negligible amounts of squid. Conversely, squid totaled nearly 20% of all mass consumed by large hake. Differences in squid predation among size classes were significant ($H_{adjusted}$=7.58, P=0.023, n=132). Longfin squid was the dominant species of squid identified in the silver hake diet.

Summer flounder Of the 830 summer flounder analyzed, only 28% were found to be actively feeding. Summer flounder spend the juvenile stage of their life cycle in estuaries along the Northwest Atlantic coast; hence few flounder <280 mm were present in the analysis. Fish ranged in size from 250 to 750 mm TL (average=450.7 mm). Overall, diets consisted primarily of fish, squid, and stomatopods. Perciforms and clupeiforms were the dominant piscine prey.

Table 2

Seasonal stomach contents of fish collected in shelf waters of the Northwest Atlantic. Values presented are percentages of mass consumed (in grams). Fish lengths are measured in millimeters. No bluefish (*Pomatomus saltatrix*) were collected during the winter and spring seasons. "Percent feeding" means the percentage of stomachs analyzed that contained prey. Bluefish were measured in fork length; goosefish, silver hake, and summer flounder were measured in total length.

	Bluefish				Goosefish			
Prey type	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Squid	—	—	58.2	10.7	2.9	—	—	3.9
Longfin inshore squid	—	—	31.7	3.2	2.9	—	—	3.9
Northern shortfin squid	—	—	7.2	7.5				
Unidentified squid	—	—	19.3	—				
Fish	—	—	38.7	88.6	83.7	100.0	96.5	96.0
All other prey	—	—	3.1	0.7	13.39	0.00	3.45	0.13
Number of stomachs analyzed	—	—	236	67	206	22	259	49
Number containing prey (percent feeding)	—	—	114 (48)	45 (67)	58 (28)	8 (36)	175 (68)	28 (57)
Mean length (mm, SE)	—	—	495.0 (12.4)	405.9 (24.6)	462.1 (16.3)	523.8 (26.2)	273.4 (13.4)	462.1 (25.4)
Length range (mm)	—	—	230–737	90–780	160–780	420–620	75–818	170–690

	Silver hake				Summer flounder			
Prey type	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Squid	15.6	1.6	0.0	0.7	49.0	0.5	22.1	12.4
Longfin inshore squid	11.4	0.3	0.0	0.6	41.2	0.5	5.2	8.6
Northern shortfin squid	—	0.4	0.0	—	7.6	—	—	—
Unidentified squid	4.1	1.0	—	0.1	0.2	—	16.9	3.9
Fish	30.3	35.7	34.6	65.4	49.6	99.5	37.9	81.8
All other prey	54.1	62.7	65.3	33.8	1.40	0.04	39.93	5.76
Number of stomachs analyzed	308	365	165	143	407	103	120	196
Number containing prey (percent feeding)	163 (53)	165 (45)	146 (88)	64 (45)	77 (19)	22 (21)	65 (54)	66 (34)
Mean length (mm, SE)	270.7 (4.7)	262.8 (5.7)	198.5 (4.8)	268.0 (6.9)	477.5 (12.6)	446.9 (30.1)	431.2 (11.1)	439.7 (12.9)
Length range (mm)	60–484	79–480	103–410	110–450	270–710	300–750	268–645	250–690

The proportion of squid consumed by summer flounder fluctuated significantly among seasons ($H_{adjusted}$=14.29, P=0.003, n=43). Predation on squid was at its maximum during winter, and elevated during the summer in comparison to spring and fall (Table 2). Although differences in squid predation among size classes were not significant ($H_{adjusted}$=2.33, P=0.312, n=132), squid contributed the greatest relative amount to the diet of medium flounder (Table 1). The dominant species of squid identified in all size classes and for all seasons was longfin squid. Shortfin squid was found only in the diets of large flounder (Table 1) and only during the winter season (Table 2).

Discussion

Seasonal predation on squid

Previous descriptions of predation on squid in the Northwest Atlantic have been based on sampling in the fall and, to a lesser extent, during the spring seasons. Survey cruises conducted by the NMFS during these two periods were the primary data source for these prior analyses. The present study indicates that these two seasons are not wholly representative of total predation pressure on squid; indeed, winter and summer may be primary periods for predation on squid. Consequently, previous estimates of the total predatory demand imposed on squid populations by these predators may have been underestimated (Buckel et al., 1999b; Overholtz et al., 2000). It should be noted that in order to collect adequate numbers of fish during all four seasons, fishery-dependent sources were used. However, nonrandom sampling could have influenced seasonal differences seen in the present study.

It is likely that heightened predation on squid during the winter season reflects an increase in habitat overlap by both predator and prey. All species of squid and fish evaluated in this study are known to retreat to warmer waters of the outer shelf and slope during the colder months of the year. This movement may act to concentrate fish and squid and lead to elevated predator-prey encounter rates. Predicted nighttime and crepuscular catches during winter indicate that longfin squid are at higher concentrations in the demersal environment than at other seasons and reflect diminished vertical migrations by squid (Hatfield and Cadrin, 2002). Increased residence time in bottom waters may make squid more susceptible to demersal predators and may explain their marked increase in silver hake and summer flounder diets during winter. Although the present study has made contributions to increase knowledge of predation rates during summer, data on squid abundance levels were insufficient to make inferences about predator interactions during this season.

Historically, longfin squid seasonal biomass on the shelf has been estimated to be at its maximum during the fall (Cargneli et al., 1999). This trend was reflected in catch results for prerecruits during the time period evaluated; however, this supposed increase in availability was not reflected in predator diets. Instead, summer flounder and bluefish both exhibited diminishing reliance on squid and increased predation on similar piscine prey (Staudinger, 2004). It is unclear whether predator and squid size relationships or predator preference is mediating bluefish and summer flounder foraging behavior; therefore further studies are warranted. Alternatively, it has been acknowledged that the NMFS fall bottom-trawl survey has better coverage of the shelf than the winter and spring surveys, as well as the greatest overlap with the distribution range of longfin squid.[10] Both of these factors could influence seasonal historical abundance estimates and inaccurately represent the fall population in relation to other times of year.

Size-based shifts in predation by fish

Ontogenetic shifts in feeding commonly take place in the early life stages of a fish. However, for many species, less is known about progressive shifts through the adult stages of growth (Gerking, 1994). Bluefish showed a dramatic shift in diet at lengths of approximately 450 mm, transitioning from a diet primarily of piscine prey to that of squid. Longfin squid was the dominant cephalopod identified in the diets across all sizes of bluefish; however, shortfin squid was found to increase in importance in large bluefish. It is at this larger (551+ mm) size that bluefish begin to inhabit outer-shelf and offshore waters (Fahay et al., 1999). Because shortfin squid are more pelagic than longfin squid (Brodziak and Hendrickson, 1999), this change in diet may reflect an ontogenetic shift towards offshore food resources as bluefish mature.

Silver hake also exhibited a strong and positive increase in predation on squid with increasing size. Significant differences were observed among size classes—the greatest amount of squid being consumed by fish 300 mm and greater. The size at which silver hake were found to begin feeding on squid is similar to that found in previous studies (Garrison and Link, 2000). However, the relative proportions consumed by large hake were found to be nearly double those previously reported. It is possible that the findings of the present study represent an expanded view of the silver hake diet at larger body sizes because of intensified sampling over all seasonal periods. Alternatively, increased squid consumption could reflect decadal differences in squid availability.

Summer flounder spend the juvenile stage of their lives in bays and estuaries. Link et al. (2002) reported squid in the diets of individuals smaller than those examined in the present study. Therefore, the initial shift toward squid by young flounder as they transition from inshore to offshore waters may not have been realized. In fish that were sampled on the continental shelf, squid were found to be an important constituent of diets across all body sizes. Although a statistically significant shift among size classes was not detected, predation on squid was observed to peak in medium-size fish. This finding is similar to that of Bowman et al. (2000), who determined squid consumption peaked between 500 and 600 mm and then declined again for larger fish.

Bowman et al. (2000) reported cephalopods as a major constituent (>20%) of the goosefish diet in the southern New England region. In a study conducted by Armstrong et al. (1996), longfin squid were found in small goosefish (<400 mm TL) stomachs during summer and represented approximately 10% of the diet. In contrast, the present study found that squid contributed trivial amounts to the diet of goosefish across all size classes and seasons. It is unclear why such vast discrepancies were observed between these studies. One possible ex-

[10] NEFSC (Northeast Fisheries Science Center). 2002. Report of the 34th northeast regional stock assessment workshop (34th SAW): stock assessment review committee (SARC) consensus summary of assessments. Northeast Fish. Sci. Cent. Ref. Doc. 02-06, 356 p. National Marine Fisheries Service, 166 Water St., Woods Hole, MA 02543.

planation is that the opportunistic foraging strategy of goosefish is more sensitive to variation in relative and overall abundances of prey and results in erratic food habits over various time scales.

Predator–prey behavior

Differences in the amount of squid consumed among species, among predator sizes, and seasonal periods indicate that aspects of predator and prey behavior must be playing a pivotal role in influencing the susceptibility of squid to predation. Seasonal inshore-offshore habitat use and diurnal vertical migrations are two mechanisms that may act to mediate predator-prey encounter rates. Other behaviors that influence encounter rates are the times of day that each predator is actively hunting and the areas of the water column being searched. Of the four predators evaluated, seasonal movements by summer flounder are most similar to the migration patterns of longfin squid. Summer flounder are primarily daytime feeders and spend the majority of their time on or near the seafloor (Packer et al., 1999). Conversely, silver hake are a demersal species known to be active hunters primarily in the late afternoon and evening (Bowman, 1984). Large vertical movements in the water column are not customary for silver hake (Bigelow and Schroeder, 1953), therefore nighttime feeding limits interactions during seasons when squid exhibit strong diurnal migrations. Bluefish are the only predator in this study considered to be pelagic and that actively pursue prey throughout the water column. Although bluefish have been shown to forage primarily during the day (Juanes and Conover, 1994), it is possible that there is a seasonal shift in depth at which bluefish forage (Bigelow and Schroeder, 1953). A shift from feeding at depth in the late spring and summer to feeding in the surface waters during fall may explain, in part, seasonal differences in importance of squid to bluefish because few (if any) squid are present in the upper water column during daylight.

In general, daytime foraging behavior, combined with positioning in the demersal environment, create the optimal setting for regular encounters between squid and fish predators and explain differences in the proportion or even presence of squid in the diet between species with similar geographical ranges.

Implications for management

Since the late 1980s, squid harvests have increased substantially during the winter. Offshore harvests have been, on average, three times greater than inshore catches between October and March (Cadrin[11]). The combination of increased fishing pressure and elevated predation rates concentrated within a single season may not be sustainable for a species, such as squid, with a life span of less than a year and that has little overlap between generations (Pierce and Guerra, 1994). If not properly accounted for, this increase in total mortality on squid during the winter could affect the number of squid surviving to spawn during spring and summer and limit available biomass for predators such as bluefish and summer flounder.

Another area of concern stems from potential increases in top-down pressure from recovering predator populations. Regionally, management has emphasized age-truncation of predators as one of the most serious factors affecting summer flounder and silver hake populations. The age classes of summer flounder (age-2) (Terceiro[12]) and silver hake (age-3) (Brodziak[13]) targeted for expansion in their respective management plans, correspond to the lengths and associated ages identified in the present study as being the most voracious predators of squid. If management objectives are met and summer flounder and silver hake stocks are fully rebuilt, predation on squid could rise substantially as fish that have been functionally absent from the population begin increasing in abundance.

Other species, such as bluefish, that have been severely overfished are also showing signs of recovery (ASMFC[14]). Consumption of squid by bluefish has been estimated to exceed the mass removed by the fishing industry (Buckel et al., 1999b) and is contingent on predator population abundance (Overholtz et al., 2000). If one includes summer foraging habits, total consumption of longfin squid by bluefish may be much greater than previously estimated. In light of this new information, a reassessment of the predatory demand imposed by bluefish and other recovering predators on squid is clearly needed before fish stocks are fully rebuilt.

The simultaneous exploitation of predators and their prey, when there is limited information about species interactions, is a precarious practice that can have unintended and potentially detrimental consequences for one or both stocks. Depletion of biomass that supports higher predators may decrease biological production. Conversely, prey populations may become overextended. A greater understanding of species relationships is necessary, especially in ecosystems where fishing occurs at multiple trophic levels. The present study shows that consideration of predation year-round and for a range of predator sizes is imperative to accurately assess

[11] Cadrin, S. X. 2001. Status of fishery resources off the northeastern United States: longfin inshore squid. Website: http://www.nefsc.noaa.gov/sos/spsyn/iv/lfsquid/ [accessed on 8 March 2006].

[12] Terceiro, M. 2003. Stock assessment of summer flounder for 2003. Northeast Fisheries Science Center Reference Document, 179 p. National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA, 02543.

[13] Brodziak, J. 2001. Status of fishery resources off the northeastern United States: silver hake. Website: http://www.nefsc.noaa.gov/sos/spsyn/pg/silverhake/ [accessed on 8 March 2006].

[14] (ASMFC) Atlantic States Marine Fisheries Commission. 2003. Website: http://www.asmfc.org [accessed on 8 March 2006].

predation pressure on squid populations. As predator populations in the Northwest Atlantic are recovered under current management initiatives, a multispecies management approach will be crucial to avoid conflicts between squid and finfish fisheries and should be applied to species beyond those presented in this article.

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