Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons

W. J. Overholtz, J. S. Link, and L. E. Suslowicz

The fish biomass on the continental shelf off the eastern USA and Southeastern Canada has shifted towards a higher proportion of pelagic fishes in the 1990s. This study provides estimates of consumption by 12 piscivorous fishes on Atlantic mackerel (*Scomber scombrus*), Atlantic herring (*Clupea harengus*), butterfish (*Peprilus triacanthus*), sand lance (*Ammodytes* sp.), short-finned squid (*Illex illecebrosus*), and long-finned squid (*Loligo pealei*) during 1977–1997. Results suggest that total consumption (all prey) by the 12 predatory fish species is probably large relative to standing stocks of the above prey. Total consumption by these piscivores (all prey) ranged from 1.5–3.0 million tonnes during this period. The flow of fish biomass from these prey pelagic species to these 12 predators is an important and large fraction of the overall energy budget of the Northeast USA shelf ecosystem. The abundance of prey fishes and squids was reflected in the diets of individual predators; for example several prey species, such as sand lance and Atlantic herring, were very prominent at specific times during the period 1977–1997. Consumption of pelagic fish and squid by predatory fish appears to equal or exceed landings in most years from 1977–1997. In several cases, notably for long-finned squid, Atlantic herring and butterfish, consumption by piscivores may approach or exceed the current estimates of maximum sustainable yield, suggesting that changes in predator abundance may have important implications for long-term fishery yields of pelagic species.

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Introduction

The northeast shelf ecosystem in the Northwest Atlantic (Fig. 1) has undergone significant changes in biomass and relative abundance of fishes during the past four decades (Clark and Brown, 1977; Mayo *et al.*, 1992; Fogarty and Murawski, 1998). Important groundfish (i.e. gadids and flounders) and pelagic species experienced major declines in abundance and fishery yields due to large increases in foreign and domestic fishing effort from the late 1960s through the mid 1980s (NEFSC, 1998a). Following these reductions, fisheries developed for previously under-utilized species, such as goosefish (*Lophius americanus*), white hake (*Urophysis tenuis*), and spiny dogfish (*Squalus acanthias*) became important sources of landings in the 1990s. These stocks have also declined in a pattern of sequential depletion (NEFSC, 1998a). Lack of any major directed fishery by domestic fleets in the mid 1980s, a decline in predator stocks, and improved spawning stocks and recruitment, allowed for recovery of the Atlantic herring and Atlantic mackerel stocks after stock depletions followed high landings in the late 1960s and early 1970s. The finfish community off the northeast USA is now dominated by pelagic fishes (NEFSC, 1998a).

Reported landings of Atlantic herring and Atlantic mackerel peaked at 470 000 mt and 437 000 mt in 1968 and 1973 respectively. These landings were not sustainable and resulted in resource collapse within a few years (NEFSC, 1996, 1998a). Stock rebuilding of these species to historical levels was complete by the mid 1990s and current biomass for each stock is in the order of
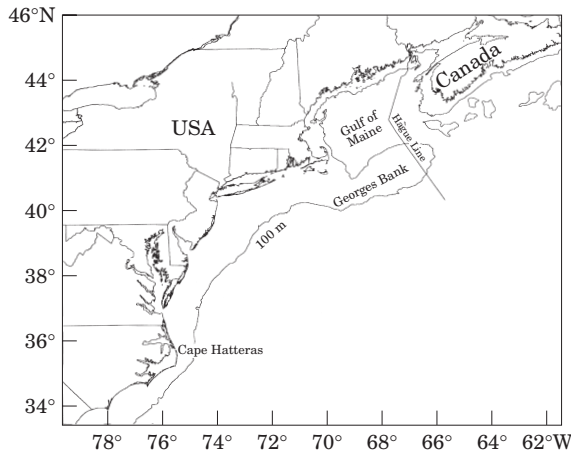
Figure 1. Area of coverage for stomach collections from research bottom trawl surveys conducted during 1977–1997 from Maine to Cape Hatteras, North Carolina.

1–3 million mt (NEFSC, 1996, 1998). These species and other pelagic fishes and squids comprise major portions of the diets of piscivorous fish, seabirds, and marine mammals (Cohen *et al*., 1982; Bowman and Michaels, 1984; Overholtz *et al*., 1991a; Link and Almeida, 2000) and piscivorous fish may consume a greater biomass than the current harvest of many pelagic species (Cohen *et al*., 1982; Overholtz *et al*., 1991a; Bax, 1991).

Knowledge of the interactions that occur within the pelagic complex and among the pelagic and demersal components is important for understanding and managing biomass and yields of both predator and prey species in this ecosystem. Management regimes may benefit greatly from an increased understanding of the role that biological interactions play in the region (*sensu* Larkin, 1996). Current fishery management in the USA is focused on sustainable levels of fishing as mandated in the Sustainable Fisheries Act of 1996. Consumption of pelagic prey by predatory fish may equal or exceed the MSY of various stocks, with considerable overalap of size distributions between commercial landings and predators (Overholtz *et al*., 1999). The flow of fish biomass to other predators such as marine mammals and seabirds, can also be substantial (Bax, 1991; Kenny *et al*., 1997). Thus, management regimes that significantly change the biomass of predators or prey species may have a substantial influence on fishery yields.

The objective of this research is to produce estimates of consumption of the more important pelagic species (Atlantic mackerel, Atlantic herring, butterfish, sand lance, short-finned squid, and long-finned squid, referred to as sf squid and lf squid below) by predator fishes. Estimates of species-specific and total consumption (i.e. all prey and pelagic components) for a set of 12 piscivorous fishes were produced. Fish consumption is

scaled to landings, current estimates of MSY, and size composition of commercial landings and predators.

Methods

Data and analyses

We provide a brief description of the stomach sampling protocol, design, and methods used, but a more detailed description is provided by Link and Almeida (2000) and also at (www.nefsc.nmfs.gov/pbio/wdp/FWDP.htm.). Starting in 1973, individual stomach samples were preserved at sea in 10% buffered formalin for later prey identification. Prey weight (0.01 g), number, percentage composition, total stomach weight (0.01 g), and lengths (mm) of fish prey were determined upon examination in the laboratory. Prey identification was to the lowest taxon feasible. Unidentified fish were categorized to family if possible, otherwise placed in the unidentified fish category. In 1981 the stomachs of major species such as Atlantic cod, haddock, silver hake, yellowtail founder, winter flouder, Atlantic herring, and Atlantic mackerel continued to be individually preserved, but prey of all other species were examined and identified at sea. Data on prey composition (%), numbers, and lengths were also collected and stomach contents were estimated in volumetric units (cc). Since 1985, all stomach samples have been processed and the prey identified at sea. To account for potential differences in the resolution of prey taxonomy between in-lab and at-sea sampling, we grouped most prey, particularly invertebrates, into broad prey categories. The exception to this was fish prey, which were maintained at the lowest level feasible. A conversion factor for volume to weight of 1.1 has been used to convert volumetric data (Link and Almeida, 2000; N=10 806, r^2=0.906, p<0.0001); this coefficient is similar to those used in other studies (R. Bowman, unpublished results; Tanasichuk *et al*., 1991). This allowed us to use consistent units (i.e. grams) across the time-series during 1973–1997.

Diet composition data from spring and autumn research bottom trawl survey cruises for 1973–1997 were examined to determine a list of significant predators of Atlantic mackerel, Atlantic herring, sand lance, butterfish, and short-finned and long-finned squid. We analysed data for 12 piscivorous fish spiny dogfish, winter skate (*Raja ocellata*), silver hake (*Merluccius bilinearis*), Atlantic cod (*Gadus morhua*), pollock (*Pollachius virens*), red hake (*Urophysis chuss*), white hake, spotted hake (*Urophysis regia*), summer flounder (*Parallichthys dentatus*), blue fish (*Pomatomus saltatrix*), weakfish (*Cynoscion regalis*), and goosefish, based on the consistency of the time-series and the percentage of pelagic prey in the diets (Table 1). Data were grouped into 5 cm length intervals for each predator to determine the minimum

Table 1. Descriptive statistics of predatory fish including season (A, autumn, S, spring), Min L (minimum length, cm), Max L (maximum length, cm), Mean L (mean length, cm), Mean S (mean stomach contents, g), Var S (variance of S), s.d. (standard deviation of S), and N (number of stomachs) during 1977–1997.

Species	Season	Min L	Max L	Mean L	Mean S	Var S	s.d.	N
Spiny dogfish	A	30	112	65.24	10.30	1165.9	34.15	10 651
	S	30	114	73.42	17.21	2644.3	51.42	18 656
Winter skate	A	40	109	67.13	8.38	348.8	18.68	3133
	S	40	107	66.93	11.56	837.5	28.94	3661
Silver hake	A	20	76	28.41	3.12	137.7	11.73	13 537
	S	20	66	29.70	2.97	164.3	12.82	8072
Atlantic cod	A	25	150	54.32	23.08	5680.1	75.37	4669
	S	25	140	58.50	32.65	7898.5	88.87	6140
Pollock	A	35	120	61.02	17.11	1403.8	37.47	1108
	S	35	108	64.97	24.14	3745.2	61.20	1406
White hake	A	30	136	48.73	20.82	3516.4	59.30	4753
	S	30	128	46.47	16.94	4358.5	66.02	2386
Red hake	A	30	73	37.09	5.56	282.5	16.81	3507
	S	30	71	36.48	4.32	177.8	13.33	2296
Spotted hake	A	25	290	30.37	4.26	64.0	8.00	1369
	S	25	818	30.39	2.83	41.1	6.41	641
Summer fld	A	25	300	37.26	2.87	80.8	8.99	2488
	S	25	82	36.57	2.30	193.7	13.92	1021
Bluefish	A	20	118	38.77	24.79	5454.7	73.86	2243
	S	20	78	47.13	27.17	2204.6	46.95	111
Weakfish	A	30	79	38.91	9.16	282.9	16.82	581
	S	30	59	41.53	2.12	48.4	6.96	115
Goosefish	A	30	116	56.60	67.31	69 608.3	263.83	1116
	S	30	124	58.24	45.32	26 179.0	161.80	1031

size at which pelagic fish and squid began to comprise a significant portion in its diet. Minimum lengths for sizes of predators, below which predation on pelagics ceased to be important, averaged 30 cm and ranged between 20–40 cm (Table 1).

Since sampling of some of the predator species began in 1977, we limited our analysis to the 1977–1997 time-frame. The numbers of predator stomachs collected during 1977–1997 were examined to determine the possibility of using annual data to calculate average stomach contents. Too few samples were available to use an annual aggregation for most predators. Based on several trials with two or more years of aggregation, a subjective decision to aggregate data in two year intervals was made for all predators except spotted hake, bluefish, and weakfish which were averaged across 5 yr intervals. These decisions were based on having a minimum number of predator stomachs (50–75), available in each season (i.e. spring and autumn). We assumed, based on previous studies (Cohen *et al.*, 1982; Overholtz *et al.*, 1991, 1999) and recent analysis (J. Link, unpublished data), that spring data would serve as a proxy for winter, and autumn for the summer periods of the year (e.g. half year resolution). We examined the diet compositions of the 12 predators for each season and year block.

Spring and autumn bottom temperatures were obtained from research survey cruises during 1977–1997.

Average bottom temperatures for the two seasons covering the entire region from the Gulf of Maine to Cape Hatteras, North Carolina were estimated using methods developed by Holzwarth and Mountain (1992), to interpolate between stations and regions (Fig. 2).
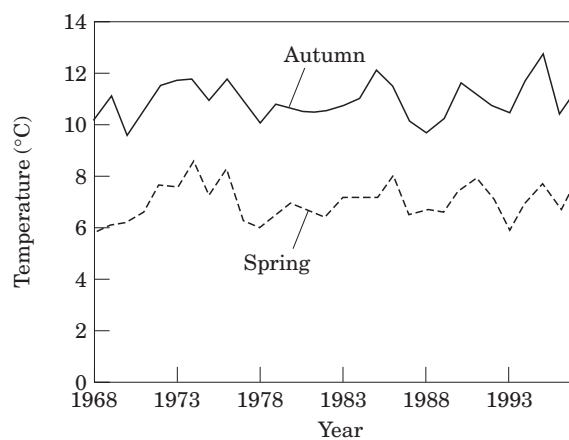

Figure 2. Average spring and autumn bottom temperature (°C) during 1968–1997 for the region from Maine to Cape Hatteras, North Carolina.
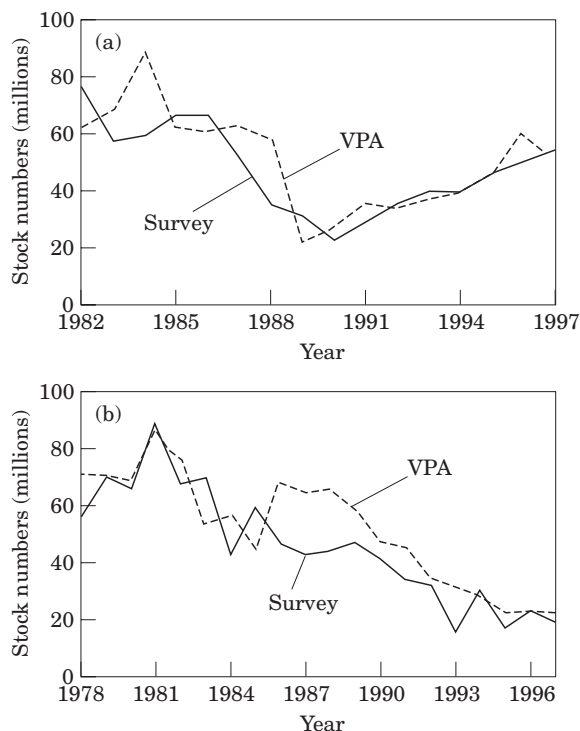
Figure 3. Total stock numbers from virtual population analysis (VPA) and survey q method (Survey) for (a) summer flounder during 1982–1997 and (b) Georges Bank cod during 1978–1997.

Predator abundance

Estimates of annual predator biomass and numbers were obtained from abundance data collected during spring and autumn bottom trawl surveys conducted during 1977–1997 (Azarovitz, 1981). Survey indices (number per tow) were truncated to account for the abundance of predators greater than the minimum predator sizes (Table 1). Area swept abundance for the entire survey region was estimated for each predator species during each year. Coefficients of variation in the trawl survey abundance estimates averaged 20–40% for most species with occasional values at 50% or greater in specific years (Overholtz et al., 1999).

For species within existing virtual population analysis (VPA) analyses, an average catchability coefficient (q) relating relative abundance to absolute stock size (numbers) was calculated from age-specific results appropriate for each predator (Table 1). These values were estimated as weighted means of the age-specific q values and estimated stock sizes from the VPA for ages above the predator cut-off length (i.e. usually age 2+). This average q was divided into area swept numbers to produce abundance estimates for each year. This method produces results similar to current VPAs, to the extent that catchability is constant over time (Fig. 3a, b), and is necessary for estimating predator numbers during

years prior to the first year in the VPA. For species without a VPA, catchability coefficients determined by Clark and Brown (1977) were applied in the same manner to produce estimates of total population size. Exceptions to this were for spiny dogfish and winter skate where area swept numbers were used without a correction for survey catchability. Spiny dogfish are highly vulnerable to bottom trawl survey gear, and following the same procedures used in the assessment for this stock (NEFSC, 1998b; Rago et al., 1999), an area swept estimate of numbers was used in our analysis. The estimate for winter skate was also based on area swept numbers, but lacking any collaborative analysis, a swept-area stock size estimate based on night tows (higher vulnerability) was used. Availability to survey gear can be influenced by many factors in any given year, resulting in high inter-annual variability in bottom trawl time-series data. To compensate for this problem we used LOWESS (Cleveland, 1979) methods to produce smoothed estimates of predator biomass over time. This approach is consistent with the current methodology applied in the spiny dogfish assessment (NEFSC, 1998b; Rago et al., 1999).

Consumption

Although many aproaches to estimate consumption are available, we chose the approach developed by Eggers (1977), Elliot and Persson (1978), and Pennington (1985) based on average stomach content and gut evacuation rate:

$$C = 24RS^\gamma, \tag{1}$$

where C is total daily consumption in grams per day, 24 is the number of hours in a day, S is the mean stomach content weight in grams, γ is a derived constant which we assumed equal to 1, and the evacuation rate R:

$$R = \alpha \, e^{\beta T}, \tag{2}$$

where α and β are fitted constants and T is average ambient temperature (°C). Values for the parameters, α and β in equation (2), were assumed to equal 0.004 and 0.115 respectively, conservative values for teleost fishes (Durbin et al., 1983).

Daily consumption estimates were then expanded to half-year estimates by pro-rating over 182.5 days for both the spring and autumn. This provided an estimate of consumption (all prey) for each predator species for each half year period. These estimates were apportioned by applying the spring and autumn diet composition percentages for the six pelagic prey types and multiplied by predator numbers to produce estimates of the biomass of each pelagic fish or squid consumed during each half-year period. This relationship expressed for a particular predator on a half year basis is:

$$FC_{ijky} = [N_{iky} \times C_{iky} \times P_{ijky}] \times 182.5 \tag{3}$$

where FC is the consumption of a particular fish or squid, N is the predator abundance, C is the daily total consumption, P is the percent by prey type, i is the subscript for predator, j for prey, k for spring or autumn, and y for year. The two half-year estimates for each prey type were then summed to obtain an estimate of annual consumption for each pelagic prey.

To investigate the possible overlap of predator and fishery size distributions, data on prey lengths of Atlantic mackerel and Atlantic herring from spiny dogfish, Atlantic cod, and silver hake during 1992–1997 were summarized. Size composition data from commercial landings for Atlantic mackerel and Atlantic herring during 1994–1997 were also summarized. These data were used in comparisons of the size compositions in predators and fisheries for these two prey species.

Interactions between predators and fishing operations that are competing for the same species may be important in understanding how to design proper fisheries management programs. Ratio estimates may be useful for measuring the potential of these effects. The ratio of consumption to landings (C/L) gives an index of how strong the competition may be between a predator or predators and a fishery. Three prey species were chosen to illustrate this concept.

Although our primary focus was on the Gulf of Maine-Georges Bank region, we assumed homogeneity in distributions of predators and prey for the entire continental shelf from Cape Hatteras to the Gulf of Maine, and thus have a coarse spatial resolution for this initial estimate of consumption. The pelagic prey species analysed change distribution on a seasonal basis, which should be approximated in the half-year approach we used. We assumed that fishery-independent trawl surveys collect both pelagic prey and their predators consistently (albeit with different relative catchabilities among species) across the time series. We recognize that several sources of observation error and general uncertainty may affect our results, including our estimates of predator abundance, catchability coefficients, average stomach contents, volume-to-weight conversion, and parameter homogeneity, but these estimates are a valuable contribution to understanding the magnitude and importance of fish consumption in this ecosystem.

Results

Predator abundance

Estimates of predator stock size were variable during 1977–1997, but generally the 12 species were most abundant during the earlier part of the time series and declined thereafter (Fig. 4). Silver hake, spiny dogfish, and red hake were the most abundant species on average during 1977–1997. Several species/stocks were at a medium level of abundance, including summer flounder,
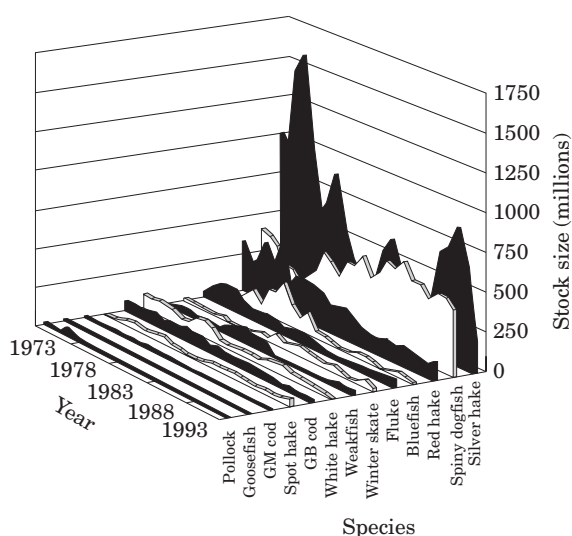

Figure 4. Population sizes (millions) of predatory fish species used to estimate consumption during 1977–1997, GM=Gulf of Maine, GB=Georges Bank.

witer skate, bluefish, white hake, weakfish, and Georges Bank cod, while pollock, goosefish, Gulf of Maine cod, and spotted hake stock sizes were relatively low during the 1977–1997 time period (Fig. 4).

Prey abundance

The biomass of pelagic fish and squid, based on spring bottom trawl research surveys, varied considerably during 1977–1997, some experiencing major declines, while others increased to historically high levels (Fig. 5). Butterfish, lf squid, and sf squid (relative abundance not corrected for trawl efficiency) were generally more abundant during the late 1970s and early 1980s, but did not fluctuate to any great degree during the entire period. Conversely, sand lance were very abundant during the late 1970s and early 1980s, but declined to very low abundances thereafter. Atlantic mackerel biomass recovered from the low abundance observed during the late 1970s, increasing steadily from 1984 and through the 1990s (Fig. 5). Atlantic herring biomass was very low during the late 1970s and early 1980s, but in 1986 this stock complex began a steep increase that has continued throughout the 1990s (Fig. 5).

Total consumption

Total annual consumption (all prey) by the 12 predatory fish averaged 1.5 million mt and ranged between 1.3 and 2.9 million mt during 1977–1997 (Fig. 6). The total annual consumption by individual predators was lowest by goosefish and summer flounder and highest by spotted hake, silver hake, and spiny dogfish, yet varied with
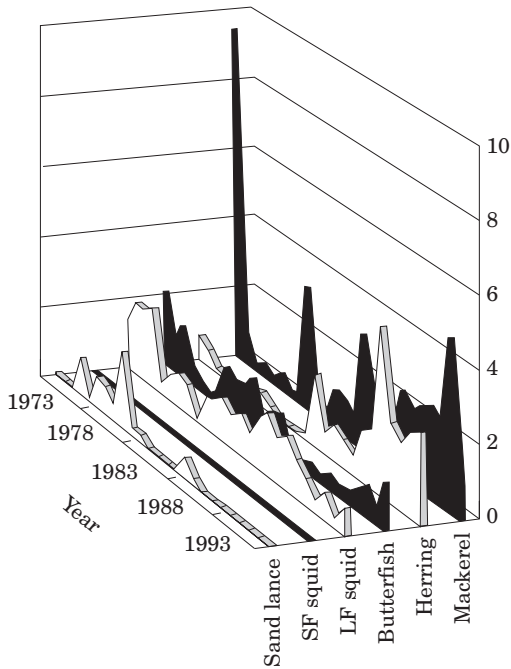
Figure 5. Biomass indices (kg/tow) of long-finned squid, short-finned squid, butterfish, Atlantic mackerel, Atlantic herring, and sand lance from spring research bottom trawl surveys during 1977–1997.
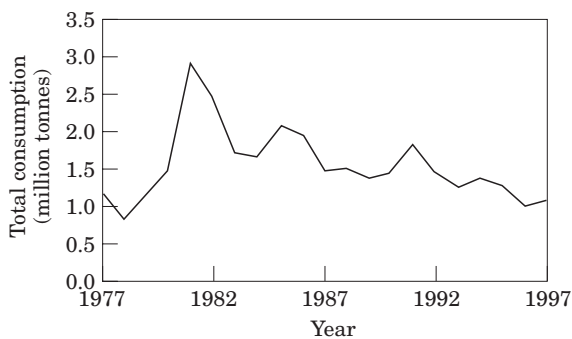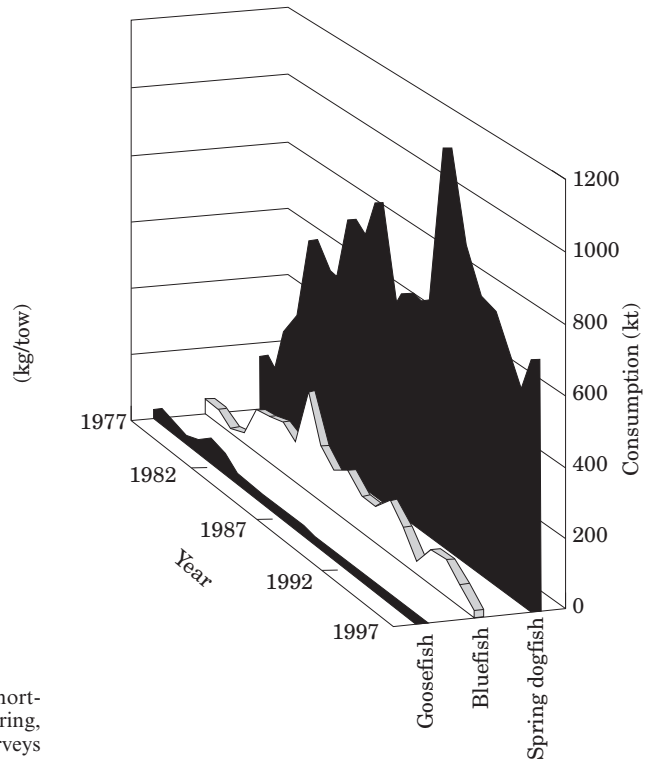

Figure 7. Total estimated consumption (thousand mt) by (a) spiny dogfish, (b) bluefish and (c) goosefish, off the northeastern USA during 1977–1997.

Figure 6. Total estimated consumption (all prey taxa) (million mt) by twelve predatory fish off the northeastern USA during 1977–1997.

predator abundance in any given year. Consumption estimates for individual predator species span three orders of magnitude, mainly reflective of predator abundance. For example, total annual consumption (all prey) during 1977–1997 averaged 619 000 mt (range 113 000–890 000 mt) for spiny dogfish, 108 000 mt (range 16 000–167 000 mt) for bluefish, and 14 000 mt (range 3600–61 000 mt) for goosefish (Fig. 7).

Consumption by individual predators

A complete examination of the stomach contents, annual per capita consumption, seasonal diet compos-ition, and fish consumption for each of the 12 predators would be too voluminous to be presented here, but examining these details for one predator is informative. We chose silver hake because it is an ecologically and commercially important species in this ecosystem (Sissenwine *et al*., 1984). The average weight of stomach contents in silver hake were generally higher in summer–autumn than in winter–spring and did not vary widely with a few exceptions (Fig. 8a). Average stomach weights were 2.9 g in the winter–spring and 3.8 g in summer–autumn with ranges between 1 and 7 g. Seasonal per capita consumption averaged 118.7 g in the winter–spring and 234.5 g in summer–autumn, consist-ent with larger mean stomach weights and higher tem-peratures in the summer–autumn (Fig. 8b). There are no obvious trends between average stomach contents, seasonal consumption, and stock size (Fig. 8c). Seasonal diet compositions, reflecting the proportion of fish and squid prey in silver hake diets during 1977–1997 are informative because of the seasonal and annual differ-ences in prey type and percent composition (Fig. 8d, e). Silver hake consumed all six prey items in both the spring and autumn, but diets varied across season and year. Spring diet compositions appeared to be focused on particular prey such as sand lance in the late 1970s
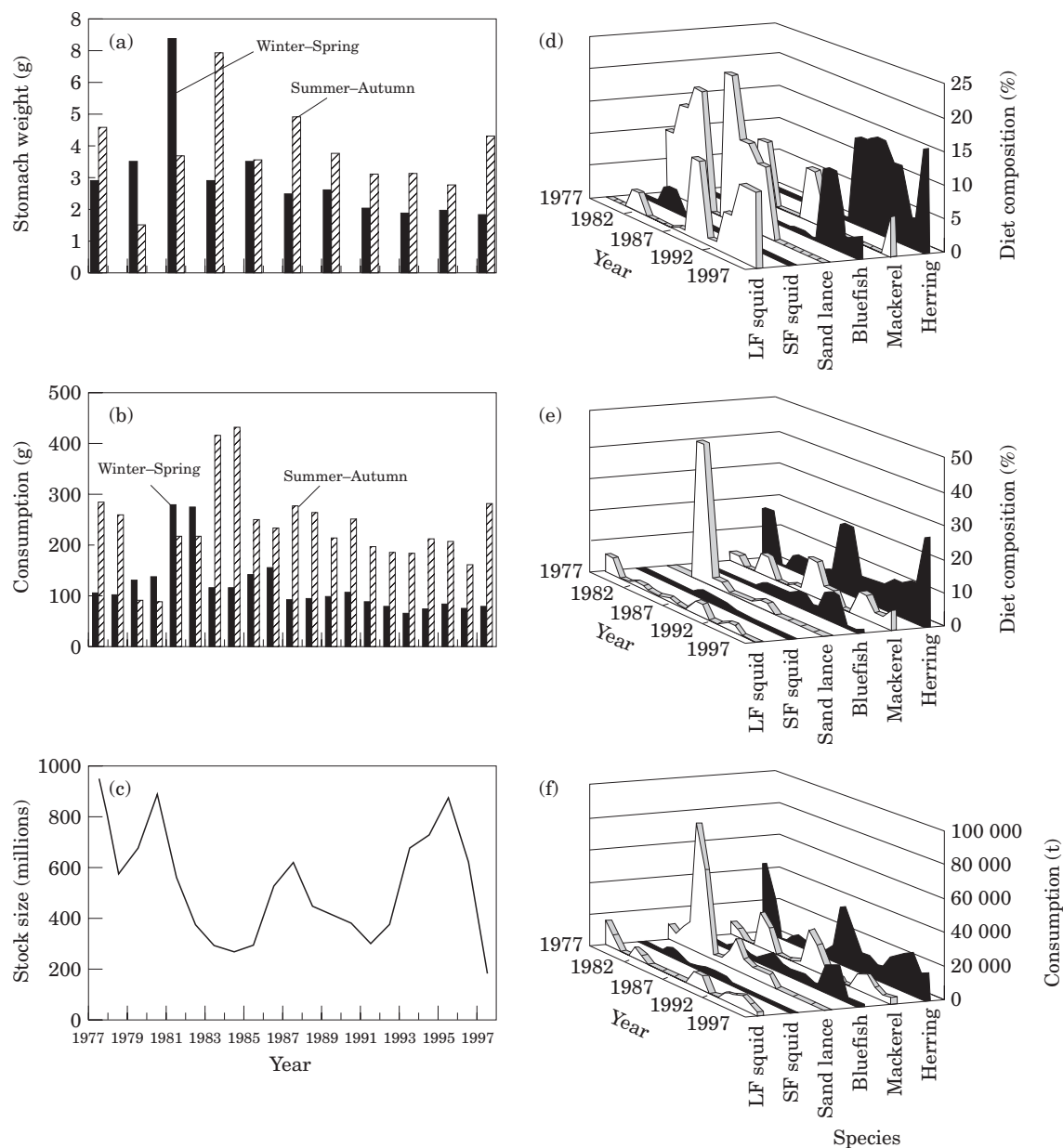
Figure 8. Silver hake (a) average stomach contents (g) in winter–spring and summer–autumn for two-year intervals, (b) seasonal per capita consumption (g) during winter–spring and summer–autumn, (c) stock size (millions), (d) spring diet composition (%) of pelagic fishes and squids, (e) autumn diet composition (%) of pelagic fishes and squids, and (f) consumption (t) of pelagic fishes and squids, during 1977–1997.

through the 1980s and lf squid, and herring in the 1990s (Fig. 8d). In contrast, during the autumn, silver hake consumed the two squids and butterfish in almost background amounts throughout the series and focused on sand lance in the early 1980s (Fig. 8e). Consumption of Atlantic mackerel and herring was characterized by peak years and was more consistent and higher over the entire 1977–1997 period during the autumn. Particularly

abundant prey such as sand lance and Atlantic herring were characterized by notable peaks in percent of the diet of silver hake during periods of years in both spring and autumn when these two fish were abundant. Conversely mackerel, an abundant species in the late 1980s and throughout the 1990s, never comprised more than a few percent of the diet in either spring or autumn. Overall, in terms of tonnes consumed, silver hake are
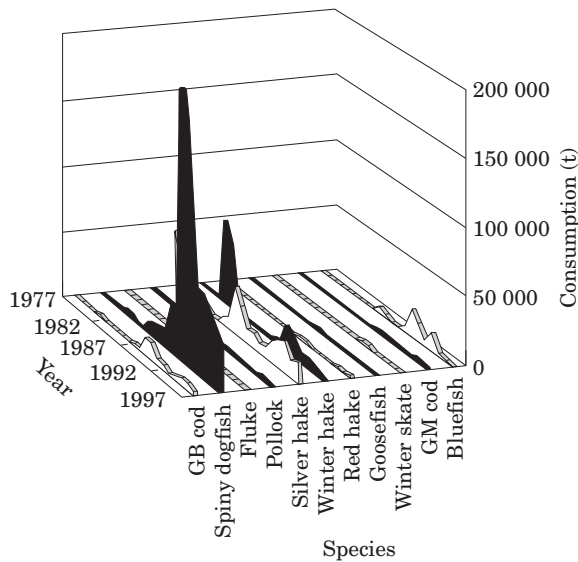
Figure 9. Consumption of Atlantic herring (t) by twelve predatory fish off the northeastern USA during 1977–1997.

Figure 10. Consumption of pelagic prey (fishes and squid, thousand mt) by 12 predatory fish off the northeastern USA during 1977–1997.

light consumers of lf squid, sf squid, and butterfish, a moderate predator of Atlantic mackerel, and a significant predator of land lance and Atlantic herring (Fig. 8f).

Consumption of individual prey by each predator

Observations on the consumption of particular prey items by the individual predators is equally informative, but similarly can be best addressed by choosing a particular prey fish to illustrate key features. We choose Atlantic herring because it is an abundant fish that is available seasonally and spatially over a large area of the eastern USA shelf, and was consumed by ten of the predatory species/stocks we studied. We found no incidence of predation on Atlantic herring by weakfish and spotted hake during the 1977–1997 period of study. Consumption of Atlantic herring by fluke, pollock, red hake, goosefish winter skate, and GM cod was relatively low (range 200–3100 t), but consistent during this period (Fig. 9). The larger, more abundant mobile predators such as GB cod, spiny dogfish, silver hake, white hake, and bluefish, consumed Atlantic herring throughout the entire period, but focused on herring during 1987–1997. Consumption by GB cod ranged from 1900–13 000 t, spiny dog fish ranged from 36 000–214 000 t, silver hake from 11 500–36 000 t, white hake from 500–20 000 t, and bluefish from 500–13 600 t during 1987–1997 (Fig. 9). It appears that all 10 predators responded to the increase in the abundance of herring in the late 1980s and throughout the 1990s. Additionally, declines in the abundance of GB cod, spiny dogfish, silver hake, white hake, and bluefish in the late 1990s resulted in a major
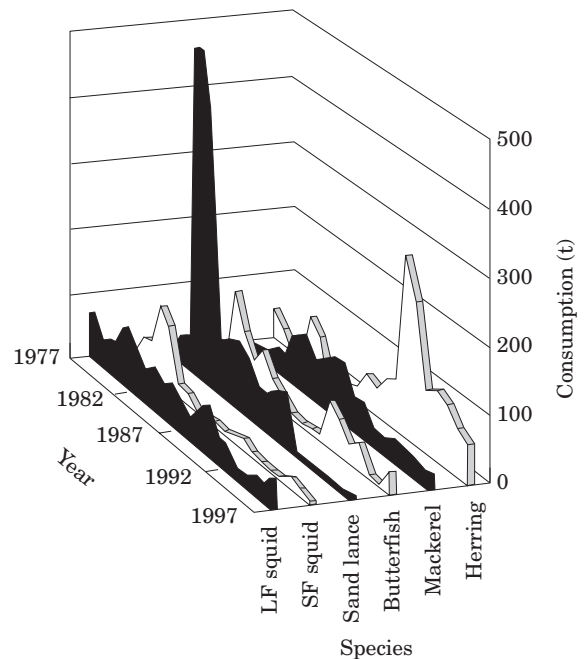
decrease in consumption of herring during this period (Fig. 9).

Total consumption of pelagic fishes and squids

Consumption of pelagic fishes and squids by the 12 predators varied over the time-series and was particularly large in some years on herring and sand lance (Fig. 10). Predation on sand lance reached high levels in the late 1970s and early 1980s coincident with the large biomass of this species present at this time and the collapse of the Atlantic mackerel and Atlantic herring stocks. As the Atlantic mackerel stock began to recover in the early 1980s, predation on mackerel increased, reaching 89 000 t in 1988, but then declined. Consumption of Atlantic herring reached over 200 000 mt during 1992 and 1993, declining thereafter to less than 100 000 mt in 1997. Consumption of sf squid and lf squid averaged 24 000 mt and 46 000 mt respectively during 1977–1997, but, remained relatively constant over this period, with a minor peak during the late 1970s and early 1980s for sf squid (Fig. 10). Predation on butterfish was more variable than the other species, but with the exception of a few years, was relatively low.

Consumption vs. available biomass of Atlantic mackerel and Atlantic herring

Consumption of Atlantic mackerel during 1977–1997 generally paralleled stock biomass until 1989, when a
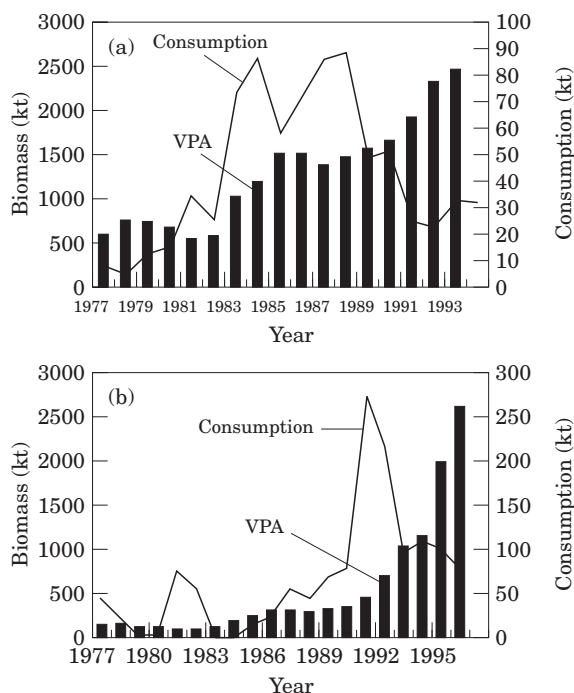
Figure 11. Consumption of (a) Atlantic mackerel (thousand mt) by twelve predatory fish and average stock biomass (VPA, thousand mt) during 1977–1997 and (b) Atlantic herring (thousands mt) by twelve predatory fish and average stock biomass (VPA, thousands mt) off the northeastern USA during 1977–1997.

sharp decline in consumption relative to VPA biomass occurred (Fig. 11a). The reduction in Atlantic mackerel consumption by piscivorous fishes continued through 1993 in spite of large increases in Atlantic mackerel biomass (Fig. 11a). Consumption of Atlantic herring was relatively low during 1977–1988, and then increased rapidly as stock biomass began to increase after 1989 (Fig. 11b). Consumption of Atlantic herring remained high from 1991–1995 (Fig. 10b). Overall consumption of Atlantic herring by the 12 predators followed increases in Atlantic herring stock biomass until it began to decline in 1993 (Fig. 11b).

Consumption and fishing

Commercial landings of prey species during 1973–1997 ranged over two orders of magnitude (Fig. 12). Squid and butterfish landings were relatively constant and low, except for sf squid in the mid 1970s. Atlantic herring and Atlantic mackerel landings were very large in the early to mid 1970s and then dropped to much lower values thereafter (Fig. 12). There is no commercial fishery on sand lance in the Northwest Atlantic.

Atlantic mackerel consumption and landings were similar during this period and both were wel below the
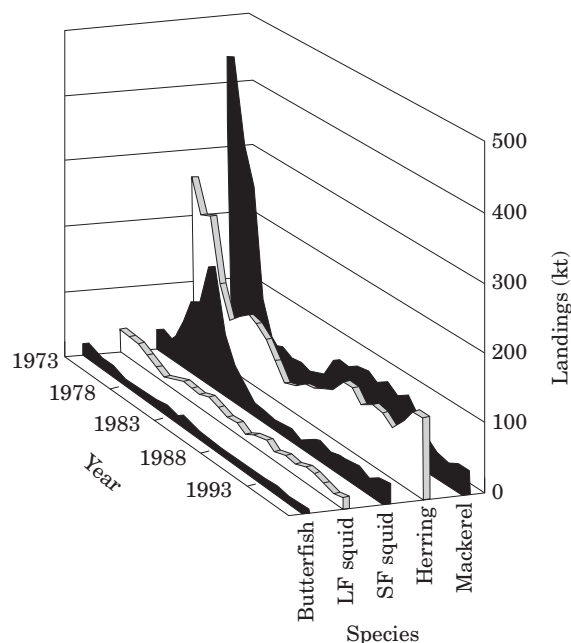

Figure 12. Total commercial landings (kt) of butterfish, long-finned squid, short-finned squid, Atlantic mackerel, and Atlantic herring off the northeastern USA during 1977–1997.

MSY for this stock (326 000 t; Applegate *et al.*, 1998) (Fig. 13a). Consumption of lf squid exceeded landings and MSY (24 000 t; Applegate *et al.*, 1998) for this stock in all years except 1993–1994 (Fig. 13b). Atlantic herring landings averaged 82 000 t during 1977–1997 ranging from 36 000–120 000 t (Fig. 13c). Consumption on this species was below 50 000 t from 1977–1987 and then increased dramatically in the 1990s, ranging from 63 000–273 000 t (Fig. 13c). Consumption by 12 piscivorous fish approached the estimated MSY (317 000 t, Applegate *et al.*, 1998) in 1991 (273 000 t) for herring, declined to 216 000 t in 1992, averaged about 100 000 t during 1993–1995, and declined to 63 000 t in 1997 (Fig. 13c).

Consumption to landings ratios for Atlantic mackerel averaged 0.68 during 1977–1997 (Fig. 14a). The ratio exceeded one during 1982 and 1983, coincident with the very large 1982 year class of Atlantic mackerel (NEFSC, 1996). Consumption to landings ratios for lf squid exceeded one during the entire period from 1977–1997 with the exception of 1993 and 1994 (Fig. 14b). Most of the C/L values for this species were relatively high, averaging 2.36 and ranged from 0.58–4.88 (Fig. 14b). As the Atlantic herring stock increased in the late 1980s and early 1990s, C/L ratios increased, exceeding three in 1991 (Fig. 14c). The C/L ratios were all low prior to the mid 1980s and increased to above one for this species during 1991–1995 (Fig. 14c).
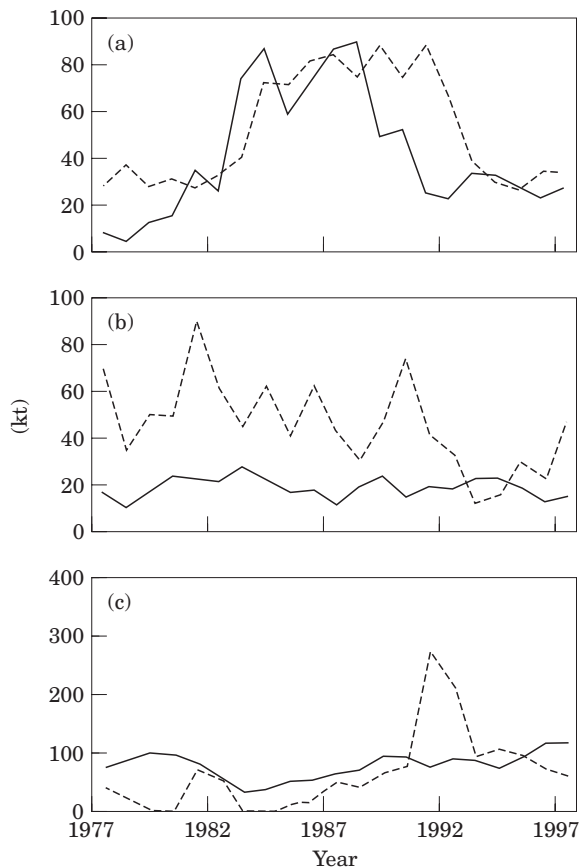
Figure 13. Consumption by 12 predatory fish (broken line) and commercial landings (continuous line), (kt) for (a) Atlantic mackerel, (b) LF squid and (c) Atlantic herring off the northeastern USA during 1977–1997.

Figure 14. Consumption to landings ratios for (a) Atlantic mackerel, (b) LF squid, and (c) Atlantic herring off the northeastern USA during 1977–1997.

Size composition in landings and predators

Atlantic herring and mackerel are eaten by predators and captured in fisheries in the region; exhibiting some overlap in size composition on both mortality components (Fig. 15a, b). Three important predators were chosen to illustrate the relationship between size distributions in predators and the fishery. Spiny dogfish, Atlantic cod, and silver hake consume Atlantic mackerel, but appear to focus on a smaller size range than the fishery for this species (Fig. 15a). The size range of mackerel for predators was between 130 and 310 mm during 1992–1997 and 210–430 mm in the fishery during 1994–1997. The average size of Atlantic mackerel found in these predators was 211.1 mm, while the average in the commercial fishery was much larger at 324 mm (Fig. 15a). Some overlap (20%) between predators and the fishery occurs, centring on fish in the 270–300 mm range.

These three predators focused on Atlantic herring between 90–330 mm during 1992–1997, while the fishery concentrated on the 190–330 size range during 1994–
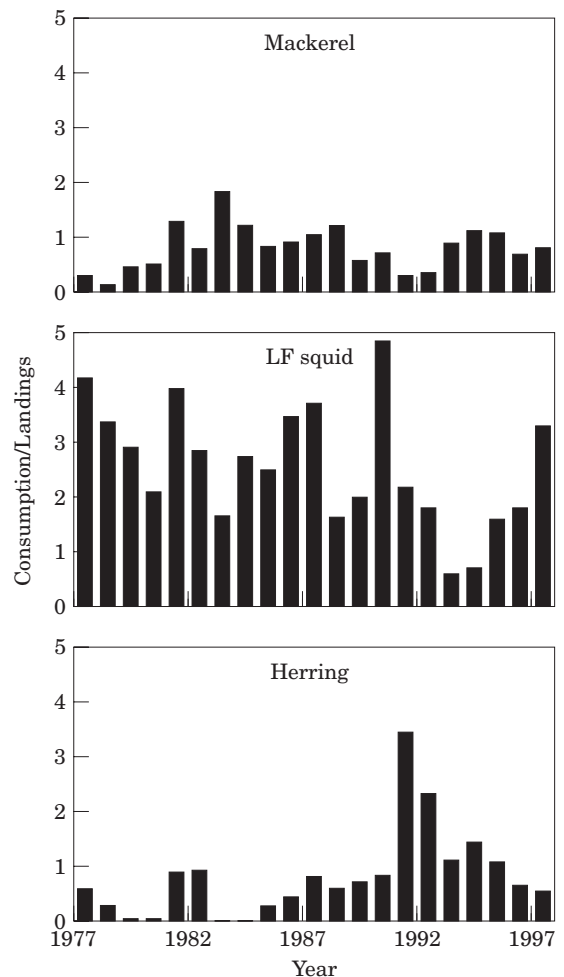
1997 (Fig. 15b). For Atlantic herring the average size in predators was 217 mm and 271 mm in the fishery (Fig. 15b). Overlap in the size distributions of predators and the fishery is significant (48%) for Atlantic herring and the overlap range of 210–330 mm is much wider than in the case of Atlantic mackerel (Fig. 15b).

Discussion

Our results agree with other studies demonstrating that predation on pelagic fish and squid is an important component of the trophic dynamics of this northeastern USA continental shelf ecosystem (Cohen *et al.*, 1982; sensu Fogarty *et al.*, 1991). The 12 predators we studied are part of a large, diverse and highly linked food web (Link, 1999). Predation on small pelagic fishes and squids appears to be far more important than predation
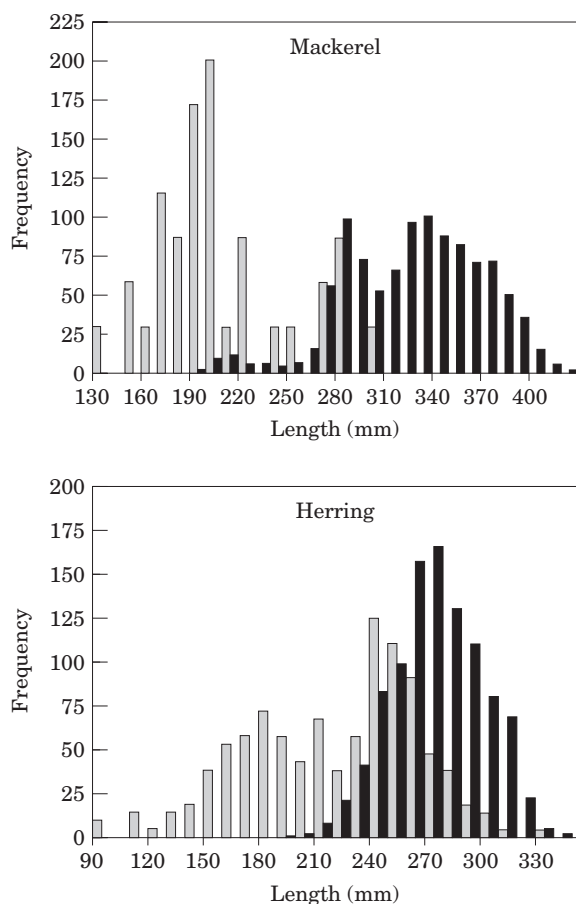
Figure 15. Size compositions (per mille) of two prey species in stomachs of spiny dogfish, Atlantic cod, and silver hake (light bar) during 1992–1997 and in the commercial fishery (dark bars) off the northeastern USA during 1994–1997 for (a) Atlantic mackerel and (b) Atlantic herring.

on the demersal fish assemblage of this ecosystem (Overholtz *et al.*, 1991a). Consumption of pelagic fish and squid often equalled or exceeded landings for these stocks during 1977–1997, and for some species such as Atlantic herring, consumption was much greater than landings in the 1990s.

Consumption by this set of predators appeared to track prey abundance closely, as evidenced by the major changes in the flow of fish biomass to predators observed during 1977–1997. This was particularly so for sand lance, Atlantic mackerel, and Atlantic herring. After the collapse of the Atlantic herring and Atlantic mackerel stocks in the mid 1970s, increased sand lance abundance during the late 1970s and early 1980s (Fogarty *et al.*, 1991) was reflected in predator diets. Similarly, Atlantic mackerel from the large 1982 year class (NEFSC, 1996) were reflected in the diets of an array of predators in 1983 and 1984 as sand lance were declining in abundance. Stock rebuilding of Atlantic

herring in the 1990s was also apparent in predator diets as percentages increased considerably during this period. Predators appear to have fed interchangeably, depending on the relative abundance of these three pelagic fishes. Consumption of Atlantic herring declined as the abundance of mobile predators such as spiny dogfish, white hake, and cod declined in the late 1990s, despite continued increases in the herring stock and a continued high proportion of herring in the diet of these predators (NEFSC, 1998a).

Silver hake diet compositions confirm these aggregate results, showing that the relative proportions of these small pelagic fishes and squids changed dramatically in the diet of this species during 1977–1997. Changes in prey abundance were reflected in the diet as major changes in the percent composition of these prey. For example, the percent of herring in the spring and autumn diet of silver hake increased markedly in the 1990s, paralleling the increase in herring abundance. However, total consumption of herring by silver hake appears to be declining since 1995, reflecting a decline in silver hake abundance, even though the relative proportion of herring in the diet of silver hake may still be consistent or increasing.

Atlantic mackerel, although abundant in the late 1990s, appeared to be less important than Atlantic herring in the diets of piscivorous fish. This may be related to relative preference or availability (e.g. spatial overlap of predator and prey) of these prey fish to predators. Atlantic mackerel grow rapidly and are probably only vulnerable to predation by virtue of preferred predator–prey size ratios for the first several years of their life (Overholtz *et al.*, 1991b; Scharf *et al.*, 1998). Atlantic herring, on the other hand, are smaller and vulnerable to most mid-size predatory fishes in the system. They are thus subject to predation by these fish over most, if not all, of their life (Overholtz *et al.*, 1991b; Scharf *et al.*, 1998). Consumption may be positively related to the available biomass of mackerel and herring, but consumption of mackerel appears to have declined in conjunction with major increases in herring biomass, at least for the set of predators examined.

It appears that even low-frequency monitoring of predator stomach contents, such as the current program at the Northeast Fisheries Science Centre, can provide important conclusions concerning the importance of biological interactions on fishery systems. This program provides continuous, albeit low-resolution, monitoring that follows long-term trends in diet, similar to stock assessment programs. One shortfall of such long-term programs is the lack of resolution between seasons when biological interactions may alter. Alternative programs (e.g. in the North Sea; ICES, 1993) use intense seasonal sampling, intermittently across several years, to calibrate different predator-prey and multi-species models. These programs address the seasonal time scale, but assume

stationarity between sampling periods. Certainly, aspects of both types of programs are valuable. Collecting large sample, seasonally focused diet composition data would be important information to contrast with the current low-frequency monitoring program on bottom trawl surveys currently employed. Such data would improve knowledge of diet stochasticity and allow us to explore the feasibility of extrapolating to half-year intervals based on spring and autumn sampling.

A prior sensitivity analysis conducted indicates that consumption estimates are very dependent on the choice of parameters (Overholtz et al., 1999). Our results may underestimate losses to fish since we chose to use relatively conservative parameters in our analysis. The accuracy of our assumption of fixed α and β parameter values for all species is difficult to determine. If only cod, silver hake and spiny dogfish are considered, our results are about the same order of magnitude as another study that used bioenergetics methods to estimate losses to fish consumption (Overholtz et al., 1991a). In another study that used a similar approach, our results would be lower for these same three species or stocks (Bax, 1991).

Stomach content data can be variable, and our estimates appear to be no exception (Table 1). Although we did not produce confidence intervals around our estimates of consumption, they could be wide, judging from the s.d. of the average stomach content information (Table 1). The diet-composition data utilized in this study includes a large proportion of unidentified fish remains (Overholtz et al., 1999). The small pelagic fish that were the focus of the current study probably comprised a major proportion if one assumes constancy of proportionality to this unidentified component (10–30%, J. Link, unpublished data, Woods Hole, MA). Thus, the diet percentages used probably underestimate consumption of these species by the 12 predators. Our estimates of abundance for predators are reasonably accurate for most of the species we studied, although we may have underestimated goosefish, winter skate, and spotted hake abundance. In spite of all these factors, our estimates provide a useful perspective on consumption of small pelagics in this ecosystem and are in agreement with other studies (Cohen et al., 1982; Overholtz et al., 1991a). However, further work on these important issues would allow for even more refined statements about the importance of predation in this ecosystem.

Maximum sustainable yields (MSY) were recently re-evaluated for a wide spectrum of Northeast fish stocks, based on traditional single-species methods (Applegate et al., 1998): MSYs for the pelagic fishes and squids discussed here were a part of that process. The MSYs for mackerel and herring are 326 000 mt and 317 000 mt, while for butterfish, sf squid, and lf squid the MSYs are 16 000 mt, 24 000 mt, and 21 000 mt, respectively (Applegate et al., 1998). Consumption of pelagic fish and squid by predatory fish appears to equal

or exceed landings in most years from 1977–1997. In several cases, notably for lf squid, Atlantic herring and butterfish, consumption also may equal or exceed the current MSY for these stocks. Other studies have also concluded that the impact of predation often exceeds potential yields from fisheries (Overholtz et al., 1991a; Bax, 1991; Christensen, 1996; Bax, 1999). It is important to consider other factors such as size composition when estimating the significance of predation, since piscivores generally remove smaller individuals (ICES, 1993), and thus may or may not compete directly with fisheries. However, when considering the estimation of yields for these small pelagic and squid fisheries, predator-fishery competition may be an important consideration.

Length compositions of Atlantic mackerel in landings and predators do not greatly overlap because most of the commercial fishery is centred on age 2 and older fish, but the interaction may be important. For Atlantic herring, there appears to be a large amount of overlap between the fishery and predators, thus the two components are competing for the same fish. The historic fishery for Atlantic herring in this region harvested juvenile fish (Anthony and Waring, 1980), and a resurgence of this fishery would place predators and fleets in even a more direct competition for the same fish. The same conclusion probably applies to butterfish, sf squid, and lf squid, due to the smaller size range of these species and the fishery that occurs on similar sizes. It may be necessary to account for predation impacts in assessments for small pelagic fishes and squids because yields and biological reference points from traditional single species approaches may be too optimistic (Overholtz et al., 1991b; Christensen, 1996; Bax, 1999). For pelagic species such as these, there may be important implications in the species dynamics and management regimes that might result from these technological and biological interactions.

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