Abstract.—The bluefish, *Pomatomus saltatrix*, has long been considered a key predator on U.S. east coast fish species. Many of its prey species are also landed by humans, but no comparison of prey biomass harvested by bluefish versus fishermen has been attempted previously. We used data on growth, mortality, gross growth efficiency, and abundance to model the total prey consumption rate by bluefish at the population level. This estimate and previously published information on diet were used to calculate the biomass of individual resource species "harvested" by bluefish. The prey biomass consumed by bluefish annually along the U.S. Atlantic coast is equal to eight times the biomass of the bluefish population. Bluefish consume a much higher biomass of squid and butterfish than is currently harvested by commercial fisheries for these species. Bluefish consumption of Atlantic menhaden, however, was below the current fisheries landings for this species. For resource species that are shared with bluefish, our findings highlight the need for multi-species assessment and management.

Mutual prey of fish and humans: a comparison of biomass consumed by bluefish, *Pomatomus saltatrix*, with that harvested by fisheries*

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The bluefish, *Pomatomus saltatrix*, has long been regarded as one of the most voracious piscivores of the western North Atlantic. In 1873 the U.S. Commissioner of Fisheries, S. F. Baird, stated in a report to congress that: ". . . I am quite inclined to assign to the bluefish the very first position among the most injurious influences that have affected the supply of fishes . . . a daily loss of 25 hundred million pounds . . . their trail is marked by fragments of fish and the stain of blood . . ." (Baird, 1873). Baird was concerned with the possibility that the high abundance of bluefish during that period was the cause of concomitant declines in fish landings.

Bluefish abundance along the U.S. Atlantic coast has been known to fluctuate dramatically over the past two centuries (Bigelow and Schroeder, 1953). The impact of variations in bluefish abundance on their principal prey as well as on the community structure of the continental shelf as a whole may be substantial (Clepper, 1979; Kerfoot and Sih, 1987). If the major prey of bluefish are also harvested by humans, then the potential fishery landings of such species may be influenced strongly by bluefish abundance. Moreover, species management through adjustment of the fishing effort will likely be ineffective if the amount of prey consumed by a key natural predator is substantially larger than the landings and ignored as a variable component of natural mortality.

In this study, we estimate the total prey biomass consumed annually by a given biomass of bluefish using a model developed by Pauly

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(1986). Previously published data on diet and recent estimates of bluefish population size along the U.S. Atlantic coast were used to determine the "harvest" of prey by bluefish. We then compared "harvesting" of prey by bluefish to the biomass harvested by the fishery for the east coast as a whole. Prey consumption by age class was calculated to determine at which age the largest impact on prey occurs. We present these analyses not as management tools but merely as gross estimates of the probable magnitude of the bluefish harvest of fishery species so as to stimulate more detailed studies.

Methods

Estimates of population consumption rate

The total U.S. east coast bluefish population consumption of a given prey was calculated from estimates of diet, the biomass of the bluefish population, and food consumption rate. Bluefish diet information was available from the literature for various seasons and regions along the east coast (Lassiter, 1962; Richards, 1976; Buckel et al., 1999a; Morris[1]; Naughton and Saloman[2]). Bluefish biomass estimates were available for 1982 to 1995 from a virtual population analysis (VPA) performed by the Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole, MA (NEFSC[3]). However, estimates of bluefish consumption rate were available only for young-of-the-year (YOY) (Juanes and Conover, 1994; Buckel et al., 1995; Buckel and Conover, 1997) or for age-0 to age-2 bluefish in Chesapeake Bay (Hartman and Brandt, 1995a). For this reason, we used the approach described below.

The quantity of food consumed annually by the bluefish population was estimated by using Pauly's (1986) age-structured consumption rate model. The model is based on a growth function (e.g. von Bertalanffy growth function, VBGF), the instantaneous total mortality rate (Z), and the relationship of gross growth efficiency to weight. Pauly's (1986) model in simplified form is

[1] Morris, T. L. 1984. Food of bluefish. Woods Hole Ref. Doc. 84-22, 13 p. [Available from Woods Hole Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543.]

[2] Naughton, S. P., and C. H. Saloman. 1984. Food of bluefish (*Pomatomus saltatrix*) from the U.S. south Atlantic and Gulf of Mexico. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SEFC-150, 37 p.

[3] NEFSC (Northeast Fisheries Science Center). 1997. Report of the 23rd Northeast Regional Stock Assessment Workshop (23rd SAW) Stock Assessment Review Committee (SARC) consensus summary of assessments. Northeast Fisheries Sci. Cent. Ref. Doc. 97-05, 105 p.

$$\frac{Q}{B} = \frac{\int_{t_r}^{t_{max}} \frac{(dw/dt) \times N_t}{K_{1(t)}} dt}{\int_{t_r}^{t_{max}} W_t \times N_t \, dt},$$

where Q/B is the food consumption per unit population biomass (see descriptions in Pauly (1986), Pauly and Palomares (1987), and Palomares and Pauly (1989)). The numerator of the model represents the food consumption of the population (Q), which is determined from the growth increment (dw/dt), numbers of fish at age t (N_t, determined from an initial arbitrary number of recruits), and the growth efficiency (K_1) for a given weight at age t. Values are integrated over age classes from t_r to t_{max} (age at recruitment to a maximum age). The denominator is the biomass term (B) which is the weight of individual fish at age t (W_t) multiplied by the number of fish (N_t) at age t. This value is integrated over all cohorts from t_r to t_{max}. An annual Q/B estimate represents the number of times the population consumes its own weight per year (Pauly, 1986).

Pauly and Palomares (1987) have provided a BASIC program to calculate Q/B from VBGF parameters, a parameter from the relationship describing K_1 as a function of weight, and an estimate of total mortality (Z). Growth for the Q/B model is based on the VBGF model expressed in weight form:

$$W_t = W_\infty \times \left[1 - e^{-k \times (t - t_0)}\right]^b,$$

where t = time in years;
   W_t = weight of bluefish at age t;
   W_∞ = asymptotic weight;
   k = growth coefficient;
   t_0 = age at weight zero; and
   b = exponent of the length-weight relationship (i.e. $W = aL^b$).

For bluefish, Wilk's (1977) VBGF parameters were used where $k = 0.226$, $t_0 = -0.123$, $W_\infty = 8725$g, and $b = 3$ (Wilk's estimate of b was 2.89 but $b = 3$ was used owing to ease of use in Pauly's (1986) model).

The Q/B model assumes that gross growth efficiency (K_1) data depends on weight (W) according to

$$K_1 = 1 - (W/W_\infty)^\beta.$$

To estimate β for use in the calculation of Q/B, bluefish gross growth efficiency and weight data from experiments on YOY fish described in Buckel et al. (1995) were used. The linearized form of the above model described in Pauly (1986) was fitted to the data

to estimate β ($\beta = -0.0445$, $r^2 = 0.64$, $F = 45.44$, df=1,25, $P < 0.0001$).

The current stock assessment of bluefish assumes a natural mortality of $M = 0.25$. The highest fishing mortality (F) measured on the east coast bluefish population was in 1992 at 0.51 and recent estimates of F are around 0.4–0.5 (NEFSC[3]). Therefore, an estimate of $M + F = 0.75$ was used as a total mortality (Z) input into the Pauly (1986) model to estimate Q/B. The value of Z does not affect the estimate of Q/B dramatically because of its presence in both the numerator and denominator of the equation (see above). Annual consumption (Q/B) was estimated for bluefish from age-0 to age-10.

To determine if our estimate was robust, Hartman and Brandt's (1995a) equation ($C_{max} = 0.520 \times W^{-0.288}$) describing laboratory (20–25°C) estimates of maximum consumption rate (C_{max}, g/(g·d)) as a function of bluefish weight (W, g) was also used to calculate the population consumption for 1995. First, bluefish biomass by age class was calculated by multiplying bluefish numbers at age (NEFSC[3]) by the mean bluefish weight at age (W_t calculated from Wilk's (1977) VBGF function and length:weight conversion equation; W_{age0} was estimated at $t = 0.5$). Second, the maximum consumption rate was calculated for a mean bluefish weight at age from the relationship between C_{max} and bluefish weight provided by Hartman and Brandt (1995a). To do so, we extrapolated out beyond the range of fish sizes used in their laboratory experiment, assuming that values obtained in this way were accurate. Lastly, these age-specific consumption rates were then multiplied by the biomass of each age class. Summing across age classes provided us with a maximum biomass of prey consumed by the bluefish population at 20–25°C; this value was divided by the biomass of the population to obtain a daily Q/B value. To calculate an annual Q/B value, the daily Q/B value was multiplied by 365 days. Additionally, this Q/B value was temperature adjusted from 22.5°C to 17.5°C. This was done by multiplying by the ratio of bluefish consumption rate estimated at 17.5°C (average temperature for coastal bluefish [Munch, 1997]) to consumption rate estimated at 22.5°C (temperature of Hartman and Brandt's [1995a] study). This ratio was estimated from both Buckel et al. (1995) and Hartman and Brandt (1995a) data and in both cases was found to be ~0.60.

Impact by age class

From the above analysis, the age class where total biomass consumption peaks can be determined. This calculation was first made for a simulated bluefish population having constant recruitment ($N = 1 \times 10^7$) and total mortality ($Z = 0.75$, see above). However, bluefish exhibit highly variable recruitment across years. To illustrate the impact of variable age structure, we also calculated biomass consumed by age class on the basis of actual abundances in 1984 (a year when preceding recruitments had been fairly constant and age structure was typical) and in 1995 (a year when preceding recruitments were highly variable and age structure was unstable).

Comparison of biomass consumed by bluefish with that harvested by fisheries

The estimate of the annual amount of prey consumed by the western Atlantic bluefish population is the annual Q/B estimate (described above) multiplied by stock biomass. The prey consumption for three different population biomass sizes was estimated based on VPA estimates; these were the minimum, maximum, and average population sizes from 1982 to 1995 (NEFSC[3]). The total annual consumption at these three stock sizes was estimated for Atlantic butterfish (*Peprilus triacanthus*), long-finned squid (*Loligo pealei*), boreal squid (*Illex illecebrosus*), and Atlantic menhaden (*Brevoortia tyrannus*). These are primary species in the diet of bluefish that are also landed by fishermen.

Several studies were used to attribute the total biomass consumption by bluefish to different geographic regions, seasons, and prey species. To simulate the migratory patterns of bluefish, it was assumed that 100% of the population was north of Cape Hatteras during summer and autumn and 100% of the population was south of Cape Hatteras during spring and winter. Diet data from Richards (1976), Morris[1], and Buckel et al. (1999b) were used to describe bluefish diet in the summer and autumn north of Cape Hatteras. The diet studies of Naughton and Saloman[2] and Lassiter (1962) were used to describe bluefish diet south of Cape Hatteras (Carolinas and southeast Florida) during winter and spring. Details regarding these diet studies can be found in Buckel et al. (1999b).

To calibrate the relative importance of bluefish predation on squid, butterfish, and menhaden, the annual bluefish consumption of these prey was plotted along with the average, minimum, and maximum fisheries landings (1984–92) for these species as compiled by the National Marine Fisheries Service (Anonymous[4]).

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[4] Anonymous. 1993. Fisheries of the United States, 1992. U.S. Dep. Commer., National Oceanic and Atmospheric Association, National Marine Fisheries Service, Silver Spring, MD, 115 p.

Table 1

Estimate of daily and annual prey consumption of the 1995 bluefish population by age class. We used weight-at-age data from Wilk,[1] maximum consumption rate estimates from Hartman and Brandt (1995a), and the virtual population analysis (VPA) estimates of bluefish number by age from NEFSC (see Footnote 3 in main text).

Age	Bluefish weight (kg)	Bluefish numbers (millions)	Bluefish biomass (10^6 kg)	Consumption rate (kg/(kg · d))	Biomass of prey consumed daily (kg)
0.5	0.031	13.89	0.43	0.1941	82538
1	0.143	17.47	2.50	0.1245	311317
2	0.662	4.78	3.16	0.0801	253240
3	1.502	3.95	5.92	0.0633	374750
4	2.524	2.86	7.22	0.0545	393250
5	3.604	3.31	11.92	0.0492	585820
6	4.654	5.88	27.35	0.0456	1249322
7	5.622	2.76	15.53	0.0432	671889
8	6.481	1.55	10.03	0.04152	416561
9+	7.225	3.99	28.84	0.0402	1160642
		Sum of bluefish biomass (B; 10^6 kg)	112.90	Sum of biomass consumed (Q; kg)	5499328
				Q/B daily (at 22.5°C)	0.0487
				Q/B annual (at 22.5°C)	17.78
				Q/B annual (at 17.5°C)	10.84

[1] Wilk, S. J. 1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Tech. Ser. Rep. 11, 56 p. [Available from James J. Howard Marine Sciences Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 74 Magruder Rd., Highlands, NJ.]

Effects of pooling diet across ages

One potential shortcoming of this analysis was the use of diet data pooled across age or size groups. This procedure was unavoidable because of the lack of data describing bluefish diet by age or size for different seasons and geographical locations on the east coast of the United States. The use of pooled diet data may bias impact estimates given that prey such as squid, butterfish, and squid are more important diet items of older and larger bluefish. To address this potential bias, we performed a separate analysis to calculate bluefish consumption of prey using size or specific diet data (where available, see Morris[1]) as opposed to pooled data. The daily biomass of prey consumed by each age or size class (uncorrected for temperature) was calculated for the simulated population (a population with constant recruitment and mortality, see "Estimates of population consumption rate" section) and the 1995 bluefish population (a population whose biomass was dominated by older fish, see "Impact by age class" section and Table 1). These consumption-by-age estimates were multiplied by percent-contribution-by-weight data from Morris[1] for the four prey species described in the main analysis. The biomass of each prey type that was consumed was summed over all age classes to obtain the popu-lation consumption of each prey type. These values were then compared with values of population consumption of each prey type that were obtained by multiplying the total population consumption of all prey by the pooled prey contribution from Morris.

Results

Estimates of population consumption rate

The annual *Q/B* estimate from Pauly's (1986) model for the east coast bluefish population is 7.7. This means that the east coast bluefish population consumes a biomass of prey that is equivalent to ~8 times its own biomass over a one year period. The estimate of *Q/B* with Hartman and Brandt's (1995a) consumption-rate-at-weight data, adjusted for temperature, and estimated for the 1995 bluefish biomass on the U.S. east coast, was 10.8 (Table 1).

Impact by age class

For the simulated population with constant recruitment and mortality, the peak predatory impact of the bluefish population occurs between approximately age 1 and age 3 (Fig. 1). In 1984, a year with

fairly typical age structure, peak absolute consumption of prey occurred between age 2 and age 3 with a second peak at age 6 (Fig. 2). In 1995, when age structure was dominated by the 1989 year class, peak predatory impact occurred in fish that were six years of age (Table 1; Fig. 3). Therefore, much interannual variation in the age classes at which the peak predatory impact occurs should be expected in bluefish.

Comparison of biomass consumed by bluefish with that harvested by fisheries

The bluefish VPA biomass estimates from 1982 to 1995 ranged from a low of 124,024 metric tons (t) in 1995 to a high of 328,864 t in 1986 with an average stock size of 233,309 t for this period (NEFSC[3]). Given a Q/B estimate of 7.7, the minimum-size bluefish
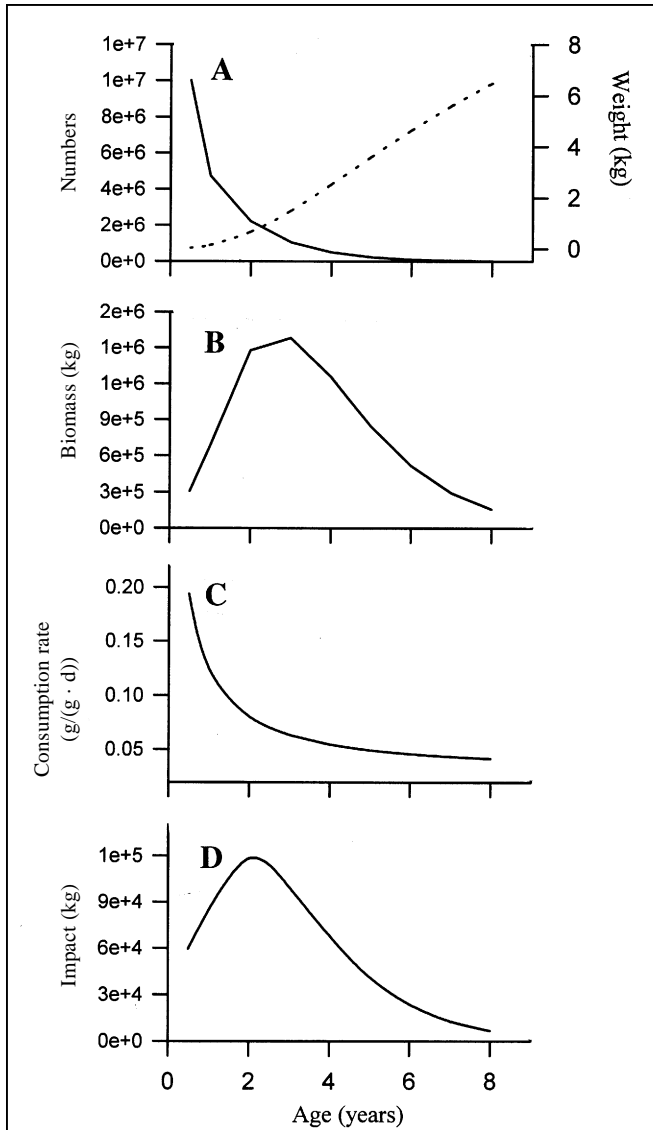

Figure 1

Estimates of bluefish impact on prey by age class for a simulated population of the U.S. east coast bluefish stock. Simulated numbers of bluefish (see text) and bluefish weight (kg; Wilk,1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by maximum consumption rate (Hartman and Brandt, 1995a) for each age class (**C**).
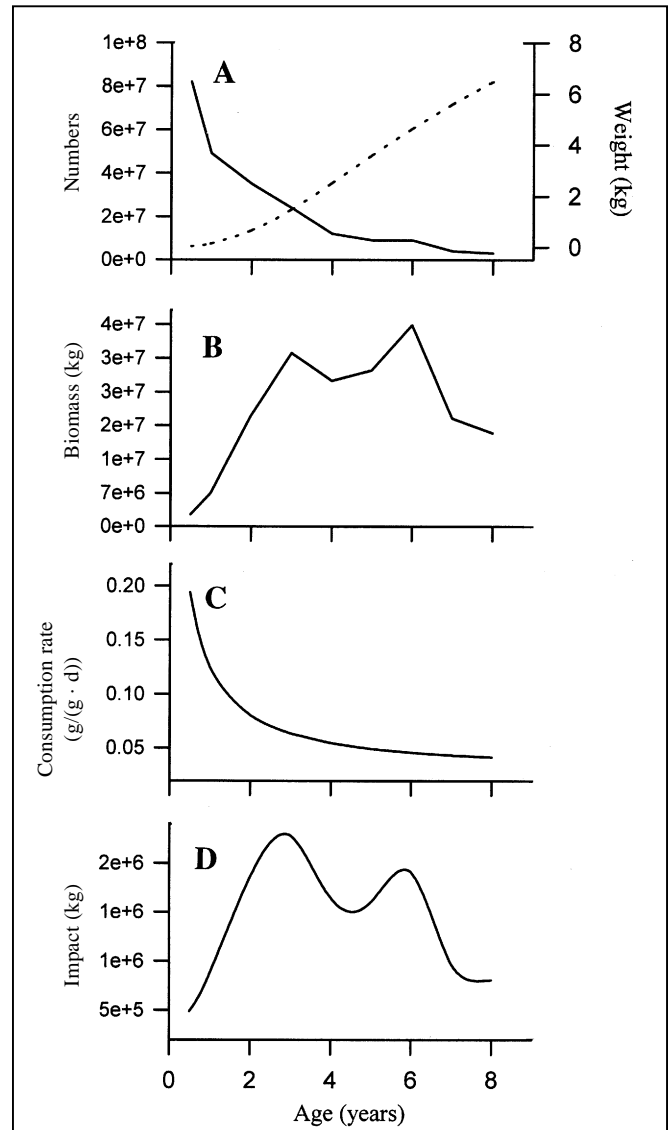

Figure 2

Estimates of bluefish impact on prey by age class for the U.S. east coast bluefish stock in 1984. Numbers of bluefish (NEFSC[3]) and bluefish weight (kg; Wilk, 1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by the maximum consumption rate (Hartman and Brandt, 1995a) for each age class (**C**).

population (1995) consumed 0.9 million t per year whereas the maximum-size population (1986) consumed 2.5 million t of prey per year. The 1982 to 1995 average population biomass consumed 1.8 million t of prey per year.

Of the total biomass of prey consumed annually by bluefish, the fraction attributed to the primary resource species is an annual average of 10% butter-

fish, 10% long-finned squid, 5% boreal squid, and 5% Atlantic menhaden. These are also averages across bluefish body size; however, these averages may be too simplistic given that bluefish diet changes with increasing size. Much of the rest of the diet of bluefish is attributed to bay anchovy (described in Buckel et al., 1999a) for which no fishery landings exist. The average (minimum-maximum) annual consumption of butterfish by bluefish is therefore 90,000 t (48,000–125,000 t); annual consumtion of long-finned squid, is 90,000 t (48,000–125,000 t); and annual consumption of boreal squid, is 45,000 t (24,000–63,000 t). The annual consumption of these species by bluefish is much higher than the annual fisheries landings over the period 1984–92 (Fig. 4). The average consumption of Atlantic menhaden by bluefish was 45,000 t (24,000–63,000 t). The menhaden fishery takes seven times the biomass of menhaden that bluefish consume (Fig. 4).
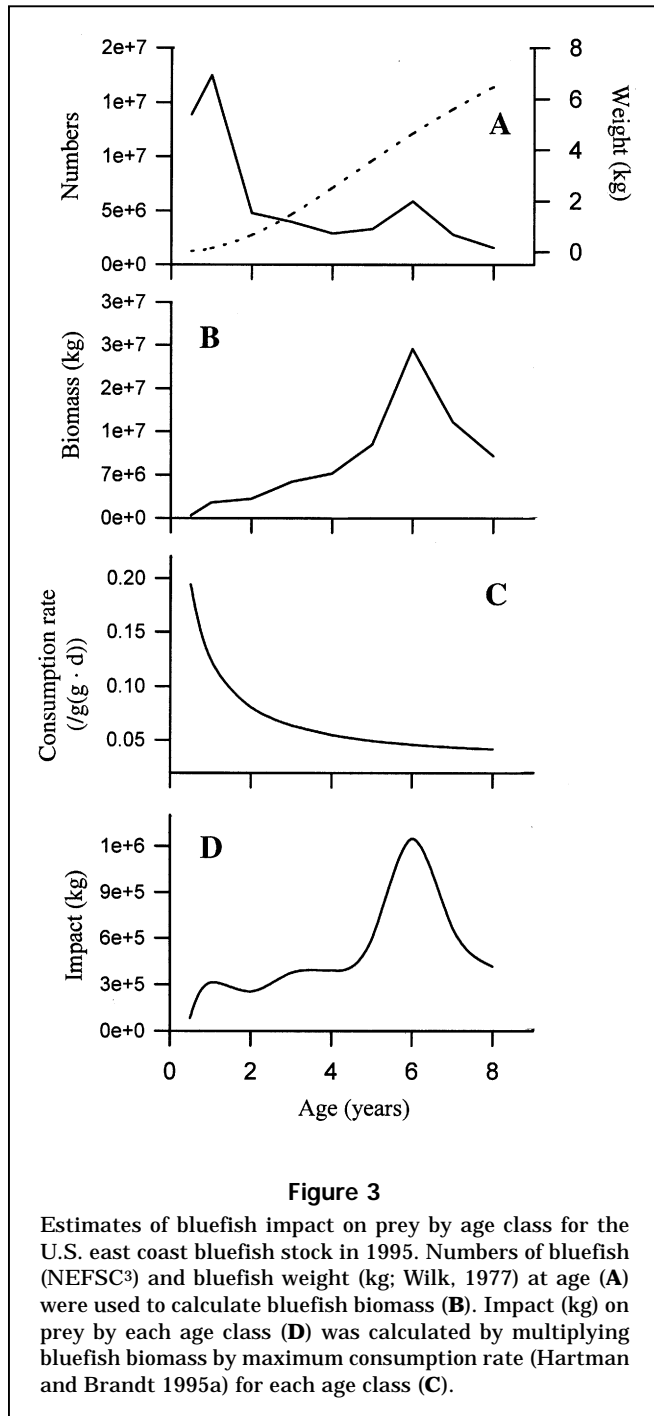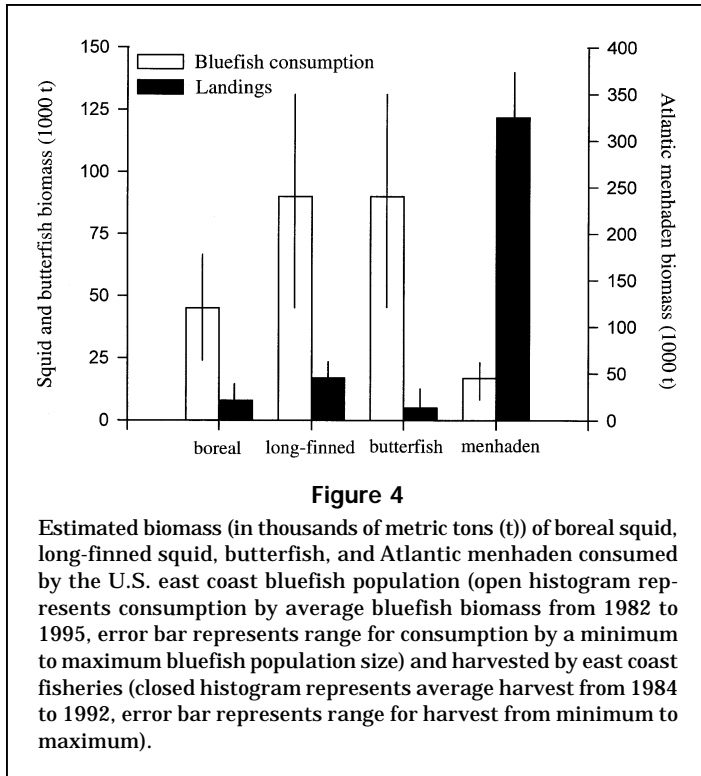
Effects of pooling diet across ages

For the simulated population, the daily consumption of long-finned squid and butterfish calculated by using age-specific data did not differ greatly from daily consumption when diets were pooled across ages (Fig. 5). However, the use of pooled diets overestimated daily consumption of boreal squid and Atlantic menhaden in comparison to values obtained with age-specific diets for both the simulated and 1995 bluefish population. For the 1995 population, age-specific diets gave daily consumption values for long-finned squid and butterfish that were higher than those that were calculated when pooled percent diet contributions were used (Fig. 5). Therefore, pooling diets can lead to under- or over-estimates of the predation pressure by bluefish; this bias can be affected by the age structure of the bluefish population.

Discussion

The results suggest that for at least three of the prey species of bluefish and humans, bluefish harvest a much higher biomass than does the fishery. This predatory loss will vary with fluctuations in bluefish abundance. We elaborate on management implications below.

Estimates of population consumption rate

Our estimate of Q/B (annual population consumption) is likely robust for two reasons. First, the estimate of bluefish annual Q/B is similar to that of other pelagic piscivores. Palomares and Pauly (1989) esti-

Figure 3

Estimates of bluefish impact on prey by age class for the U.S. east coast bluefish stock in 1995. Numbers of bluefish (NEFSC[3]) and bluefish weight (kg; Wilk, 1977) at age (**A**) were used to calculate bluefish biomass (**B**). Impact (kg) on prey by each age class (**D**) was calculated by multiplying bluefish biomass by maximum consumption rate (Hartman and Brandt 1995a) for each age class (**C**).

Figure 4

Estimated biomass (in thousands of metric tons (t)) of boreal squid, long-finned squid, butterfish, and Atlantic menhaden consumed by the U.S. east coast bluefish population (open histogram represents consumption by average bluefish biomass from 1982 to 1995, error bar represents range for consumption by a minimum to maximum bluefish population size) and harvested by east coast fisheries (closed histogram represents average harvest from 1984 to 1992, error bar represents range for harvest from minimum to maximum).

Figure 5

Daily consumption (not temperature corrected; t) of boreal squid, long-finned squid, butterfish, and Atlantic menhaden by the U.S. east coast bluefish population based on simulated (**A**) and 1995 (**B**) data (see text for calculation methods). Consumption was estimated from pooled diet indices (open histogram) and indices which were partitioned by age or size (closed histogram).

mated the annual Q/B of bar jack, *Caranx ruber,* and the dolphin *Coryphaena hippurus* at 10.6 and 8.5, respectively. Secondly, the estimate of Q/B with laboratory-measured daily rations (age 0–2 yr fish) and 1995 VPA bluefish biomass data gave us an estimate of Q/B of 10.8. This value was only slightly higher than the estimate from Pauly's (1986) model. This difference is likely a result of extrapolating C_{max} data from Hartman and Brandt (1995a) to larger fish. Assuming consumption rates of these larger fish were overestimated, values of 2.0 to 3.0 kg/(kg · d) · 100 were substituted for fish ages 4–9+. From this a Q/B value of 6.6 was estimated. This value is more similar to the Pauly model Q/B estimate of 7.7. Future estimates of bluefish population consumption should include laboratory or field estimates of feeding rates of older bluefish.

The Q/B estimate based on the 1995 VPA (10.8) incorporates the age structure existing at that time (recruitment not constant in the population), whereas the estimate from Pauly's (1986) model (7.7) assumes constant recruitment. Age structure may also contribute to the differences between the two Q/B estimates. For the 1995 bluefish stock, recent years of low recruitment have led to peak biomass in the older age classes (NEFSC[3]). These older, more abundant age classes consume a higher biomass of prey than younger age classes. In 1995, age-6 fish consumed more prey biomass than any other age class. This
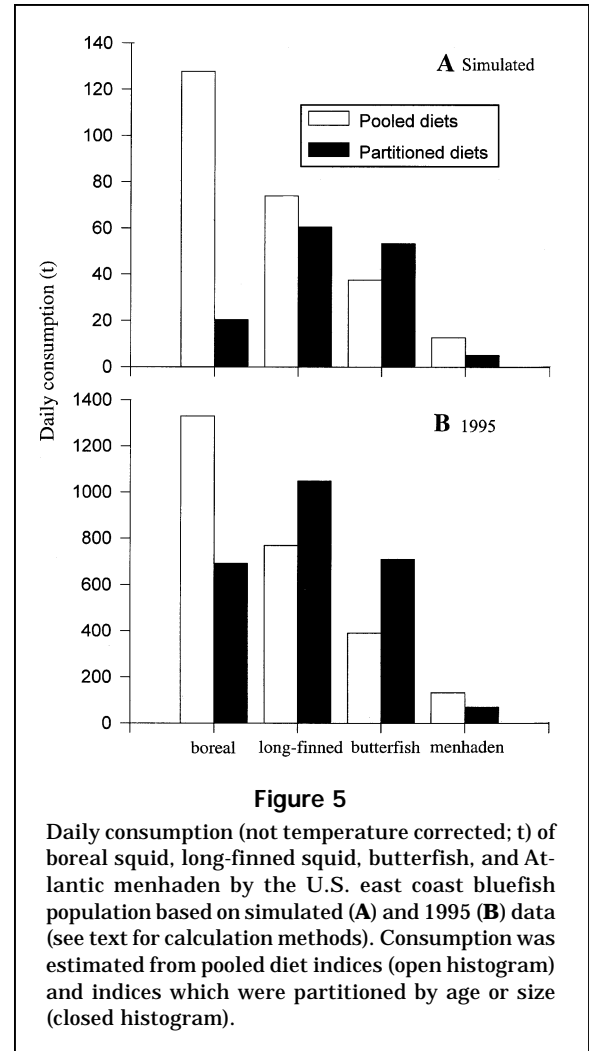
strong age class resulted from a relatively large recruitment in 1989. If recruitment and mortality are constant, our analyses predict that absolute prey consumption will peak at about age 2 (Fig. 1D). That consumption rate tends to peak in the earlier age classes has also been found in other species (Stewart and Binkowski, 1986; Yañez-Arancibia et al., 1993).

Bluefish ingest larger and a greater diversity of prey and include more resource species in their diet (e.g. butterfish, squid, Atlantic herring, and several groundfish species), with increasing body size (Buckel et al., 1999b; Morris[1]). When coupled with temporal shifts in the biomass age structure of bluefish, such ontogenetic changes in diet have important implications for impact on prey populations. For example, bluefish recruitment was relatively high from 1982 through 1984. In 1984, peak absolute consumption of prey occurred between age 2 and 3 compared with age 6 in 1995. In 1984, the biomass consumption of age-0 through age-3 fish was 40% of the entire

population's consumption, but it was only 18% of total population consumption in 1995 (Figs. 2 and 3). Similarly, Hartman and Brandt (1995b) found that relative prey consumption by bluefish at the population level in Chesapeake Bay varied with age structure.

The fact that age structure and ontogenetic diet shifts interact provides further justification for obtaining bluefish diet information by age or size. For example, the impact of the 1995 bluefish population on long-finned squid and butterfish was underestimated when pooled diet indices were used compared with diet indices that were partitioned by age or size (Fig. 5).

Comparison of biomass consumed by bluefish with that harvested by fisheries

Edwards and Bowman (1979) and Sissenwine et al. (1984) found that total piscivore consumption often exceeded fishery landings on Georges Bank. We have shown that bluefish alone consume an amount of squid and butterfish far exceeding the harvest of these species. How do our findings relate to the management of squid and butterfish? The current management plan for long-finned squid recommends a target yield of 21,000 t (Mid-Atlantic Fishery Management Council[5]). From calculations presented here bluefish consumed almost five times this amount of long-finned squid. Consistent with our findings, estimates of natural mortality for butterfish, long-finned squid, and boreal squid are high compared with other species (Anonymous, 1995; Atlantic butterfish, M=0.80; long-finned squid, monthly M=0.34; boreal squid, M>1.0). Our analysis does not allow us to determine what fraction of total prey mortality is due to bluefish consumption. Nor do we have estimates of impact of other predators on these prey. If we knew that bluefish were the dominant contributor to natural mortality in these prey, then questions regarding allocation could be dealt with more explicitly. For example, if the goal were to build larger squid stocks, would increased fishing mortality on bluefish be more or less effective than reductions in fishing mortality on squid? Future research should determine the magnitude of predation mortality resulting from bluefish and other predators. Until this information is available we must assume that predation mortality is similar to or below estimates of natural mor

tality for squid and butterfish. The management plan for these prey species assumes a high natural mortality (high predation mortality already taken into account) and fishing harvests are targeted accordingly.

However, these stock assessments assume that natural mortality is a fixed value. For prey of bluefish, this may not be true given the persistent changes in bluefish abundance on multiyear to decadal time scales. Natural mortality in squid and butterfish may vary greatly as a function of bluefish abundance. This has important management implications. For example, if bluefish abundance is high and remains so for extended periods and if this results in natural mortality rates on the prey that exceed the baseline natural mortality rates, then the biological reference points used in squid and butterfish management must be adjusted accordingly. Even if fishery removals are low in relation to those for other species, they may still contribute to population collapse by driving the prey population past the replacement level. Much more attention needs to be focused on assessment of the dynamics and predatory impact of bluefish if we wish to manage its prey, not to mention bluefish. Our results illustrate the importance of incorporating interspecific interactions in the management of marine fisheries (Sissenwine and Dann, 1991; Magnusson, 1995).

Bluefish may have limited influence on menhaden population dynamics because bluefish consumption of Atlantic menhaden was substantially below the fisheries landings of this species in our calculations. Oviatt (1977) estimated the aggregate demand for menhaden by bluefish in Narragansett Bay. She found that menhaden abundance was sufficient to meet the demands of bluefish even when the menhaden stock was low. Hartman and Brandt (1995b) found that combined predation by bluefish, weakfish, and striped bass on menhaden in Chesapeake Bay was low compared with fisheries harvest of menhaden.

There are several limitations to this analysis. The estimates of the biomass of prey consumed rely on several other estimated parameters. These include the VPA of bluefish biomass, the allometry of gross growth efficiency as a function of bluefish weight, diet estimates, and assumptions about the spatial and temporal location of the bluefish population. We therefore urge readers to view our estimates as rough approximations of the true values. At the very least, however, our analysis clearly suggests a need to greatly improve our knowledge of the population dynamics and foraging ecology of bluefish. In particular, more accurate data on bluefish abundance, spatial distribution, and diet as a function of bluefish size, season of the year, and habitat (e.g. estuary, coastal shoreline, or offshore) are required.

[5] Mid-Atlantic Fisheries Management Council. 1996. Amendment 6 to the fishery management plan and the draft environmental assessment for the Atlantic mackerel, squid, and butterfish fisheries. [Available from Mid-Atlantic Fishery Management Council, Room 2115, Federal Building, 300 South New Street, Dover, DE 19904-]6790, 16 p.]

For example, it has been shown that pooling blue-fish diet by age or size class may over- or under-estimate the impact of bluefish compared with estimates of impact obtained when using age or size partitioned diets. Additionally, the diet of bluefish in estuaries (Oviatt, 1977; Hartman and Brandt, 1995c; Buckel et al., 1999a), where YOY bluefish are known to be dominant piscivores, was not considered here. Buckel et al. (1999a) showed that YOY bluefish in the Hudson River estuary are key predators on YOY striped bass and that recruitment success of striped bass is negatively correlated with YOY bluefish abundance. In the Chesapeake Bay, the percentage of menhaden in bluefish diet can be over 80% of the diet by weight (Hartman and Brandt, 1995c), much higher than the diet proportion we used in our analyses. A synoptic study examining the diet on the shelf and estuarine environments, as well as temporal and spatial distributions, will be required to determine the exact proportions of prey items in the coastal bluefish population.

Acknowledgments

Literature cited

Anonymous.
    1995.   Status of the fishery resources off the northeastern United States for 1994.   U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NE.108, 140 p.
Baird, S. F.
    1873.   Natural history of some of the more important food fishes of the south shore of New England. Part II: the bluefish.   U.S. Commissioner of Fish and Fisheries, Washington, D.C., p. 235–252.
Bigelow, H. B., and W. C. Schroeder.
    1953.   Fishes of the Gulf of Maine.   Fishery Bulletin of the Fish and Wildlife Service, Washington, D.C., 577 p.
Buckel, J. A., and D. O. Conover.
    1997.   Movements, feeding chronology, and daily ration of piscivorous young-of-the-year bluefish (*Pomatomus saltatrix*) in the Hudson River estuary.   Fish. Bull. 95:665–679.

Buckel, J. A., D. O. Conover, N. D. Steinberg, and K. A. McKown.
    1999a.   Impact of age-0 bluefish (*Pomatomus saltatrix*) predation on age-0 fishes in the Hudson River estuary: evidence for density-dependent loss of juvenile striped bass.   Can. J. Fish. Aquat. Sci. 56:275–287.
Buckel, J. A., M. J. Fogarty, and D. O. Conover.
    1999b.   Foraging habits of bluefish (*Pomatomus saltatrix*) on the U.S. east coast continental shelf.   Fish. Bull. 99: 758–775.
Buckel, J. A., N. D. Steinberg, and D. O. Conover.
    1995.   Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish.   J. Fish Biol. 47:696–706.
Clepper, H., ed.
    1979.   Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C., 504 p.
Edwards, R. L., and R. E. Bowman.
    1979.   Food consumed by continental shelf fishes.   *In* H. Clepper (ed.), Predator-prey systems in fisheries management, p. 387–406.   Sport Fisheries Institute, Washington, D.C.
Hartman, K. J., and S. B. Brandt.
    1995a.   Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. Can. J. Fish. Aquat. Sci. 52:1647–1666.
    1995b.   Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models.   Can. J. Fish. Aquat. Sci. 52:1667–1687.
    1995c.   Trophic resource partitioning, diets, and growth of sympatric estuarine predators.   Trans. Am. Fish. Soc. 124:520–537.
Juanes, F., and D. O. Conover.
    1994.   Rapid growth, high feeding rates, and early piscivory in young-of-the-year bluefish (*Pomatomus saltatrix*). Can. J. Fish. Aquat. Sci. 51:1752–1761.
Kerfoot, W. C., and A. Sih.
    1987.   Predation:direct and indirect impacts on aquatic communities.   Univ. Press of New England, Hanover, NH, 386 p.
Lassiter, R. R.
    1962.   Life history aspects of the bluefish, *Pomatomus saltatrix* (Linnaeus), from the coast of North Carolina.   M.S. thesis, North Carolina State College, Raleigh, NC, 103 p.
Magnusson, K. G.
    1995.   An overview of the multispecies VPA-theory and applications.   Rev. Fish Biol. Fisheries. 5:195–212.
Munch, S.
    1997.   Recruitment dynamics of bluefish, *Pomatomus saltatrix*, on the continental shelf from Cape Fear to Cape Cod, 1973–1995.   M.S. thesis, State University of New York at Stony Brook, NY, 127 p.
Oviatt, C. A.
    1977.   Menhaden, sport fish, and fishermen.   University of Rhode Island Marine Technical Report 60, 24 p.
Palomares, M. L., and D. Pauly.
    1989.   A multiple regression model for predicting the food consumption of marine fish populations.   Aust. J. Mar. Freshwater Res. 40:259–273.
Pauly, D.
    1986.   A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments.   Fish. Bull. 84:827–839.
Pauly, D., and M. L. Palomares.
    1987.   Shrimp consumption by fish in Kuwait waters: a methodology, preliminary results and their implications for management and research.   Kuwait Bull. Mar. Sci. 9:101–125.

Richards, S. W.
>   **1976.**   Age, growth and food of bluefish from east-central Long Island Sound from July through November 1975. Trans. Am. Fish. Soc. 105:523–525.

Sissenwine, M. P., E. B. Cohen, and M. D. Grosslein.
>   **1984.**   Structure of the Georges Bank ecosystem.   Rapp. P.-V. Reun. Cons. Int. Explor. Mer 183:243–254.

Sissenwine, M. P., and N. Daan.
>   **1991.**   An overview of multispecies models relevant to management of living resources.   ICES Mar. Sci. Symp. 193:6–11.

Stewart, D. J., and F. P. Binkowski.
>   **1986.**   Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Trans. Am. Fish. Soc. 115:643–661.

Yañez-Arancibia, A., A. L. L. Dominguez, and D. Pauly.
>   **1993.**   Coastal lagoons as fish habitats.   *In* B. Kjerfve (ed.), Coastal lagoon processes, p. 339–351.   Elsevier Science Publishers, Elsevier Oceanography Series 60, Amsterdam.