Foraging habits of bluefish, *Pomatomus saltatrix*, on the U.S. east coast continental shelf*

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Abstract.–After spending summer months in estuaries, spring- and summer-spawned young-of-the-year (YOY) bluefish, *Pomatomus saltatrix*, migrate out to continental shelf waters of the Mid-Atlantic Bight in early autumn. Adult bluefish are found on the continental shelf throughout summer and fall. Both juveniles and adults have high food consumption rates and are generally piscivorous. To determine principal prey types on the shelf, dietary analyses were performed on YOY and adult bluefish collected from National Marine Fisheries Service autumn bottom trawl surveys in 1994 and 1995. Both spring- and summer-spawned YOY bluefish diets were dominated by bay anchovy. However, the significantly larger size of the spring-spawned cohort was associated with the consumption of other prey species such as squid, butterfish, striped anchovy, and round herring. Summer-spawned bluefish were significantly smaller in 1995 than in 1994; diet and prey size comparisons suggest that body size had a dramatic influence on the amount of piscivorous feeding in the summer-spawned cohort. Adult bluefish diet was dominated by schooling species such as squid, butterfish, and clupeids. Cannibalism was virtually nonexistent. Daily ration estimates of YOY bluefish on the shelf (4–12% body wt/d) were similar to estuarine estimates in late summer. It is estimated that during the month of September, YOY bluefish in aggregate consumed 6.0 to 6.8 billion bay anchovies in 1994 and from 2.2 to 5.3 billion in 1995. The effect of this predatory loss on population dynamics of bay anchovy and the fish community on the continental shelf is unknown.

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One of the dominant marine piscivores along the U.S. east coast is the bluefish, *Pomatomus saltatrix* (Juanes et al., 1996). Bluefish spawned in offshore waters of the South Atlantic Bight in the spring (spring-spawned) are advected northward in waters associated with the Gulf Stream (Hare and Cowen, 1996) and move into mid-Atlantic Bight estuaries in June at ~60 mm fork length (Kendall and Walford, 1979; Nyman and Conover, 1988; McBride and Conover, 1991). A second wave of recruits consisting of summer-spawned fish occur in nearshore waters from mid to late summer.

In estuaries, bluefish exhibit rapid growth rates that are fueled by high food consumption and evacuation rates (Juanes and Conover, 1994; Buckel et al., 1995; Buckel and Conover, 1996). In the Hudson River estuary, for example, predation by bluefish is high enough to account for virtually all natural mortality of young-of-the-year (YOY) striped bass during their summer–fall growing season (Buckel et al., 1999). After spending the summer months in estuaries, YOY bluefish migrate back out onto the shelf and migrate southward to overwinter (Munch and Conover, in press). Spring-spawned YOY bluefish migrate out of estuaries at a size of ~180 mm fork length (FL) and ~100 g (Nyman and Conover, 1988; McBride and Conover 1991). By age 1, these spring-spawned fish attain sizes of ~260 mm FL and weights of ~300 g (Chiarella and Conover, 1990). Therefore, an individual spring-spawned bluefish gains from 100 to 200 g during its autumn migration. Given a 15% gross growth efficiency (Juanes and Conover, 1994; Buckel et al. 1995), a single bluefish could thus consume from ~650 to 1300 g of prey.

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Compared with the nearshore phase of the early life history of bluefish, our knowledge of the foraging ecology and predatory impact of bluefish on the continental shelf is poor. Here we quantify the diet of YOY and adult bluefish and determine YOY bluefish prey type and size selectivity patterns, foraging chronology, daily ration, and biomass of prey consumed during the autumn migration on the shelf.

Methods

Study area and collections

YOY and adult bluefish and their potential prey were collected on the U.S. east coast continental shelf during the autumn of 1994 and 1995 aboard the research vessel *Albatross IV*. Collections were made during the National Marine Fisheries Service, Northeast Fisheries Science Center's (NMFS-NEFSC) autumn bottom trawl survey cruises at predetermined stations from Cape Hatteras, NC, to Nova Scotia. Cruises began in early September and ended in late October in both years (6 September to 28 October 1994 and 5 September to 27 October 1995).

Descriptions of the survey design and the trawl characteristics can be found in Azarovitz (1981). Briefly, tows were made with a no. 36 Yankee trawl equipped with rollers with an opening 3.2 m high, 10.4 m wide, with 12.7-cm stretched mesh in the opening, with 11.4-cm stretched mesh in the codend, and with a 1.25-cm stretched mesh lining in the codend and upper belly to retain YOY fishes. Tows were 30 minutes in duration at 3.5 knots in relation to bottom and were conducted on a 24-h basis.

Dietary analyses

Adult and YOY bluefish were distinguished by using length-age relationships. Munch and Conover (in press) examined the annual size distributions of bluefish from autumn bottom trawl surveys conducted since the 1970s in four different regions of the shelf: SOC=South of Chesapeake Bay; C–D=Chesapeake Bay to Delaware Bay; SNE=Southern New England (Delaware Bay to Narragansett Bay); and Georges Bank. On the basis of these size distributions and backcalculated sizes at age 1 (Chiarella and Conover, 1990, and references therein), they classified YOY bluefish in autumn as those fish ≤300 mm FL. We classified adults as those bluefish >300 mm FL and we distinguished spring- and summer-spawned YOY bluefish for each region in 1994 and 1995 on the basis of bimodality in length-frequency distributions (Munch and Conover, in press). We also adopted Munch and Conover's (in press) geographical boundaries for this analysis. In 1994, summer-spawned bluefish sizes by region were as follows: SOC, FL≤120 mm; C–D, FL≤160 mm; and SNE, FL≤160 mm. In 1995, summer-spawned bluefish sizes were as follows: SOC, FL≤100 mm; C–D, FL≤150 mm; and SNE, FL≤140 mm. Spring-spawned bluefish were those fish larger than the summer-spawned cohort by region but ≤300 mm FL.

Diets of spring- and summer-spawned juveniles and adult bluefish were quantified. Bluefish taken for stomach content analysis were wet weighed (±1.0 g) and measured for fork length, FL (to 1.0 mm). Stomachs were removed at sea and preserved in 10% formalin buffered with sea water. On some occasions, whole fish were either frozen or preserved in 10% formalin and then processed in the laboratory. Stomach contents of bluefish were identified to the lowest possible taxon, enumerated, blotted dry, weighed (±0.01 g), and measured (TL for fish prey and mantle length for squid, ±1.0 mm). Eye diameter (±0.1 mm) and caudal peduncle height (±0.1 mm) were measured for partially eaten bay anchovy and butterfish prey and converted into TL from linear regression equations (Scharf et al., 1997; Scharf et al., 1998a).

Each trawl containing bluefish provided us with a group or "cluster" of bluefish for a given station. Therefore, for our analysis, the mean and variance of diet indices were calculated with cluster sampling estimators developed at the NEFSC-NMFS, Woods Hole, MA (Cochran, 1977, Fogarty, unpubl. data). These calculations are described in a previous study that examined bluefish diet in the Hudson River estuary (Buckel et al., 1999).

Net feeding

During a 30-minute tow, bluefish may feed within the trawl (an activity known as net feeding). Net feeding could bias the diet index estimates or affect gut fullness level estimates (or do both). We tested for such bias by classifying fish or squid prey as either 1) "fresh" or 2) "digested" during our stomach content examination. "Fresh" prey had no sign of digestion and "digested" prey were either partially or well digested (e.g. they were anywhere from starting to lose skin to being only identifiable by skeleton or shape). The percent occurrence of four dominant prey (bay anchovy, striped anchovy, butterfish, and squid) were compared between fresh and digested categories in YOY bluefish. If the percent occurrence of each prey category within a cohort and region was similar for fresh and digested prey, it would suggest that either there was no net feeding or that it did not affect diet index estimates.

Prey-type selectivity

The feeding selectivity of spring-spawned bluefish on the continental shelf was determined from the relative abundance of prey in individual bluefish guts and the relative abundance of prey in trawl catches. Four prey categories were examined in 1994 (bay anchovy, butterfish, squid, and "other") and three prey categories in 1995 (bay anchovy, squid, and "other"). The "other" category included any teleost fish that did not fall into the previously mentioned groups. The relative abundance of these prey in the field was calculated by including only those prey that were of a size that bluefish could theoretically consume (prey FL<80% of bluefish FL; determined from an independent study, Scharf et al., 1997). Additionally, the index was calculated for stations where at least ten spring-spawned bluefish were captured. Chesson's (1978) index was used to determine bluefish prey preference as

$$\alpha_i = \frac{r_i / p_i}{\sum_{j=1}^{m} r_j / p_j}, \qquad i = 1,\ldots\ldots, m,$$

where α_i = the selectivity for prey type i for an individual bluefish;
r_i = the relative abundance of prey type i in an individual bluefish stomach;
p_i = the relative abundance of prey type i in the environment; and
m = the number of prey types available.

Values of α_i were averaged for each year. Random feeding occurs when mean α_i= 1/m (1994=0.25 and 1995=0.33); values of α_i > 1/m or α_i < 1/m represent "selection" and "avoidance" of prey, respectively. Random feeding was tested by using a t-test to compare mean α_i with 1/m for each prey type within each year (Chesson, 1983).

Prey-size relationships and size selectivities

Prey sizes of all bluefish prey were measured directly or determined indirectly from regression equations. The relationship between ingested prey size and bluefish length was determined for YOY and adult bluefish in both 1994 and 1995. In order to compare the relative prey size ingested by spring- and summer-spawned bluefish cohorts in 1994 and 1995, the frequency distributions of bay anchovy FL to bluefish FL ratios were examined. Ratios were calculated for all bay anchovy prey that were measured (1994, n=388; 1995, n=202).

Size-selective feeding on bay anchovy prey was examined by comparing the sizes of bay anchovy ingested by bluefish at a specific station with sizes of bay anchovy captured in the trawl at that station. Stations from 1994 and 1995 that had n>15 bay anchovy length measurements for each bluefish cohort were used in the analysis. Bay anchovy lengths at each station were obtained from archived data at NEFSC-NMFS, Woods Hole, MA.

Selectivity for bay anchovy prey size categories was measured by using Chesson's (1978) index (described above). Bay anchovy lengths ingested by bluefish and collected at each station were partitioned into four bay anchovy FL categories: 25–34, 35–44, 45–54, and 55–64 mm. Values of α_i were calculated from individual bluefish for each size bin at each station separately; these were then averaged across stations. As above, values of α_i > 1/m or α_i< 1/m represent "selection" and "avoidance" of size categories, respectively. Estimated values of mean α_i were compared with 1/m by using a t-test (1994 spring-spawned, 1/m=0.25, and summer-spawned, 1/m=0.33; 1995 spring-spawned, 1/m=0.33).

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Values of gut fullness were used to examine feeding chronology of YOY bluefish. Gut fullness values (F) were calculated as

$$F = G / W,$$

where G = prey wet weight; and
W = bluefish wet weight (total weight minus prey wet weight).

Gut fullness values for individual bluefish were pooled over eight 3-h time periods and averaged. This analysis was performed for both spring- and summer-spawned bluefish by geographic region.

In order to estimate feeding rates of bluefish on the shelf, bluefish gastric evacuation rate (GER) estimates were needed. Previous work on YOY bluefish GER showed that prey type and bluefish body size did not have a significant effect on bluefish GER; of the factors examined, temperature had the only significant effect on bluefish GER (Buckel and Conover, 1996). These laboratory experiments described bluefish GER from 21° to 30°C. In our continental shelf collections, YOY bluefish were found in water temperatures as low as 15°C (mean of surface and bottom temperature). Therefore, a laboratory experiment to measure YOY bluefish GER at 15°C was performed.

The experiment was conducted in an identical manner to previous GER experiments on YOY bluefish (Buckel and Conover, 1996). Briefly, YOY bluefish were acclimated to experimental tanks for two weeks, acclimated to 15°C for 3 days, and then held at 15°C for a 12–48 h starvation period. They were then fed a single meal of previously frozen and thawed adult bay anchovy (bluefish sizes were: mean bluefish TL=122 [range=99–146], mean wet weight=15.79 g, prey mean wet weight=0.88 g, mean prey wt/predator wt=5.8%). After a predetermined period of time, individual bluefish were sacrificed and their stomach contents removed, blotted dry, and weighed (±0.01 g).

The exponential GER model (see Buckel and Conover, 1996) was fitted to the proportion of meal remaining versus time by using nonlinear regression analysis. The GER estimate from this experiment was used along with estimates from Buckel and Conover (1996) to develop an empirical function describing YOY bluefish GER from 15° to 30°C. This function was used to estimate bluefish GER from water temperatures at which bluefish were collected on the continental shelf. Bluefish daily ration was estimated for each cohort by region in 1994 and 1995 with the Eggers (1979) equation:

$$D = \overline{F_i} \cdot R_e \cdot 24,$$

where D = is bluefish daily ration;
$\overline{F_i}$ = the mean gut fullness over 24 hour; and
R_e = the exponential gastric evacuation rate (see above).

Mean gut fullness was calculated by taking the average of the individual time period (i) gut fullness means from the feeding chronology analysis (see above). The mean of the means was used to give each time period equal weight even though sample sizes for given time intervals varied over the diel cycle. Daily ration was calculated for those geographical regions and cohorts that had a sufficient diel record (e.g. gut fullness estimates throughout the diel cycle). The standard error of the daily ration estimate was approximated by using the delta method (Seber, 1973).

Estimates of the biomass of prey consumed by the YOY bluefish population during their southward migration requires estimates of the numbers of YOY bluefish in the population. The NEFSC, NMFS, Woods Hole, MA, has used virtual population analysis (VPA) to estimate the abundance of the east coast bluefish population (NEFSC[1]). These estimates of YOY bluefish abundance in 1994 and 1995 were used to calculate the daily consumption of bay anchovy by the YOY bluefish population in the following steps. First, the biomass of the spring- and summer-spawned cohorts on the shelf was calculated. This was done by determining the numbers in each spawning cohort (this was necessary because the VPA was for all YOY combined) based on relative abundance estimated from the NMFS autumn bottom trawl survey and then multiplying by the average individual fish weight in each cohort. Secondly, this cohort biomass was multiplied by the estimates of daily ration (lowest and highest) to determine the daily biomass of prey consumed by each cohort. To determine the amount of bay anchovy consumed daily, each cohort's biomass was multiplied by the mean proportion of bay anchovy by weight in each cohort's diet. Finally, a daily estimate of the numbers of bay anchovy consumed by the YOY bluefish population was calculated by dividing the biomass of bay anchovy consumed by the average bay anchovy weight ingested by each cohort. Bay anchovy weight was calculated from mean bay anchovy length ingested with regressions from Hartman and Brandt (1995a).

[1] NEFSC. 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, 191 p. [Available from National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026.]

Results

Dietary analyses

The stomach contents of 989 young-of-the-year (626 spring- and 363 summer-spawned) and 275 adult bluefish were examined. All YOY bluefish were captured between 12 and 29 September 1994 and 7 and 23 September 1995. Continental shelf bluefish diets were dominated by teleost fish and squid prey (see Table 1 for common and scientific names of bluefish prey).

In both 1994 and 1995, the dominant fish prey of spring-spawned bluefish in all three geographical regions was bay anchovy (Table 2). Other spring-spawned bluefish prey included long-finned squid, striped anchovy, butterfish, and round herring. Butterfish were slightly more important in 1994 than in 1995. Also in 1994, amphipods made up a substantial portion of spring-spawned bluefish diets in the SNE region. In 1995, channeled whelk were a relatively important prey of bluefish in the C–D region; the foot and operculum were found in bluefish collected over a large geographical area.

The dominant fish prey of summer-spawned bluefish across all geographical regions was bay anchovy in both 1994 and 1995 (Table 3). The incidence of long-finned squid in summer-spawned bluefish diets was low; however, other invertebrates such as amphipods, mysids, crab larvae, and copepods were relatively important prey. This was particularly true for the relatively small size summer-spawned bluefish collected in the SNE in 1995; the diet of these fish were dominated by copepods (Table 3).

The diet of adult bluefish collected in the Georges Bank region was dominated by butterfish, squid, round herring, and Atlantic herring in both 1994 and 1995 (Table 4). There were several commercially important species consumed by adult bluefish on Georges Bank in 1994. These included American plaice, haddock, Atlantic cod, and several hake species. A large component of the diet of adult bluefish from Cape Hatteras to Montauk Point, NY, was bay anchovy. Butterfish, round herring, and squid were also important prey of bluefish collected from this geographical region. The diet of bluefish from both regions also included several other fish and invertebrate species (Table 4). Channeled whelk were preyed upon by adult bluefish in the same region and year that spring-spawned YOY bluefish were found to feed on them.

Table 1

Common and scientific names of bluefish prey items on the continental shelf and Georges Bank.

Common name	Scientific name
Fish	
American plaice	*Hippoglossoides plattessoides*
Atlantic cod	*Gadus morhua*
Atlantic herring	*Clupea harengus*
Atlantic mackerel	*Scomber scombrus*
Atlantic silverside	*Menidia menidia*
bay anchovy	*Anchoa mitchilli*
butterfish	*Peprilus triacanthus*
conger eel	*Conger oceanicus*
fawn cusk eel	*Lepophidium cervinum*
fourbeard rockling	*Enchelyopus cimbrius*
haddock	*Melanogrammus aeglefinus*
Northern pipefish	*Syngnathus fuscus*
Northern puffer	*Sphoeroides maculatus*
ocean pout	*Macrozoarces americanus*
planehead filefish	*Monacanthus hispidus*
red hake	*Urophycis chuss*
round herring	*Etrumeus teres*
sand lance	*Ammodytes* spp.
scup	*Stenotomus chrysops*
sea horse	*Hippocampus erectus*
searobin	*Prionotus* spp.
silver hake	*Merluccius bilinearis*
margined snake eel	*Ophicthus cruentifer*
spot	*Leiostomus xanthurus*
striped anchovy	*Anchoa hepsetus*
weakfish	*Cynoscion regalis*
white hake	*Urophycis tenuis*
windowpane	*Scophthalmus aquosus*
Invertebrates	
amphipods	*Gammarus* spp.
boreal squid	*Illex illecebrosus*
blue crab	*Callinectes sapidus*
cancer crab	*Cancer* spp.
channeled whelk	*Busycon canaliculatum*
fiddler crab	*Uca* spp.
lady crab	*Ovalipes ocellatus*
long-finned squid	*Loligo pealei*
mole crab	*Emerita talpoida*
sand shrimp	*Crangon* spp.

Net feeding

Although there was evidence of net feeding, it did not seem to bias diet indices. The percent occurrence of several different prey found to be "fresh" and the percent occurrence of these same prey found to be "digested" was similar (Table 5). Only in spring-spawned bluefish in the SNE region in 1995 were there more fresh prey than digested prey in their diet (30 fresh vs. 19 digested; Table 5). Spring-spawned bluefish had more freshly eaten prey in their diet (20–61%) than summer-spawned bluefish (0–26%).

Prey-type selectivity

Spring-spawned YOY bluefish selected positively (α>1/m) for bay anchovy in both 1994 (α=0.69, t-test vs. 0.25, t=8.05, df=154, P<0.001)) and 1995 (α=0.80, t-test vs. 0.33, t=6.40, df=74, P<0.001). However, YOY bluefish avoided (α<1/m) butterfish, squid, and "other" (determined for 1994 only) prey fish in 1994 (t-tests vs. 0.25; P<0.001) and 1995 (t-tests vs. 0.33, P<0.05) (Table 6).

Prey-size relationships and selectivities

There was a very weak but significant positive linear relationship between fish prey TL and YOY bluefish FL in 1994 (r^2=0.10, P<0.0001, n=418) and 1995 (r^2=0.02, P=0.027, n=224) (Fig. 1). A positive linear relationship also existed for fish prey TL and adult bluefish FL in 1994 (r^2=0.15, P<0.001, n=90) and 1995 (r^2=0.28, P<0.0001, n=100) (Fig. 2). Although there was a significant increase in mean prey sizes taken, juvenile and adult bluefish continued to take small prey with increasing body size.

Bay anchovy to bluefish FL ratios were higher in the summer-spawned bluefish cohort than in the spring-spawned cohort in 1994 and 1995. Additionally,

Table 2

Stomach contents of spring-spawned bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %W=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994						1995					
	Southern New England		Chesapeake–Delaware		South of Chesapeake		Southern New England		Chesapeake–Delaware		South of Chesapeake	
Prey type	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Fish												
bay anchovy	71.4 (32.9)	45.7 (21.9)	35.7 (22.9)	40.4 (23.6)	25.0 (54.1)	6.0 (28.0)	57.2 (62.9)	83.2 (59.2)	50.2 (9.0)	50.1 (14.4)	47.4 (38.1)	43.8 (39.3)
butterfish	5.5 (3.4)	8.9 (6.0)	14.7 (7.5)	38.9 (19.0)	12.5 (97.5)	48.1 (375.2)	1.7 (8.8)	1.6 (9.4)			1.9 (4.5)	3.5 (8.2)
round herring	4.4 (2.4)	10.3 (7.6)					4.3 (3.1)	0.8 (5.7)	0.6 (0.9)	3.3 (5.5)		
striped anchovy	1.4 (3.1)	1.8 (4.2)	3.9 (4.9)	10.0 (10.8)	12.5 (123.9)	33.4 (331.1)	3.0 (16.8)	5.8 (29.3)	5.1 (3.3)	8.5 (5.7)	3.8 (6.3)	2.6 (4.6)
bluefish									1.1 (1.4)	2.9 (4.1)	1.9 (4.4)	4.2 (9.8)
silver hake	2.3 (6.0)	2.9 (7.6)										
seahorse									0.6 (0.9)	0.2 (0.3)		
margined snake eel											1.9 (4.4)	7.1 (16.2)
Serranidae											3.8 (5.9)	4.6 (8.9)
Sparidae											1.9 (4.2)	6.2 (13.6)
Clupeidae							0.4 (3.1)	1.8 (12.6)	0.6 (0.9)	2.8 (4.7)		
Unidentified fish	16.0 (10.8)		11.6 (5.6)		12.5 (97.5)		7.0 (27.2)		16.6 (5.6)		14.1 (9.3)	
Invertebrates												
long-finned squid	10.5 (7.4)	14.8 (16.0)	1.6 (2.0)	1.1 (1.7)			5.7 (25.6)	3.2 (13.0)	1.7 (1.6)	7.9 (9.6)	1.9 (9.3)	4.2 (7.2)
crab[1]	2.0 (3.9)	4.0 (10.6)									3.8 (6.6)	0.6 (1.0)
amphipods	31.2 (20.2)	11.1 (10.4)					3.0 (14.1)	1.9 (9.2)				
unidentified shrimp crustacean larvae[2]			1.6 (2.2)	0.9 (1.7)					2.2 (1.7)	0.6 (1.0)		
polychaete	1.4 (3.0)	<0.1 (0.3)	0.8 (1.4)	0.3 (0.5)								
channeled whelk									9.0 (8.1)	11.6 (9.3)		
Total stomachs analyzed	182		129		8		79		177		51	
Number containing prey	157		81		5		57		140		39	
Mean FL (mm, SE)	208 (2)		243 (4)		263 (14)		212 (2)		244 (3)		261 (3)	
FL range (mm)	161–270		161–300		200–300		180–300		160–300		200–300	
Mean wt (g, SE)	124.9 (3.5)		219.2 (9.4)		247.4 (33.8)		129.7 (5.0)		203.6 (7.3)		247.5 (9.3)	
Wt range (g)	51–256		49–398		116–343		75–342		50–371		105–365	

[1] Lady crab, mole crab, unidentified crab.
[2] Lady crab, *Penaeus* spp., unidentified crustacean larvae.

Table 3

Stomach contents of summer-spawned bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %*W*=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994						1995					
	Southern New England		Chesapeake–Delaware		South of Chesapeake		Southern New England		Chesapeake–Delaware		South of Chesapeake	
Prey type	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Fish												
bay anchovy	80.1 (30.1)	90.9 (7.1)	33.7 (72.5)	71.7 (70.0)	16.7 (250.0)	50.0 (750.0)	23.6 (113.5)	34.3 (145.7)	45.1 (32.3)	86.6 (33.5)	23.5 (72.6)	76.5 (253.4)
Atlantic silverside	0.3 (1.2)	0.9 (3.7)										
searobin larvae			8.1 (60.8)	0.8 (3.1)								
Unidentified fish	15.3 (9.9)		14.8 (23.1)		33.3 (0.0)		27.9 (33.1)		50.4 (32.5)		41.2 (63.6)	
Invertebrates												
long-finned squid	0.6 (2.1)	<0.1	3.6 (33.7)	1.4 (6.6)			1.7 (10.4)	1.7 (10.4)				
crab[1]	0.5 (2.0)	1.0 (3.7)										
crab larvae[2]	1.1 (4.0)	<0.1	12.4 (24.3)	3.7 (7.4)								
amphipods	19.1 (11.0)	7.0 (5.3)	3.9 (8.5)	0.8 (1.8)								
mysids			23.6 (139.6)	20.4 (71.2)	16.7 (250.0)	12.2 (182.4)						
copepods					16.7 (250.0)	8.7 (131.8)	44.7(149.1)	48.5 (186.0)				
sand shrimp	0.1 (0.5)	<0.1										
polychaete	<0.1	<0.1			16.7 (250.0)	29.1 (435.8)						
isopod			1.4 (10.1)	1.0 (3.6)								
Total stomachs	200		66		6		61		53		17	
Number containing prey	165		56		4		52		38		11	
Mean FL (mm, SE)	135 (1)		133 (2)		96 (12)		70 (3)		90 (3)		77 (3)	
FL range (mm)	86–160		107–160		37–120		20–140		60–150		60–100	
Mean wt (g, SE)	31.2 (0.9)		29.2 (1.4)		11.3 (2.4)		4.8 (0.6)		10.9 (1.3)		5.0 (0.6)	
Wt range (g)	6–64		10–53		1–19		0.1–32		2–45		3–12	

[1] Mole crab and unidentified crab.
[2] Lady crab, blue crab and fiddler crab.

Table 4

Stomach contents of adult bluefish captured during the 1994 and 1995 National Marine Fisheries Service autumn bottom trawl survey. %*F*=proportion of bluefish stomachs containing a prey (±SE), %*W*=proportional contribution of identifiable prey to bluefish diet by weight (±SE). Note that proportions from cluster estimators do not add up to 100%. SE=standard error from variance estimators for cluster samples.

	1994				1995			
	Georges Bank		Hatteras–Montauk		Georges Bank		Hatteras–Montauk	
Prey type	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*	%*F*	%*W*
Fish								
bay anchovy			25.9 (51.8)	21.4 (47.7)			36.4 (34.6)	34.9 (44.9)
butterfish	27.8 (28.7)	18.6 (23.6)	9.4 (18.5)	12.7 (30.0)	7.6 (38.0)	16.3 (80.2)	5.6 (12.0)	9.0 (20.8)
round herring	3.7 (9.2)	2.2 (5.6)	6.8 (17.4)	26.5 (87.9)	7.6 (41.8)	10.8 (66.4)	3.7 (9.1)	3.6 (11.1)
striped anchovy			1.8 (7.9)	1.7 (7.7)	2.2 (21.4)	5.2 (51.5)	3.9 (12.3)	5.0 (13.2)
bluefish							0.5 (2.3)	0.9 (4.7)
planehead filefish							0.5 (2.3)	0.2 (1.4)
Northern puffer							0.9 (4.6)	0.8 (4.0)
Northern pipefish	1.9 (7.5)	0.6 (2.5)						
searobin			1.8 (6.2)	2.1 (8.8)	2.2 (21.9)	6.5 (65.3)	0.5 (2.3)	1.1 (5.4)
weakfish			2.2 (7.8)	3.0 (12.9)			0.5 (2.3)	0.1 (0.6)
spot								
sand lance							0.5 (2.3)	0.9 (4.7)
scup			2.7 (7.9)	1.5 (4.5)			0.5 (2.3)	0.1 (0.5)
Atlantic herring	7.4 (17.6)	11.3 (23.7)			10.9 (54.7)	17.6 (85.0)	0.5 (2.3)	0.1 (0.7)
Atlantic mackerel			0.9 (4.2)	0.9 (4.3)				
fawn cusk eel							0.5 (2.3)	<0.1
conger eel							0.5 (2.3)	1.5 (7.2)
ocean pout			0.9 (4.3)	0.9 (4.3)	2.2 (22.9)	2.2 (22.9)	0.5 (2.3)	0.3 (1.7)
fourbead rockling	1.9 (7.5)	1.7 (7.0)						
American plaice	1.9 (7.6)	0.8 (3.5)						
windowpane	5.6 (22.0)	5.6 (22.0)			2.2 (21.9)	5.2 (51.9)		
silver hake	1.9 (7.6)	1.0 (4.2)			4.3 (39.5)	8.4 (76.3)		
white hake	1.9 (7.5)	2.4 (9.9)						
red hake	1.9 (6.7)	2.1 (7.6)					1.9 (7.4)	1.7 (6.7)
haddock	1.9 (7.5)	2.0 (8.0)			2.2 (21.9)	0.8 (8.4)		
Atlantic cod	3.7 (10.3)	6.7 (20.6)						
Gadidae	1.9 (7.6)	1.9 (7.6)						
Unidentified fish	29.6 (32.1)		26.1 (43.1)		30.4 (70.7)		21.9 (23.4)	
Invertebrates								
long-finned squid	29.6 (25.6)	23.7 (29.4)	11.6 (22.1)	5.2 (11.3)	15.2 (53.6)	18.1 (89.2)	7.7 (11.8)	10.9 (27.0)
boreal squid	11.1 (23.7)	8.4 (19.4)						
lady crab	3.7 (15.0)	1.2 (4.7)						
cancer crab	1.9 (7.2)	0.6 (2.5)						
unidentified crab			0.9 (4.1)	0.8 (3.5)	2.7 (22.9)	0.4 (3.7)	1.3 (4.6)	0.1 (0.4)
amphipods			0.9 (4.3)	0.9 (4.3)				
unidentified shrimp					4.3 (30.8)	2.0 (19.1)		
polychaete							2.0 (6.8)	4.9 (16.7)
channeled whelk							9.0 (33.2)	13.0 (41.9)
Total stomachs analyzed	50		65		44		116	
Number containing prey	45		45		32		84	
Mean FL (mm, SE)	653 (10)		451 (18)		607 (17)		391 (11)	
FL range (mm)	420–780		310–780		380–750		310–730	
Mean wt (g, SE)	3837 (151)		1546 (170)		3082 (225)		991 (106)	
Wt range (g)	1209–6151		368–5965		692–6530		319–4570	

the prey to predator FL ratios for summer-spawned bluefish were higher in 1995 than they were in 1994 (Fig. 3). Summer-spawned bluefish consumed relatively larger bay anchovies in 1995 than in 1994; this was due to both the smaller size of the summer-spawned cohort in 1995 and the larger bay anchovy prey. A linear function describing bluefish capture success as a function of prey length to bluefish length ratio from Scharf et al. (1998b) is also plotted in Figure 3 (capture success data for bluefish feeding on Atlantic silversides). The distribution of ratios for both spring- and summer-spawned bluefish in 1994 and spring-spawned bluefish in 1995 are values for which bluefish have relatively high capture success;

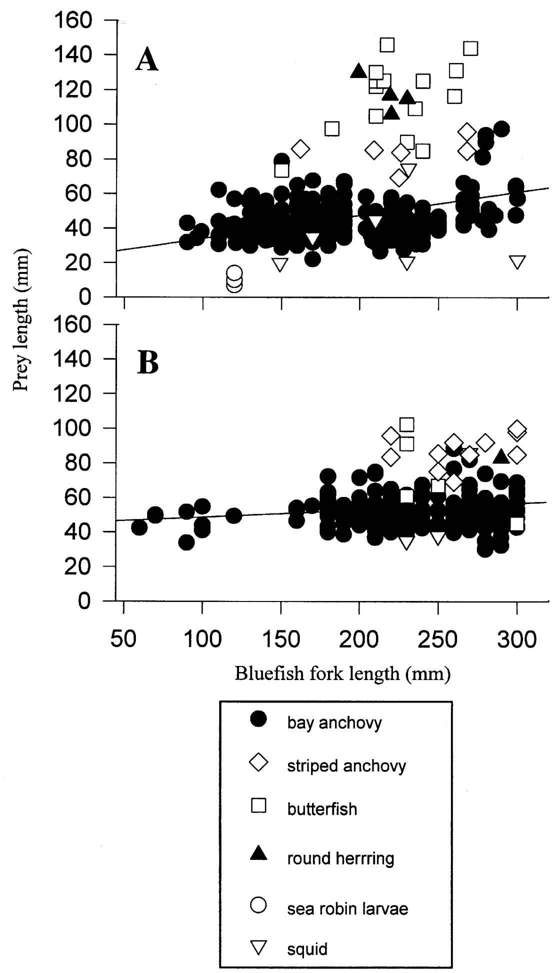

Figure 1

Prey total length (mantle length for squid) versus YOY bluefish fork length in (**A**) 1994 (*prey TL*=0.134 × *bluefish FL*+20.826, r^2=0.10, P<0.0001) and (**B**) 1995 (*prey* TL=0.041 × *bluefish FL*+44.538, r^2=0.02, P=0.027).

Table 5

The total number of prey (n) found either fresh or digested (fresh=no sign of digestion; digested=prey skinless to being only identifiable by skeleton or shape) in spring- and summer-spawned young-of-the-year bluefish stomachs and the percentage contribution of bay anchovy, striped anchovy, butterfish, and squid for these categories. Bluefish were captured during 1994 and 1995 National Marine Fisheries Service autumn bottom trawl surveys. Bluefish were collected from three geographical locations of the Mid-Atlantic Bight continental shelf (SNE=Southern New England, C–D=Chesapeake Bay to Delaware Bay, and SOC=South of Chesapeake Bay, after Munch 1997).

		Spring-spawned		Summer-spawned	
Location	Prey type	No. fresh (%)	No. digested (%)	No. fresh (%)	No. digested (%)
1994					
SNE	*n*	19	51	0	31
	bay anchovy	89.5	56.9		
	striped anchovy	5.3	7.8		
	butterfish	5.3	33.3		
	squid	0	2.0		
C–D	*n*	46	107	36	104
	bay anchovy	89.1	76.6	100	97.1
	striped anchovy	2.2	2.8	0	0
	butterfish	2.2	7.5	0	1.0
	squid	6.5	13.1	0	2.0
1995					
SNE	*n*	30	19	0	57
	bay anchovy	73.3	68.4		
	striped anchovy	6.7	10.5		
	butterfish	3.3	15.8		
	squid	16.7	5.3		
C–D	*n*	21	82	0	36
	bay anchovy	81.0	82.8		
	striped anchovy	19.0	13.8		
	butterfish	0	0		
	squid	0	3.4		

Table 6

Prey selectivity (Chesson's α, see text for calculations) in YOY bluefish collected on the U.S. east coast continental shelf in the autumn of 1994 and 1995. Values of α =1/m (where "m" is the number of prey categories) represent random feeding, whereas values of α > 1/m or α < 1/m represent "selection" and "avoidance" of prey, respectively. Values significantly different from 1/m (t-test, P<0.05) are indicated by a (+) for "selection" or (–) for "avoidance".

Prey type	1994 (1/m=0.25)	1995 (1/m=0.33)
Bay anchovy	0.69 (+)	0.80 (+)
Butterfish	0.12 (–)	0.03 (–)
Squid	0.09 (–)	0.18 (–)
Other	0.11 (–)	—

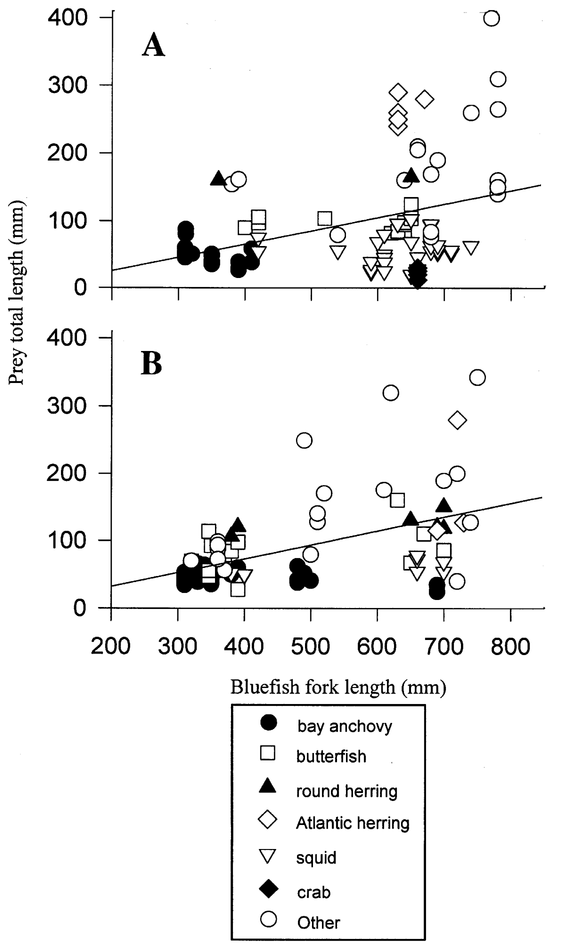

Figure 2

Prey total length (mantle length for squid) versus adult bluefish fork length in (**A**) 1994 (*prey TL*=0.199 ˙ *bluefish FL*–14.413, r^2=0.15, P<0.001) and (**B**) 1995 (*prey TL*=0.205 × *bluefish FL*–9.047, r^2=0.28, P<0.0001). "Other" prey include searobin, red hake, silver hake, unidentified gadid, scup, windowpane, haddock, Northern puffer, conger eel, cusk eel, sand lance, striped anchovy, spot, weakfish, Atlantic mackerel, fourbeard rockling, and ocean pout.

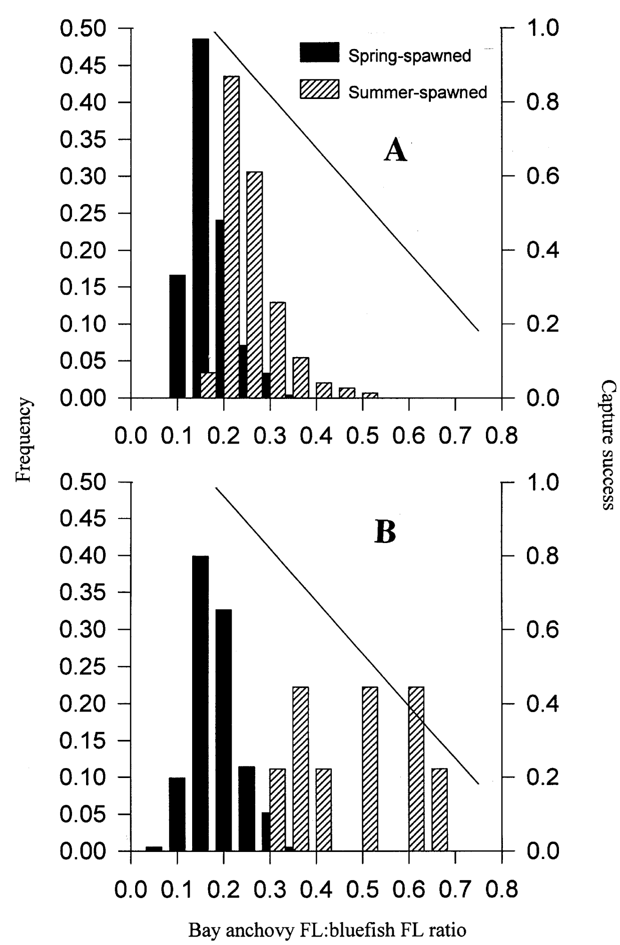

Figure 3

Bay anchovy FL to bluefish FL ratios for both spring-and summer-spawned bluefish in (**A**) 1994 and (**B**) 1995. Regression line for capture success versus prey length to predator length ratio from Scharf et al. (1998b).

however, the prey length to predator length ratios of summer-spawned bluefish in 1995 are values at which bluefish have relatively lower capture success (Fig. 3).

In 1994, there were four stations that had n>15 bay anchovy measurements for both spring and summer-spawned bluefish (n=16–20 bay anchovy measurements for summer- and n=22–39 for spring-spawned). Both spring- and summer-spawned YOY bluefish showed significant selection for relatively small bay anchovies (spring-spawned α=0.57 vs. 0.25, t=2.99, df=38, P=0.005; summer-spawned α=0.65 vs. 0.33, t=2.61, df=27, P=0.011) and avoidance of relatively larger anchovies in 1994 (spring-spawned α=0.02 vs. 0.25, t=3.83, df=38, P<0.001; summer-spawned α=0.07 vs. 0.33, t=2.86, df=27, P=0.006) (Table 7). Intermediate-size bay anchovy were taken in proportion to their abundance in 1994 (t-test; P>0.05 for all α's). In the 1995 analysis, three stations had n>15 individual bay anchovy lengths (n=17–32); an analysis of size-selective feeding of summer-spawned fish in 1995 was not possible owing to small sample size. Spring-spawned bluefish in 1995 showed no significant size selectivity (t-test; P>0.05 for all α's); however, the trend of increasing selectivity with decreasing prey sizes was present (Table 7).

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Both spring- and summer-spawned YOY bluefish gut fullness values varied over the diel cycle in the different geographical regions of the MAB shelf. Peaks in gut fullness generally occurred at dawn, dusk, and diurnal time periods, whereas gut fullness values during nighttime collections were low in relation to diurnal gut fullness values (Fig. 4).

Table 7

Size-selectivity (Chesson's α, see text for calculations) for bay anchovy in YOY bluefish collected on the U.S. east coast continental shelf in the autumn of 1994 and 1995. Values of $\alpha = 1/m$ (where "m" is the number of prey categories) represent random feeding while values of $\alpha > 1/m$ or $\alpha < 1/m$ represent "selection" and "avoidance" of prey, respectively. Values significantly different from $1/m$ (t-test, $P<0.05$) are indicated by a (+) for "selection" or (–) for "avoidance".

	1994		1995	
Bay anchovy size (mm)	Spring-spawned ($1/m$=0.25)	Summer-spawned ($1/m$=0.33)	Spring-spawned ($1/m$=0.33)	Summer-spawned
25–34	0.57 (+)	0.65 (+)	—	—
35–44	0.27	0.28	0.44	—
45–54	0.14	0.07 (–)	0.37	—
55–64	0.02 (–)	—	0.19	—

Table 8

Daily ration g/(g · d) · 100 ±SE) and weighted mean temperature at which spring- and summer-spawned YOY bluefish were collected during National Marine Fisheries Service autumn bottom trawl survey in 1994 and 1995. Bluefish juveniles were collected from three geographical areas of the Middle Atlantic Bight continental shelf (SNE=Southern New England, C–D=Chesapeake Bay to Delaware Bay, and SOC= South of Chesapeake Bay, after Munch 1997). Daily ration was calculated using the Eggers' (1979) approach (see text). NA=not applicable due to low number of samples for diel series.

	Summer-spawned			Spring-spawned		
Year and geographical region	n	Temp. °C	Daily ration g/(g · d) · 100 (SE)	n	Temp. °C	Daily ration g/(g · d) · 100 (SE)
1994						
SNE	200	18.9	8.5 (3.1)	182	18.8	6.6 (2.5)
C–D			NA	129	20.0	4.8 (1.9)
1995						
SNE	61	20.7	12.4 (3.9)	79	19.9	3.7 (1.4)
C–D			NA	177	23.7	9.0 (2.9)
SOC			NA	51	24.3	8.1 (2.8)

In order to use the gut fullness data to estimate bluefish daily ration, gastric evacuation rate (GER) estimates were needed for bluefish at shelf water temperatures. The exponential GER model adequately described the evacuation of bay anchovy at 15°C from our laboratory experiment (r^2=0.87, n=22, P<0.001; Fig. 5). Incorporation of the 15°C GER estimate (R_e=0.102) into the evacuation rate vs. temperature function of Buckel and Conover (1996) gave the following equation: $R_e = 0.017\ e^{0.099\ Temp}$, n=16, r^2=0.82 (Fig. 5). The largest deviation from the equation describing R_e and temperature is from the single estimate of GER at 15°C. This is likely not due to differences in experimental protocol; the 15°C GER experiment was conducted identically to the experiments described in Buckel and Conover (1996). The larger deviation may result from there being only one estimate of GER at 15°C whereas each GER estimate for the higher temperatures represents a mean of four estimates (Fig. 5). Estimates of GER from this equation were used to estimate bluefish daily ration.

The daily ration of summer-spawned bluefish in the SNE region in 1994 and 1995 was 8.5 and 12.4 g/(g · d) · 100, respectively (Table 8). Spring-spawned bluefish daily ration estimates ranged from 4.8 to 6.6 g·/(g · d) · 100 for the SNE and C–D region in 1994 and 3.7–9.0 g/(g · d) · 100 in the SNE, C–D, and SOC regions of the MAB in 1995. There was insufficient diel records to calculate feeding rates for the SOC region in 1994 or the remaining region and cohort combinations (Table 8).

The VPA estimates of YOY bluefish abundance in 1994 and 1995 were 24 million and 14 million, respectively. These estimations were partitioned into spring- and summer-spawned bluefish on the basis of relative abundances of these cohorts for each year (Table 9). It was estimated that spring-spawned bluefish consumed from 70 to 96 million bay anchovy per day in 1994 and from 68 to 170 million bay anchovy per day in 1995 during the September period of their migration (Table 9; the range is based on the lowest to highest daily ration estimate). Summer-spawned bluefish consumed 130 million bay anchovy per day in 1994 and 5 million per day in 1995 (there is no range for summer-spawned bluefish because there was only one estimate of summer-spawned daily ration for each year).

Discussion

Dietary analyses

Bay anchovy was the predominant fish prey of both spring- and summer-spawned YOY bluefish in both 1994 and 1995. A previous gut contents analysis of NEFSC-NMFS bottom-trawl-collected bluefish (south of Cape Hatteras to Georges Bank) was conducted by Morris[2] from 1978 to 1980. Bay and striped anchovy dominated the diet of the 292 YOY bluefish (110–300 mm) that he examined; butterfish and squid were also important prey. The migration of YOY bluefish onto the shelf is thought to be controlled by declines in estuarine temperature and day length (Olla and Studholme, 1972). Schools of bay anchovy migrate out onto the shelf beginning in September and are concentrated off New York, New Jersey, and the Delmarva peninsula in the autumn (Vouglitois et al., 1987) in a similar pattern to that of concentrations of YOY bluefish (Munch and Conover, in press). The timing of bluefish estuarine emigration may be linked with bay anchovy movements offshore.

Invertebrates were an important part of the diet of YOY bluefish in several regions. In 1994, there was a large amount of gammarid amphipods in the diets of spring- and summer-spawned bluefish in the SNE region. In addition, mysids contributed to the diet of summer-spawned fish in the C–D and SOC regions of the continental shelf in 1994. Diets of juvenile bluefish in estuaries are usually dominated by fish prey, but at times invertebrates, such as shrimp, are a major prey (Friedland et al., 1988; Juanes and Conover, 1995). This pattern is likely a function of prey availability and prey size. Bluefish prey selectivity was related to prey abundance in the Hudson River (Buckel et al., 1999). Bay anchovy schools and invertebrate swarms are likely to have patchy distributions on the shelf; the diet of bluefish at any location will be dependent on local prey availability.

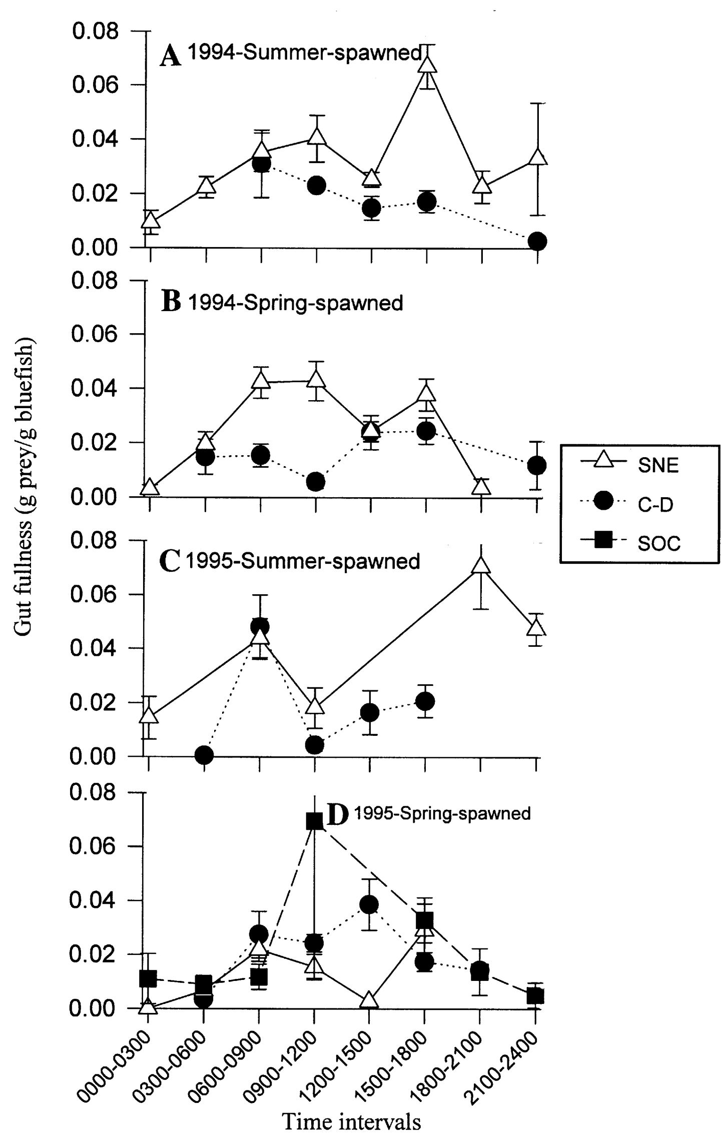

Figure 4

Gut fullness (g prey/g bluefish) for spring-and summer-spawned bluefish collected from SNE, C–D, and SOC regions of the continental shelf in 1994 (**A, B**) and 1995 (**C, D**) versus time interval of collection. Sunrise fell between the 0600 and 0900 time interval and sunset fell between the 1800 and 2100 time interval. Error bars are ±1 SE.

Channeled whelk has not been reported previously as a prey of bluefish. The foot of channeled whelk with the operculum still attached was found in several bluefish in the C–D region in 1995. This may have been due to opportunistic feeding on whelk that had shell damage related to some fishery activity. However, whelk occurred in bluefish gut contents over a fairly broad geographic area and not at a single

[2] Morris, T. L. 1984. Food of bluefish. Woods Hole Laboratory Reference Document 84-22, Woods Hole Laboratory, Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543 MED/NEFC 84-26, 13 p.

station (Cape May, NJ, to Lewes, DE). Bluefish may attack whelk when the foot is extended out of the shell and may sever that section alone. This would explain the presence of only the foot portion of the animal.

Summer-spawned bluefish diet was dominated by copepods in the SNE region in 1995. Marks and Conover (1993) found that the diet of summer-spawned bluefish collected in surface waters of the New York Bight was dominated by copepods. Summer-spawned bluefish size ranged from 17 to 64 mm TL in their samples and ranged from 20 to 140 mm FL in our samples from the SNE region in 1995. The large presence of copepods in this cohort's diet compared with other regions on the shelf in 1995 and with summer-spawned bluefish diets in 1994 is most likely a result of their small size (see "Prey-size analysis" section).

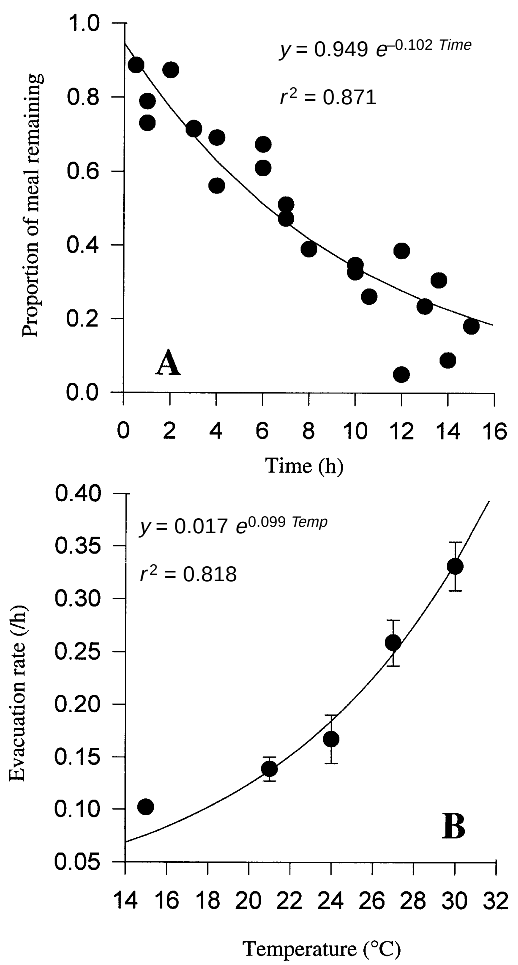

Figure 5

(**A**) Proportion of meal remaining vs. time for bluefish fed a single bay anchovy meal at 15°C (*proportion of meal remaining* = 0.949 $e^{-0.102 \cdot time}$), and (**B**) YOY bluefish evacuation rate versus temperature (data for temperatures of 21 to 30°C are from Buckel and Conover, 1996; *evacuation rate*=0.017$e^{0.099 \cdot temp}$). Error bars are ±1 SE.

McBride et al. (1995) found that age-0, spring-spawned bluefish abundance appeared to be regulated by density-dependent (compensatory) losses in Narragansett Bay, Rhode Island. One potential density-dependent mechanism is cannibalism. There were very few cases of bluefish cannibalism on the continental shelf; spring-spawned bluefish cannibalism of summer-spawned bluefish occurred in the C–D and SOC region in 1995, a year when individuals in the summer-spawned cohort were relatively small in size. However, past diet studies of bluefish have found a higher incidence of cannibalism, particularly off the Carolinas (Lassiter, 1962; Naughton and Saloman, 1984). Bluefish abundance is currently low (NEFSC[1]) and cannibalism may be frequent only when bluefish are more abundant or other prey abundances are low.

We found slight regional differences in the diet of adult bluefish; diets of bluefish in 1994 and 1995 were similar to those found in past studies. In the Georges Bank region in 1994 and 1995, the dominant prey of adult bluefish were butterfish, long-finned squid, boreal squid, round herring, and Atlantic herring. Bay anchovy, butterfish, round herring, and long-finned squid were the dominant prey of adult bluefish collected from Cape Hatteras, NC, to Montauk Point, NY. Morris (1984) found that long-finned squid, boreal squid, butterfish, round herring, and bay and striped anchovies dominated the diet of adult bluefish (n=226) captured in NEFSC-NMFS bottom trawls (1978–80, spring, summer, autumn combined) from these same regions. Richards (1976) examined the diet of adult bluefish angled near Long Island, NY, in the summer and autumn. The diet of bluefish in this area included bay anchovy, long-finned squid, menhaden (*Brevoortia tyrannus*), butterfish, and silver hake (n=66, FL range: 490–750 mm).

There were very few bluefish for our diet analysis from south of Cape Hatteras; however, Naughton and Saloman (1984) collected 729 bluefish from this region using hook and line during 1977–81 and reported the diet of bluefish in this area as dominated by Scianidae, Clupeidae, Mugilidae, Labridae, and Atherinidae. Scianids, clupeids, engraulids, sparids, atherinids, and squids were important prey in Lassiter's (1962) study of over 900 bluefish captured by beach haul seining or hook and line August–December 1960 and March, June–August 1961. The diet of bluefish (n=42) collected south of Cape Hatteras in the autumn by bottom trawling was dominated by squid, butterfish, and striped anchovy (Morris, 1984).

There were several commercially important groundfish species in the diet of adult bluefish on Georges

Table 9

Estimated spring- and summer-spawned bluefish daily consumption of bay anchovy on the U.S. east coast continental shelf in the autumn of 1994 and 1995. We used mean size of bluefish, daily ration estimates, proportion of bay anchovy in the diet, and mean bay anchovy size that were measured for each cohort in this study. Estimates of the numbers of YOY bluefish for 1994 and 1995 are from virtual population analysis (VPA) performed by NEFSC (see Footnote 1 in main text); we partitioned the numbers between spring- and summer- spawned bluefish using relative abundances of each cohort from the NEFSC-NMFS autumn groundfish survey cruises.

Cohort	Bluefish numbers	Biomass of bluefish cohort (10^6 kg)	Amount of bay anchovy consumed daily (kg/d; low ration)	Amount of bay anchovy consumed daily (kg/d; high ration)	Number of bay anchovy consumed daily (no./d; low)	Number of bay anchovy consumed daily (no./d; high)
1994						
Total	24×10^6					
Spring-spawned	7.2×10^6	1.20	25,000	34,000	70×10^6	96×10^6
Summer-spawned	16.8×10^6	0.50	35,000		130×10^6	
1995						
Total	14×10^6					
Spring-spawned	9.8×10^6	1.86	45,000	110,000	68×10^6	170×10^6
Summer-spawned	4.2×10^6	0.032	2,000		5×10^6	

Bank in 1994. Morris (1984) also found gadids in stomach contents of adult bluefish. This finding is of interest because there is a large effort to understand the factors that regulate fish populations on Georges Bank (Peterson and Powell, 1991). The biomass of skates (Rajidae) and dogfish sharks (Squalidae) has increased in this area of the shelf and in some locations makes up the largest part of fish biomass (Overholtz et al., 1991). However, cartilaginous fishes were not found in the diet of adult bluefish. Bluefish predation will have no direct effect in regulating the population sizes of these fishes. However, bluefish may play a role in the recovery of commercially important groundfish species on Georges Bank. Because bluefish distribution is closely linked with temperature (Munch, 1997), an increased warming trend may allow a larger proportion of the bluefish population to extend northward onto Georges Bank. Ware and McFarlane (1995) found that Pacific hake (*Merluccius productus*) biomass and hake predation on herring (*Clupea harengus*) increased with recent increases in temperature off the west coast of Vancouver Island. They concluded that this recent increased predation explains recent declines in the herring stock. The importance of bluefish predation to recovery of groundfish species warrants further investigation.

Net feeding

Postcapture net-feeding can bias diet indices and gut fullness level estimates. Net feeding is known to occur in a variety of Pacific midwater fish (Lancraft and Robison, 1980). There was little evidence that net feeding biased our estimates of bluefish diet given the similarities between percent of fresh versus digested prey; however, any net feeding would lead to biased estimates of gut fullness level and inflated estimates of consumption rate. Lancraft and Robison (1980) found that larger fish were more likely to ingest artificial prey. The larger spring-spawned cohort had more fresh prey in its diet than the smaller summer-spawned bluefish which may be a result of a higher incidence of net feeding by this cohort.

Prey-type selectivity

Spring-spawned YOY bluefish selected for bay anchovy over all other prey types in both 1994 and 1995. Butterfish, squid, and "other" potential prey were avoided. This is most likely due to both the relative abundances of these prey as well as interspecific size differences. Bay anchovy tended to be the smallest prey available; the only smaller prey of spring-spawned bluefish were invertebrates such as amphipods (ranging from 3 to 15 mm TL). In the Hudson River estuary, the prey with the highest relative abundance were selected for, whereas the prey with the lowest abundance were selected against (Buckel et al., 1999). A second possible explanation for the strong selection of bay anchovy could be sampling bias. Chesson's (1978) index assumes that prey abundance is large in relation to the amount consumed (likely true for the shelf) and that the catchability or availability of the different prey groups to the trawl are the same. We do not have estimates of the catchability for each of the prey species used in this analysis. Our results would be biased if these differ. For example, catchabilities for squid and butterfish may be higher than that of bay anchovy and may explain the strong selection for bay anchovy.

Prey-size analysis

Although there was a weak positive linear relationship between ingested bluefish prey sizes and bluefish length, it was mainly due to prey other than bay anchovy. The slope of the regression of bay anchovy length on bluefish length alone was 50% and 75% less than the slope of the regression of all prey on bluefish length in 1994 and 1995, respectively. The sizes of bay anchovy taken by the smallest YOY bluefish were similar to those taken by the largest YOY bluefish, especially in 1995. Juanes and Conover (1995) and Scharf et al. (1997) saw a similar relation for bluefish feeding on piscine prey in New York estuaries.

Most ratios of bay anchovy length to bluefish length were similar to those seen in past estuarine work (Juanes and Conover, 1995; Scharf et al., 1997). Juanes and Conover (1995) hypothesized that the shift in spring-spawned bluefish diet from Atlantic silversides to bay anchovy in Great South Bay, NY, was a result of the higher capture success on the relatively smaller bay anchovy. The capture success of bluefish feeding on bay anchovy is likely higher than that of bluefish feeding on the relatively larger butterfish and squid. Our size selectivity analysis shows that even within bay anchovy there is preference for smaller sizes (Table 7).

The relatively small size of the 1995 SNE summer-spawned bluefish (1994 mean FL=135 vs. 1995 mean FL=70) influenced the extent of piscivorous feeding in this cohort. The capture success was plotted for bluefish feeding at different ratios of prey length to bluefish length from laboratory work on Atlantic silversides (Scharf et al., 1998b). Summer-spawned, small-size bluefish in 1995 would have experienced greatly reduced capture success when feeding on bay anchovy.

Feeding chronology, daily ration estimates, and impacts on bay anchovy

Bluefish appear to feed mainly during the day or at dawn or dusk. This was also noted in past work on juvenile bluefish in estuarine environments (Juanes and Conover, 1994; Buckel and Conover, 1997). In the Hudson River estuary, the diel feeding patterns of bluefish appeared to be linked to their diel movement patterns (Buckel and Conover, 1997). This may also be the case for shelf bluefish; Munch (1997) found that the catch per unit of effort (CPUE) of YOY bluefish in NEFSC-NMFS bottom trawl collections was significantly higher in diurnal than in nocturnal collections. Munch (1997) hypothesized that this diel movement to near bottom habitat (which makes them available to bottom trawling) during the day may be in response to the vertical migration of bay anchovy. Bay anchovy exhibit diel vertical migration and are significantly more available to bottom trawl sampling during the day compared with at night (Vouglitois et al., 1987).

Our daily ration estimates for spring-spawned bluefish (3.7–9.0 g /(g · d) · 100) are similar to past estimates of daily ration for September. Measurements of bluefish maximum daily ration from a laboratory mesocosm experiment (18.5–23°C) for mid-September were ~10 g/(g · d) · 100 (Buckel et al., 1995). Field estimates of bluefish daily ration in the Hudson River estuary were 10.1–12.6 in mid to late August and 7.3 in mid-September (Buckel and Conover, 1997). Mean spring-spawned bluefish size was larger and mean temperatures were slightly lower on the shelf compared with bluefish sizes and temperatures in the above laboratory and field experiments. This finding may explain our slightly lower daily ration estimates for spring-spawned bluefish on the shelf in the autumn. Hartman and Brandt's (1995b) laboratory estimates of maximum daily ration (C_{max}) are also similar to our field estimates of spring-spawned bluefish daily ration estimates on the shelf. From their experiments, estimates of C_{max} for bluefish ranging from 100 to 350 g at 20°C (temperature at which bluefish were found on the shelf) are 7.5 to 12.5 g/(g · d) · 100.

Owing to low sample sizes and an inadequate diel record, the daily ration of summer-spawned bluefish was determined only in the SNE region in 1994 and 1995. The daily ration estimate in 1994 was lower at 8.5 g/(g · d) · 100 than the estimate of 12.5 g/(g · d) · 100 in 1995. The mean size of fish in this cohort varied substantially between 1994 (31.2 g) and 1995 (4.8 g). The size and the temperature difference (1994= 18.9°C vs. 1995=20.7°C) may explain the differences in daily ration. The daily ration estimates of these fish are slightly lower than would be predicted from laboratory estimates of maximum daily ration of bluefish at these sizes and temperatures (Buckel et al., 1995; Hartman and Brandt, 1995b); however, both shelf estimates fall into the 95% confidence interval of the summer-spawned bluefish daily ration estimate (19–20 September 1992) in the Hudson River (Buckel and Conover, 1997).

For our estimates of bay anchovy consumption by the YOY bluefish population during their September migration, it was assumed that the entire YOY bluefish population occurred on the shelf from Cape Hatteras, NC, to Montauk, NY. Support for this comes from sharp declines in YOY bluefish CPUE in early autumn estuarine beach seine surveys (Nyman and Conover, 1988; McBride and Conover, 1991) and an abrupt decline in average bluefish size on the shelf during early autumn (Munch, 1997). Our estimates show that given a 30-d migration period in September, the population of YOY bluefish could consume from 6.0 to 6.8 billion bay anchovies in 1994 and from 2.2 to 5.3 billion in 1995.

Summer-spawned bluefish consumed two orders of magnitude less bay anchovy per day in 1995 (5 million) compared with 1994 (130 million). This was partly due to the low abundance of this cohort in 1995 (4.2 million) compared with that in 1994 (16.8 million). The amount of bay anchovy in the diet of summer-spawned bluefish (80% in 1994 vs. 60% in 1995) and the absolute size of bay anchovy prey taken by the two cohorts (0.27 g in 1994 vs. 0.54 g in 1995) explained the remainder. Interannual variation in the size structure of the summer-spawned cohort and their predominant piscine prey (bay anchovy) can have dramatic effects on the predatory impact of this bluefish cohort on bay anchovy populations. Although the importance of size-dependent processes in freshwater fish predator-prey interactions is well described (Kerfoot and Sih, 1987; Ebenman and Persson, 1988), their importance for piscivore-prey interactions in marine systems is just beginning to be recognized (Juanes and Conover, 1995).

There are no estimates of coastwide bay anchovy abundance for 1994 and 1995; hence, no direct examination of the impact of this estimated bay anchovy loss to the continental shelf bay anchovy population was made. There are bay anchovy biomass density estimates for estuaries on the east coast of the U.S. Vouglitois et al. (1987) estimated that the bay anchovy standing crop in Barnegat Bay, NJ, ranged from 830 to 4830 kg/km^2. In Chesapeake Bay, Luo and Brandt's (1993) bay anchovy biomass density estimate for September was ~8000 kg/km^2. We calculated the standing stock of bay anchovy on the shelf by multiplying the estimated ranges of estuarine bay anchovy densities by the area (km^2) in which bluefish were collected on the shelf. This area (km^2) estimate was calculated by summing all the NEFSC stratum areas in which YOY bluefish were captured in the autumn groundfish survey in 1994 and 1995.

During the month of September, bluefish (spring- and summer-spawned combined) consumption of bay anchovy could account from ~2 to 22% of bay anchovy standing stock in 1994 and from 1% to 24% of the bay anchovy standing stock in 1995. Bay anchovy are probably less dense on the shelf than in the estuary and our estimates of bluefish impact may be underestimates. However, the latest bluefish stock assessment (Mid-Atlantic Fishery Management Council[3]) has found that bluefish abundance may be lower than that reported in the VPA (NEFSC[1]). This could mean that our impact estimates are overestimates. At the upper range of the impact estimates, it is clear that the YOY bluefish population on the continental shelf consume a significant quantity of bay anchovy biomass. The effect of this loss on the population dynamics of bay anchovy or the fish community on the continental shelf is unknown.

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