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 (*Morone saxatilis*)

Jeffrey A. Buckel, David O. Conover, Nancy D. Steinberg, and Kim A. McKown

Abstract: We measured bluefish (*Pomatomus saltatrix*) weights, densities, and prey sizes during the summers of 1992 and 1993 and diets over a 4-year period (1990–1993) in the Hudson River estuary. This information was used to estimate the loss of young-of-the-year (YOY) striped bass (*Morone saxatilis*) resulting from YOY bluefish predation. We then compared this predation mortality with the total loss of striped bass in the system. Data from sampling surveys conducted since the mid-1970's were used to examine relationships between bluefish abundance and striped bass recruitment levels. YOY striped bass, bay anchovy (*Anchoa mitchilli*), Atlantic silverside (*Menidia menidia*), and *Alosa* spp. dominated YOY bluefish diets. There were ontogenetic and interannual differences in YOY bluefish diets. Bluefish avoided striped bass at low densities but selected for them at high densities, suggesting a density-dependent feeding response. In the early summer of 1993, bluefish predation accounted for 50–100% of the total estimated loss of YOY striped bass. A significant negative correlation exists between the relative magnitude of striped bass recruitment and bluefish abundance. We conclude that YOY bluefish are important predators of estuarine fish and can have a substantial impact on their recruitment.

Résumé : Nous avons mesuré le poids et la densité de tassergals (*Pomatomus saltatrix*) et la taille de leurs proies durant les étés 1992 et 1993, ainsi que leur régime alimentaire sur une période de 4 ans (1990–1993) dans l'estuaire de l'Hudson. Ces données ont été utilisées pour estimer la diminution de l'abondance des jeunes bars rayés (*Morone saxatilis*) de l'année due à la prédation par les jeunes tassergals de l'année. Nous avons ensuite comparé cette mortalité par prédation à la diminution totale de l'abondance du bar rayé dans le milieu. Nous avons utilisé les données de campagnes d'échantillonnage menées depuis le milieu des années 70 pour examiner la relation entre l'abondance du tassergal et les niveaux de recrutement du bar rayé. Les jeunes bars rayés de l'année, les anchois américains (*Anchoa mitchilli*), les capucettes (*Menidia menidia*) et les *Alosa* spp. constituaient la plus grande partie du régime alimentaire des jeunes tassergals de l'année. Il y avait des différences ontogénétiques et interannuelles dans les régimes alimentaires des jeunes tassergals de l'année. Les tassergals évitaient les bars rayés quand ces derniers étaient présents en faible densité, mais s'en nourrissaient quand leur densité était élevée; il y aurait donc chez les tassergals une réponse alimentaire dépendante de la densité. Au début de l'été de 1993, 50 à 100% de la diminution totale estimée de l'abondance des jeunes bars rayés de l'année était attribuable à la prédation par les tassergals. Une corrélation négative significative existe entre l'importance relative du recrutement des bars rayés et l'abondance des tassergals. Nous concluons que les jeunes tassergals de l'année sont d'importants prédateurs des poissons estuariens et peuvent avoir un impact substantiel sur leur recrutement.

[Traduit par la Rédaction]

J.A. Buckel,[1] **D.O. Conover, and N.D. Steinberg.**[2] Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794-5000, U.S.A.
K.A. McKown. New York Department of Environmental Conservation, Anadromous Fish Unit, 205 Belle Meade Road, East Setauket, NY 11733, U.S.A.

[1]Author to whom all correspondence should be addressed. Present address: NOAA, National Marine Fisheries Service, James J. Howard Marine Laboratory, 74 Magruder Road, Highlands, NJ 07732, U.S.A. e-mail: jbuckel@sh.nmfs.gov
[2]Present address: Hudson River Foundation, 40 West 20th Street, New York, NY 10011, U.S.A.

Introduction

Determination of the factors that affect recruitment of marine fish populations is an area of intense study. Biotic (food availability, predation, etc.) and abiotic factors (temperature, loss to advection, etc.) have both been shown to influence recruitment (for a review, see Leggett and DeBlois 1994), necessitating a multifactorial approach to understanding recruitment variation (Fogarty et al. 1991; Leggett and DeBlois 1994). Much research has focused on factors affecting egg and larval stages; however, there has been a resurgence of interest in processes affecting juvenile mortality (Hixon 1991; Walters and Juanes 1993; Bailey 1994).

In freshwater systems the effects of predation on juvenile fish are well documented. For example, piscivores directly

Can. J. Fish. Aquat. Sci. **56**: 275–287 (1999)

© 1999 NRC Canada

affect recruitment in many freshwater fishes (Nielsen 1980; Tonn et al. 1992). Evidence of indirect effects of predation on prey fish populations in freshwater systems also exists (Kerfoot and Sih 1987; He and Wright 1992).

Far fewer studies have examined the effects of piscivores in open marine systems such as estuaries and the coastal ocean. Campbell (1979) and Sykes and Manooch (1979) reviewed piscine predation studies in rivers and estuaries, respectively. No studies found conclusive evidence of a direct predatory effect on prey fish populations. More recently, Rieman et al. (1991) determined the amount of juvenile salmonid (*Oncorhynchus* spp.) losses that resulted from fish predation in the Columbia River. They found that mortality from fish predators (mostly northern squawfish (*Ptychocheilus oregonensis*)) accounted for a previously unexplained source of mortality during the out-migration of juvenile salmonids. Experiments designed to investigate the effects of piscivory on estuarine juvenile fish populations have been conducted in salt pond or mesocosm enclosures (Wright et al. 1993; Gleason and Bengtson 1996*a*), but direct in situ measurements of the impact of piscivores on juvenile prey fish populations in estuaries are lacking (but for a coastal nursery example, see van der Veer and Bergman 1987).

The bluefish (*Pomatomus saltatrix*) is a marine piscivore of circumglobal distribution that occurs nearshore in its juvenile stage (Juanes et al. 1996). In the western Atlantic, spawning occurs offshore over the continental shelf and juveniles migrate abruptly into U.S. east coast estuaries at ~ 60 mm fork length (Kendall and Walford 1979; Nyman and Conover 1988; McBride and Conover 1991). Bluefish spawned in the South Atlantic Bight in the spring are advected northward in waters associated with the Gulf Stream (Hare and Cowen 1996) and move into New York – New Jersey estuaries in June (Nyman and Conover 1988; McBride and Conover 1991). A second wave of recruits consisting of summer-spawned fish recruit into estuaries in middle to late summer (Nyman and Conover 1988; McBride and Conover 1991). The offshore to inshore habitat shift coincides with a feeding shift from zooplanktivory to piscivory (Marks and Conover 1993).

A large number of studies have determined the diet of age-0 bluefish along the east coast of the United States (see references in Buckel and Conover 1997). Age-0 bluefish prey includes the larval and juvenile stages of a variety of fish species. In the Hudson River estuary, Juanes et al. (1993) found that juvenile bluefish prey includes several important anadromous species such as American shad (*Alosa sapidissima*) and striped bass (*Morone saxatilis*). Friedland et al. (1988) found year-to-year differences in diets of age-0 bluefish in a New Jersey marine embayment. Bluefish are believed to be opportunistic predators and appear to feed in relation to prey abundance (Juanes et al. 1993).

Here, we present diet and prey selectivity data from bluefish collected over a 4-year period (1990–1993) throughout a large portion of the Hudson River estuary (24 km). Using field estimates of bluefish consumption rates (Buckel and Conover 1997), prey sizes, and bluefish and prey densities, the loss of age-0 striped bass resulting from age-0 bluefish predation in the Hudson River estuary is estimated. This predation mortality is compared with the total loss of striped bass in the system. Additionally, data from sampling surveys conducted since the mid-1970's were used to examine relationships between striped bass recruitment and bluefish abundance.

Materials and methods

Study area and fish collections

The lower Hudson River is one of several major estuaries along the east coast of the United States (41°00′N, 73°54′W). It functions as a nursery for a diverse ichthyofaunal community consisting of several anadromous (clupeid and percichthyid) and estuarine (engraulid and atherinid) fishes (Beebe and Savidge 1988).

There were two sources of bluefish from the Hudson for diet analysis. The first included bluefish specimens collected by the New York State Department of Environmental Conservation's (NYDEC) juvenile striped bass sampling program over a 4-year period (1990–1993). This survey has been conducted since 1976 and involves nine biweekly samples of 25 stations from mid-July through early November. Sampling gear consists of a 61 × 3 m beach seine (13-mm-mesh wings and a 6-mm-mesh bag) deployed by boat. The survey samples a 24-km section of the lower Hudson River estuary from river kilometre ~39 to 63 (see fig. 1 in Juanes et al. 1993). This area of the estuary contains the majority of the summer age-0 striped bass population (Versar, Inc. 1988; available from Versar, Inc., 9200 Rumsey Road, Columbia, MD 21045, U.S.A.).

The second source of bluefish (early field collection, EF) was from biweekly collections at a subset (eight sites) of the NYDEC beach seine locations. These collections were performed from mid-June to early July 1992 and 1993 to determine the timing of first bluefish recruitment to the lower Hudson and diet during this time period. Collections were with identical gear as described above.

In both surveys, one seine haul was conducted at each station during daylight hours. This is a time period when bluefish are known to feed (Buckel and Conover 1997). The contents of the net were identified, enumerated, and put back into the river with the exception of bluefish and subsamples of potential prey, which were preserved in 10% buffered formalin.

Diet

Diets of bluefish captured throughout the sampling seasons of 1990–1993 were evaluated. Bluefish were measured for total length (TL) and their stomachs extracted. Stomach contents of bluefish were identified to the lowest possible taxon, enumerated, blotted dry, weighed (± 0.01 g), and measured (TL, ± 1.0 mm; eye diameter, ± 0.1 mm; caudal peduncle depth, ± 0.1 mm). Regressions relating prey eye diameter and caudal peduncle depth to TL were used to estimate prey TL of partially eaten prey (see Scharf et al. 1997). A reference collection of Hudson River fish species (whole fish, scales (see Lassiter 1962), and bones) was used to aid in identification of digested prey. Differences in dentition and anal fin morphologies were used to aid in identification of the congeners white perch (*Morone americana*) and striped bass (Fritzsche and Johnson 1980; Waldman 1986). Differences in mouth morphologies were used to aid in the identification of *Alosa* spp.

Each beach seine haul provided us with a group or "cluster" of bluefish for a given station as in a cluster sampling design (Cochran 1977). The mean and variance of diet indices were calculated with cluster sampling estimators developed at the Northeast Fisheries Science Center, National Marine Fisheries Service, Woods Hole, Mass. (M.J. Fogarty, University of Maryland System, Chesapeake Biological Laboratory, Solomons, MD 20688, U.S.A., unpublished data). For each sampling date, an estimate of the mean proportion of stomachs (frequency of occurrence) that contain prey type k (F_k) was calculated as

$$F_k = \frac{\sum\limits_{i=1}^{n} M_i p_{ik}}{\sum M_i}$$

where

$$p_{ik} = \frac{m_{ik}}{m_i}$$

and where n is the number of seine hauls containing bluefish, M_i is the number of bluefish captured in a beach seine haul at station i, m_i is the number of bluefish in a subsample of the fish from station i that were analyzed for diet, and m_{ik} is the number of bluefish in the subsample with food type k at station i. The estimator of variance for F_k is

$$v(F_k) = \frac{1}{n\overline{M}^2} \frac{\sum\limits_{i=1}^{n} M_i^2 (p_{ik} - F_k)^2}{n-1}$$

where $\overline{M}$ is the average number of fish in a seine haul on that date. The estimate of the mean proportional contribution of a prey type by weight (W_k) was calculated as

$$W_k = \frac{\sum\limits_{i=1}^{n} M_i q_{ik}}{\sum M_i}$$

where

$$q_{ik} = \frac{w_{ik}}{w_i}$$

and where w_i is the total weight of all identifiable prey in a subsample of the fish from station i that was analyzed for diet and w_{ik} is the weight of prey type k in the subsample at station i. The estimator of variance for W_k is

$$v(W_k) = \frac{1}{n\overline{M}^2} \frac{\sum\limits_{i=1}^{n} M_i^2 (q_{ik} - W_k)^2}{n-1}.$$

Prey type selectivity

Feeding selectivity of juvenile bluefish in the Hudson River estuary was determined from relative abundance of prey in bluefish stomachs and beach seine catches (see Fig. 1). Four fish prey categories were examined: striped bass, clupeids (American shad and blueback herring (*Alosa aestivalis*)), Atlantic silverside (*Menidia menidia*), and other fish (white perch, *Fundulus* spp., Atlantic menhaden (*Brevoortia tyrannus*), hogchoker (*Trinectes maculatus*), and Atlantic tomcod (*Microgadus tomcod*)). These prey, along with bay anchovy (*Anchoa mitchilli*), made up 90–98% of the potential fish prey collected during beach seine collections during all 4 years of collection (1990–1993). Bluefish selectivity for bay anchovy was not calculated because the larval and early juvenile stages that were often found in bluefish guts were not collected efficiently in the beach seine gear. Chesson's (1978) index was used to determine bluefish prey preference as

$$\alpha_i = \frac{r_i/p_i}{\sum\limits_{j=1}^{m} r_j/p_j}, \quad i = 1, \ldots, m$$

where α_i is the selectivity for prey type i for a group of bluefish from a given beach seine haul, r_i is the relative abundance of prey type i for the group of bluefish stomachs in a given beach seine haul, p_i is the relative abundance of prey type i in the environment calculated from the combined seine catches in which bluefish stomachs were collected on a given date, and m is the number of prey types available ($m = 4$). Values of r_i for prey that were not identified to the species level (e.g., *Morone* spp.) were partitioned to identifiable categories based on the relative occurrence of the identifiable species making up each category. Values of α_i were calculated for each beach seine haul. The mean α_i for each date was calculated using the cluster sampling estimators described above. The variance was not estimated because of the lack of independence between estimates of α_i on a given date — an identical value of p_i was used for each beach seine haul estimate of α_i. For statistical purposes, a unique value of p_i for each seine haul estimate of α_i would have been preferred, but the absence of prey species from individual beach seine hauls precluded this technique (zeros often occurred in the denominator). Pooling prey across seine hauls to develop estimates of relative abundance for the four prey types on each date may be more ecologically realistic given the movements of bluefish in the system. Random feeding occurs when $\alpha_i = m^{-1}$ (0.25); values of $\alpha_i > 0.25$ or $\alpha_i < 0.25$ represent "selection" and "avoidance" of prey, respectively. Values of α_i can be compared among dates even if the relative abundances of prey types differ (Chesson 1983).

A nonparametric Kruskal–Wallis test was used to examine the influence of year on prey selection of striped bass; within-year variation could not be measured given the different sampling dates from one year to the next. To determine if bluefish feed disproportionately on prey as prey density changes, a Pearson correlation coefficient was calculated between striped bass α_i values and striped bass catch-per-unit-effort (CPUE).

Prey loss calculations

Daily loss of juvenile striped bass to bluefish predation was calculated from bluefish density (number per 100 m², $D \pm SE$), weight (grams, $W \pm SE$), daily ration (grams per gram per day, $C \pm SE$), the proportion of striped bass by weight in bluefish diet ($P \pm SE$), and striped bass sizes eaten by bluefish (grams, $S \pm SE$). Values for D, W, P, and S are from EF/NYDEC collections. Values of D were calculated from bluefish CPUE data (Table 1) assuming that the 61-m seine sampled a 500-m² area (McBride et al. 1995). Bluefish C values (Table 2) were measured in the lower Hudson River during the summers of 1992 and 1993 by sampling bluefish gut fullness levels over a diel period (Buckel and Conover 1997); additional bluefish W (Table 1) and S data came from these diel sampling collections.

Equations to estimate striped bass lengths consumed by bluefish were developed using sizes of striped bass retrieved from bluefish guts throughout the summers of 1992 and 1993 (1992: striped bass TL eaten (millimetres) = 0.682·(day) + 3.573, $r^2 = 0.70$, $n = 66$; 1993: striped bass TL eaten (millimetres) = 0.965·(day) – 9.081, $r^2 = 0.80$, $n = 135$; day 0 = June 1); these length equations were then substituted into the following equation to predict striped bass prey weights consumed by bluefish on a given date (S (grams) = 7.0×10^{-6}·TL$^{3.06}$, $r^2 = 0.99$, $n = 246$). The delta method (Seber 1973) was used to approximate a standard error for the resulting 1992 and 1993 functions describing prey weight as a function of date.

In order to obtain a daily value of D, W (log$_e$ transformed to linearize), C, and P, linear interpolations were used between actual estimates. Daily values of SE's for these quantities were estimated from the general relationship for the variance of a linear function of two independent random variables (Hogg and Craig 1970). The number of striped bass eaten by bluefish per 100 m² ($\pm$ SE) of the

Table 1. Weight and CPUE of YOY bluefish collected with a 61-m beach seine in the lower Hudson River estuary for 1992 and 1993.

Date	Survey	Weight (g)		CPUE	
		No. of fish	Mean (SD)	No. of hauls	Mean (SD)
1992					
June 18	EF	1	1.54	3	0.33 (0.58)
June 26	EF	20	2.39 (0.41)	8	2.25 (1.83)
July 7	EF	85	3.04 (1.24)	8	6.57 (5.35)
July 16–17	24-h	179	4.48 (2.43)	na	na
July 22–23	NYDEC	90	9.26 (5.95)	25	3.76 (3.77)
July 28–29	24-h	85	11.30 (6.40)	na	na
August 5–6	NYDEC	47	18.73 (10.46)	25	2.00 (1.94)
August 13–14	24-h	119	26.79 (14.18)	na	na
August 18–19	NYDEC	17	21.04 (9.90)	25	1.92 (2.45)
August 26–27	24-h	85	41.16 (25.49)	na	na
September 1–2	NYDEC	22	45.40 (18.92)	25	0.92 (1.29)
September 15–16	NYDEC	8	54.88 (24.05)	25	0.52 (1.12)
September 19–20	24-h	96	43.71 (19.73)	na	na
October 1–2	NYDEC	1	68.71	25	0.04 (0.20)
1993					
June 16	EF	na	na	8	0
June 30	EF	57	3.87 (1.43)	7	8.14 (1.86)
July 7–8	24-h	248	4.96 (1.60)	na	na
July 13–14	NYDEC	117	6.17 (6.55)	25	4.52 (4.73)
July 20–21	24-h	136	8.96 (5.94)	na	na
July 28–29	NYDEC	73	21.55 (12.44)	25	3.92 (3.98)
August 4–5	24-h	119	19.84 (10.24)	na	na
August 10–11	NYDEC	161	22.87 (11.90)	25	5.26 (8.48)
August 11–12	24-h	47	23.29 (9.64)	na	na
August 18–19	24-h	130	33.30 (18.02)	na	na
August 24–25	NYDEC	23	47.31 (31.98)	25	1.64 (1.98)
September 7–8	NYDEC	34	84.57 (35.15)	25	2.00 (4.80)
September 11–12	24-h	23	75.67 (42.16)	na	na
September 29–30	NYDEC	2	119.66 (7.25)	25	0.20 (0.41)

Note: See text for description of the NYDEC and EF surveys. Weight data from 24-h surveys are from Buckel and Conover (1997). na, not applicable.

nearshore per day was calculated in three steps. First, nearshore bluefish biomass ($B \pm SE$) was calculated as

$$B \ (\mathrm{g \cdot 100 \ m^{-2}}) = D \ (\mathrm{no. \cdot 100 \ m^{-2}}) \times W \ (\mathrm{g}).$$

Second, the grams of striped bass consumed by bluefish per 100 m^2 per day (SBC $\pm$ SE) was calculated as

$$\mathrm{SBC} \ (\mathrm{g \cdot 100 \ m^{-2} \cdot day^{-1}}) = B \ (\mathrm{g \cdot 100 \ m^{-2}})$$
$$\times C \ (\mathrm{g \cdot g^{-1} \cdot day^{-1}}) \times P.$$

Third, the number of striped bass consumed by bluefish per 100 m^2 per day ($N \pm SE$) was calculated as

$$N \ (\mathrm{no. \cdot 100 \ m^{-2} \cdot day^{-1}})$$
$$= \mathrm{SBC} \ (\mathrm{g \cdot 100 \ m^{-2} \cdot day^{-1}})/S \ (\mathrm{g}).$$

Estimates of N were calculated from the date that bluefish were first captured in substantial numbers (June 26, 1992, and June 30, 1993) until bluefish densities declined to a low level (September). Standard errors of products or quotients in the above equations were approximated using the delta method (Seber 1973). The cumulative consumption of striped bass was calculated for N and $\pm$ 1 SE of N. These cumulative consumption curves were compared with beach seine striped bass density estimates (number per 100 m^2)

from the EF/NYDEC survey and with an independent estimate of striped bass abundance (beach seine CPUE) from an identical area of the Hudson River conducted by the Hudson River Estuary Monitoring Program (HREMP) (described below).

Striped bass mortality resulting from bluefish predation (M_{pred_i}, per day) was calculated for each interval length i between striped bass sampling dates as

$$M_{\mathrm{pred}_i} = \frac{N_i}{\overline{X}_i}$$

where N_i is the total number of striped bass consumed by bluefish per 100 m^2 for the interval i and $\overline{X}_i$ is the geometric mean number of striped bass per 100 m^2 (EF/NYDEC) over that same time interval. The intervals used to estimate total loss and predation loss of striped bass were based on striped bass sampling dates. These calculations were also performed using the sum of striped bass consumed at $\pm$ 1 SE of N_i. Estimates of striped bass predation mortality (M_{pred_i}) were divided by the interval length i in days to get daily estimates of predation mortality. Values of daily striped bass mortality resulting from bluefish predation were compared with estimates of total striped bass loss. Striped bass loss (mortality plus the sum of emigration and immigration) was determined from EF/NYDEC data from the end of June until early August using

Table 2. Estimated YOY bluefish consumption rates from Buckel and Conover (1997).

Date	Consumption rate $(g \cdot g^{-1} \cdot day^{-1} \cdot 100)$	SE
1992		
July 16–17	22.20	5.71
July 28–29	17.45	3.70
August 13–14	14.73	2.67
August 26–27	12.62	2.82
September 19–20	7.34	3.00
1993		
July 7–8	10.05	1.92
July 20–21	14.67	3.40
August 4–5	13.90	4.77
August 18–19	10.06	1.94

catch curve analysis; the instantaneous mortality rate (Z, per day) was calculated as the slope of the linear regression of $\log_e$(CPUE) against day (Ricker 1975). Daily conditional mortality rates (percent per day) were calculated as $1 - e^{-M}$ and $1 - e^{-Z}$.

Relationship between bluefish and striped bass abundance

HREMP has conducted an extensive ichthyoplankton and juvenile fish sampling survey since 1974 (for methodologies, see Dey 1981; Barnthouse et al. 1988; Pace et al. 1993). The program is considered among the most intensive long-term studies of fish populations ever conducted (Pace et al. 1993). A Pearson correlation coefficient was calculated between the NYDEC young-of-the-year (YOY) striped bass index (geometric mean) measured in the lower Hudson River estuary and HREMP's striped bass post-yolk-sac larvae (PYSL) index. There were 18 years that had coincident data (1977–1978, 1980–1995) from the two surveys.

An annual YOY bluefish index from the HREMP beach seine survey from 1974 to 1995 was calculated. The index is the arithmetic mean bluefish CPUE for the Tappan Zee and Croton-Haverstraw regions of the lower Hudson River (river kilometres 39–63) averaged for the month of July. This area of the Hudson is identical to the area sampled by the NYDEC YOY striped bass survey. The bluefish index was determined for those years in which there was at least 2 weeks of sampling in the month of July. This excluded 1981–1984. A Pearson correlation coefficient between the NYDEC YOY striped bass index and the YOY bluefish index was calculated for the 14 years of coincident data.

Results

Diet

The diets of 1585 spring-spawned and 197 summer-spawned bluefish (cohort determined from size differences) were examined from fish collected in the Hudson River during the summers of 1990–1993 (1990: 575 spring, 99 summer; 1991: 258, 25; 1992: 290, 60; 1993: 462, 13). In all four years, the dominant prey type of spring- and summer-spawned bluefish was teleost fish.

Spring-spawned bluefish had not recruited to the lower Hudson River during the mid-June EF collection in 1992 or 1993 (one bluefish was captured on June 18, 1992; no bluefish were captured on June 16, 1993; see Table 1). However, in both years, bluefish were captured in large numbers by the end of June. Fish prey was the largest diet component of recently recruited bluefish (see Buckel (1997) for values of

bluefish diet by percent; the diet data presented in Fig. 1 have been normalized because percentages from cluster estimators do not add up to 100%). The dominant prey of bluefish captured in EF collections was striped bass in both 1992 and 1993 (Fig. 1; Table 3). Other bluefish prey during this time period included *Alosa* spp., blueback herring, bay anchovy, and Atlantic silverside. Invertebrate prey, crab zoea (mostly *Rhithropanopus harisii*) and calanoid copepods, were also an important part of the diet of recently recruited spring-spawned bluefish (Fig. 1).

The dominant prey of spring-spawned bluefish collected from mid-July to September–October in the four years studied (1990–1993) were bay anchovy, striped bass, Atlantic silverside, American shad, and blueback herring (Fig. 1). The importance of these prey varied from year to year. Bay anchovy was the most consistently taken prey for all four years (Fig. 1). Striped bass, white perch, and *Morone* spp. were important dietary items of spring-spawned bluefish in 1990, 1992, and 1993 but not in 1991. Atlantic silverside and clupeids were more variable. The Atlantic silverside was not an important prey in 1990 and was a dominant part of the diet on only one date in 1992 (Fig. 1). However, it was a major prey item of spring-spawned bluefish in 1991 and 1993. Clupeids (American shad, blueback herring, alewife (*Alosa pseodoharengus*), and *Alosa* spp.) were nearly absent in bluefish stomachs in 1993, intermediate in occurrence in 1991, but dominated the diet on some collection dates in 1990 and 1992 (Fig. 1).

Invertebrate prey of spring-spawned bluefish collected from mid-July to September–October included crab zoea (mostly *R. harisii*), unidentified copepods, unidentified isopods, unidentified amphipods, blue crab (*Callinectes sapidus*), sand shrimp (*Crangon* spp.), and grass shrimp (*Palaemonetes* spp.). These invertebrate prey were usually rare in bluefish stomachs with the exception of some dates where zoea and copepods and sand and grass shrimp were relatively important dietary items.
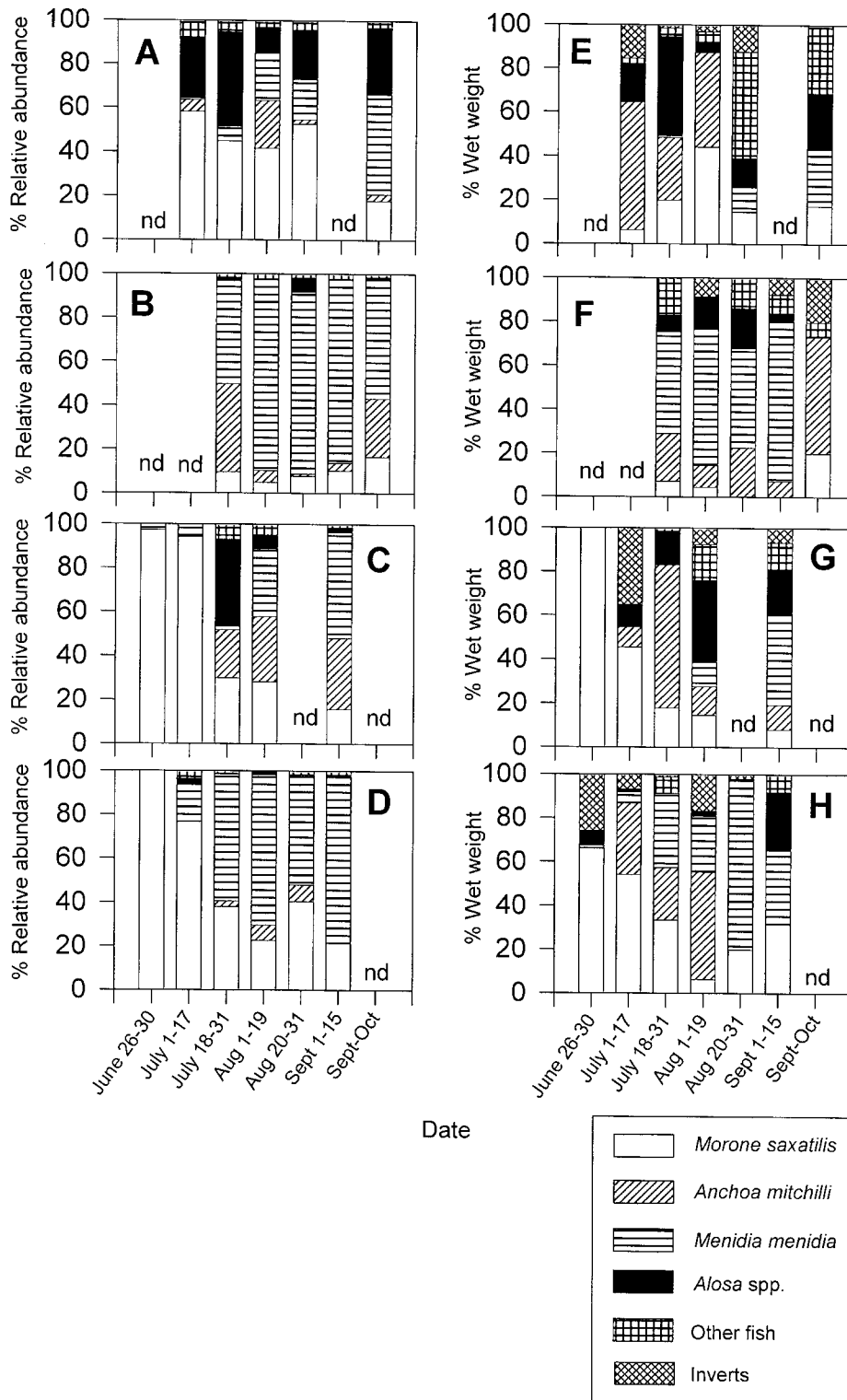
The diets of summer-spawned bluefish were dominated by bay anchovy in all four years (see Buckel 1997). Striped bass were not an important prey of summer-spawned bluefish (Table 3).

Prey type selectivity

Selectivity values (Chesson's α) indicated that spring-spawned bluefish showed considerable variation in prey preference. Bluefish often fed randomly with respect to prey abundance but, on occasion, also appeared to select or avoid prey (Table 4). There were both seasonal and interannual differences in selectivity for a given prey type. For example, there was a significant (Kruskal–Wallis ANOVA, $\chi^2 = 8.53$, df = 3, $p = 0.036$) interannual difference in selection of striped bass by bluefish. Bluefish often fed randomly with respect to striped bass abundance in 1990 and 1993 while avoiding them in 1991 (Table 4). In June and July of 1992 and 1993, bluefish showed positive selection for striped bass but then fed randomly or avoided them in later months.

Bluefish preference for striped bass was positively correlated with EF/NYDEC-measured striped bass CPUE ($r = 0.73$, $p = 0.001$) (Fig. 2). Hence, bluefish appear to select striped bass as prey when they are abundant.

280

Can. J. Fish. Aquat. Sci. Vol. 56, 1999

Fig. 1. Percent relative abundance of potential YOY bluefish prey from beach seine CPUE data during EF/NYDEC sampling in the Hudson River estuary for (A) 1990, (B) 1991, (C) 1992, and (D) 1993 and the mean percent wet weight contribution of prey to YOY bluefish diet in the Hudson River estuary estimated from a cluster sampling design (see Buckel (1997) for cluster estimator percentages; values are normalized to 100%) for (E) 1990, (F) 1991, (G) 1992, and (H) 1993. nd, no data.

Bluefish showed a preference for clupeids on at least one date in all four years. Bluefish mostly selected for Atlantic silverside in 1991 and 1993 while avoiding them on most dates in 1990 and 1992.

Prey loss calculations

Estimates of mean daily predation loss were made for three intervals in 1992 and 1993. In 1992, the loss of striped bass during June 26 – July 7, July 7–22, and July 22 –

Table 3. Proportion of striped bass in spring- and summer-spawned bluefish diets during 1990–1993 beach seine collections in the Hudson River estuary.

Date	1990		1991		1992		1993	
	%F	%W	%F	%W	%F	%W	%F	%W
Spring-spawned bluefish								
June 26–30	nd	nd	nd	nd	9.5 (7.4)	28.6 (22.1)	17.5 (4.9)	56.3 (15.2)
July 1–17	4.6 (2.3)	6.0 (3.7)	nd	nd	9.5 (4.7)	37.5 (21.0)	18.8 (5.0)	51.0 (13.7)
July 18–31	8.2 (3.7)	17.7 (7.8)	3.4 (2.2)	6.7 (5.6)	5.5 (3.2)	15.5 (10.0)	11.3 (5.2)	25.6 (17.6)
August 1–19	4.3 (3.2)	20.5 (18.6)	1.5 (2.2)	3.8 (5.5)	6.3 (7.0)	12.3 (14.7)	1.2 (1.3)	3.9 (4.7)
August 20–31	1.5 (1.9)	4.9 (6.7)	0	0	6.3 (7.0)	12.3 (14.7)	9.1 (22.5)	17.1 (42.5)
September 1–15	nd	nd	0	0	3.3 (9.1)	4.5 (12.4)	2.9 (6.8)	24.8 (57.4)
September–October	5.3 (4.7)	6.4 (5.7)	3.8 (9.5)	11.5 (28.4)	nd	nd	nd	nd
Summer-spawned bluefish								
August–October	0	0	0	0	1.6 (9.6)	4.9 (28.9)	0	0

Note: %F, proportion of bluefish stomachs containing striped bass (±SE); %W, proportion contribution of identifiable prey to bluefish diet by weight (±SE). SE, standard error from variance estimators for cluster samples (see equations in the text); nd, no data.

August 5 was 15.4, 13.1, and 3.3 fish·100 m^{-2}, respectively (Table 5). The loss of striped bass during June 30 – July 13, July 13–28, and July 28 – August 10, 1993, was 36.8, 14.0, and 4.4 fish·100 m^{-2}, respectively. Predation mortality estimates ranged from 2.6 to 25.9%·day^{-1} in 1992 and from 2.1 to 5.3%·day^{-1} in 1993 (Table 5). Both the EF/NYDEC and HREMP beach seine survey estimates of striped bass abundance did not decline from late June to early August 1992; during this time period, they either stayed level or increased slightly (Fig. 3). In contrast, there was a dramatic decline in striped bass abundance in late June through mid-July for both surveys in 1993. The EF/NYDEC survey estimates of striped bass abundance continued to decline from mid-July through early August (Fig. 3). The total loss (mortality plus the sum of immigration and emigration) from the 1993 EF/NYDEC striped bass density data from late June to early August was 4.1%·day^{-1}. Bluefish predation in 1993 accounted for 51–129% of total striped bass loss from late June to early August (Table 5).

Relationship between bluefish and striped bass abundance

The NYDEC annual juvenile striped bass index was negatively correlated ($r = -0.61$, $p = 0.022$) with July YOY bluefish abundance (Fig. 4). However, the correlation between the NYDEC annual juvenile striped bass index and the HREMP annual PYSL striped bass index was not significant ($r = 0.08$, $p = 0.746$) (Fig. 4). Hence, striped bass PYSL abundance is not a good predictor of juvenile striped bass abundance, but juvenile striped bass recruitment is significantly related to the abundance of bluefish.

Discussion

Bluefish have long been suspected of causing declines in prey fish abundance (Baird 1873). Here, evidence is presented that bluefish can directly affect the mortality rate of estuarine fish. There were intra- and inter-annual differences in YOY bluefish diets that appear to result from changes in bluefish selectivity as relative abundances of prey change; bluefish avoid striped bass at low densities but select for them at high densities, suggesting a density-dependent feed-

ing response. Striped bass mortality resulting from bluefish predation is at times equal to total juvenile striped bass mortality. Correspondingly, a significant negative correlation exists between striped bass recruitment and bluefish abundance across years. Bluefish predation may account for a significant amount of the previously unexplained density-dependent loss of striped bass between the post-yolk-sac larval and late summer juvenile stages.

Diet and prey type selectivity

Fish prey dominated YOY bluefish diet. This result is similar to past YOY bluefish diet studies in the Hudson River estuary (Texas Instruments Inc. 1976; Juanes et al. 1993; Buckel and Conover 1997) as well as other estuarine and marine systems on the U.S. east coast (see references in Buckel and Conover 1997). Bay anchovy, clupeids (American shad and blueback herring), striped bass, and Atlantic silverside were the most common prey of YOY bluefish in the Hudson River from 1990 to 1993. The dominant prey of Hudson River spring-spawned bluefish from July to September 1974 was bay anchovy, clupeids (American shad and blueback herring), and Atlantic tomcod (Texas Instruments Inc. 1976). These prey accounted for 75% of the diet, while striped bass represented <2%. Juanes et al. (1993) found that bay anchovy, striped bass, clupeids, and Atlantic tomcod dominated the diet of Hudson River spring-spawned bluefish in 1989. Our study confirmed earlier findings that anadromous fish (*Morone* spp. and *Alosa* spp.) often dominate the diet of YOY bluefish in the Hudson River estuary.

Striped bass was a prevalent bluefish prey in 1990, 1992, and 1993 but nearly absent from the diet of bluefish in 1991. This corresponds to low relative abundance of striped bass in 1991 (Fig. 1). Texas Instruments Inc. (1976) found very few striped bass in bluefish diet in 1974, which they attributed to low striped bass abundance. This was in contrast with their preliminary study in 1973 (large striped bass year-class) that found that seven out of the 33 (21%) bluefish examined had striped bass in their stomachs. Other prey types also show interannual variability. Clupeids were more prevalent as prey in 1990 and 1992 compared with 1991 and 1993. Atlantic silverside showed the opposite pattern. It was

Table 4. Prey selectivity (Chesson's α, see text for calculations) in spring-spawned bluefish collected in the Hudson River estuary.

Date	No. of hauls	Striped bass	Clupeids	Atlantic silverside	Other
1990					
July 17–18	8	0.21	0.78	0	0.01
July 31 – August 1–2	12	0.23	0.54	0.04	0.19
August 14–15	6	0.88	0.06	0.06	0
August 28–29	5	0.06	0.33	0.02	0.59
September 11 and October 18	6	0.11	0.23	0.33	0.33
1991					
July 23–24	15	0.12	0.20	0.43	0.25
August 6–7	11	0.11	0.33	0.56	0
August 21–22	5	0	0.24	0.58	0.18
September 3–4	8	0	0.50	0.75	0.13
1992					
June 26 and July 7 and 22–23	14	0.54	0.41	0	0.05
August 5–6 and 18–19	11	0.08	0.75	0.03	0.13
September 1–2 and 15–16	5	0.04	0.74	0.08	0.14
1993					
June 30 and July 13–14	16	0.89	0.07	0.04	0
July 28–29	8	0.53	0	0.39	0.07
August 10–11	6	0.29	0.40	0.32	0
August 24–25	7	0.21	0	0.69	0

Note: Values of α = 0.25 represent random feeding, while values of α > 0.25 or α < 0.25 represent "selection" and "avoidance" of prey, respectively.

a more dominant prey in 1991 and 1993 and less so in 1990 and 1992. Bay anchovy was important in all four years.

Within-year variability in bluefish diet was prevalent in 1990, 1992, and 1993. For example, striped bass was the dominant prey of YOY bluefish immediately after recruitment to the Hudson River estuary in 1992 and 1993. During this time period, striped bass was the primary piscine prey of appropriate size for bluefish. Later in the summer, bluefish began to prey upon bay anchovy, clupeids (1992), and Atlantic silverside (1993) as the relative abundances of these prey increased.

Inter- and intra-annual differences in diet appear to result from changes in the relative abundance of prey. The positive relationship between selectivity and striped bass CPUE suggests that bluefish may exhibit "prey switching" behavior (Murdoch et al. 1975). Switching occurs when the prey that has the highest relative abundance is attacked at a disproportionately higher rate than would be expected from random feeding (Murdoch et al. 1975). The clupeid and Atlantic silverside selectivity data appear to suggest switching behavior as well. For example, in years where clupeids were selected positively (1990 and 1992), the Atlantic silverside was selected against. If bluefish exhibit a type 3 functional response in the presence of multiple prey, then changes in relative abundance of prey that induce switching behavior would result in density-dependent mortality (see Bailey 1994). Other such demonstrations of predator switching behavior are rare (see Townsend et al. 1986).

The positive relationship between selectivity and striped bass CPUE could potentially result from covariance between the ratio of striped bass length to bluefish length and the striped bass density. Juvenile striped bass are more vulnerable to bluefish predation at lower prey length to predator
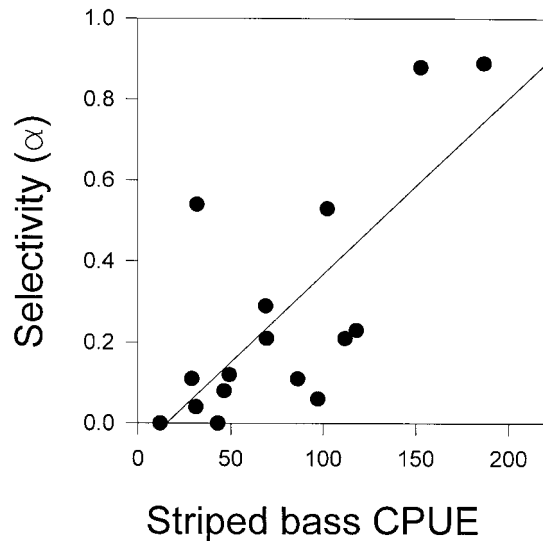
length ratios (Scharf et al. 1998). In the Hudson River estuary, the lowest mean striped bass length to bluefish length ratios (measured as mean striped bass length divided by mean bluefish length on a given date) often occur in early summer coincident with higher densities of striped bass. However, the estimates of striped bass selectivity are not significantly related to mean striped bass length to bluefish length ratios ($r = -0.05$, $p = 0.858$).

The amount of overlap that bluefish have with their prey in an estuary will depend partly on bluefish and prey salinity preferences. Bluefish distribution throughout the section of the estuary measured by NYDEC CPUE data does not suggest preference for any area. There are slightly higher CPUE's at the more southern stations, but there was no significant relationship between percent bluefish captured and distance from the mouth of the estuary ($r = -0.16$, $p = 0.067$). Our sampling did not extend as far upriver as bluefish have been captured by HREMP. In years where the salt front is higher and freshwater prey such as clupeids are not found at our beach seine stations, bluefish may still prey on them further upriver where overlap occurs. Therefore, different assemblages seen in the lower Hudson River may result from the salinity level or from real interannual variations in prey fish abundance.

Striped bass loss calculations

Our estimates of striped bass predation mortality show that bluefish predation directly influences prey abundance. For example, our estimates of striped bass density and predation mortality ($25.9\% \cdot day^{-1}$) suggest that the standing numbers of striped bass would disappear in a relatively short time period. This did not occur in 1992 given that the numbers of striped bass actually increased slightly throughout

Fig. 2. Relationship between bluefish selectivity (Chesson's α) for striped bass and striped bass CPUE in the Hudson River estuary ($r = 0.73$, $p = 0.001$).

the summer. Cohorts that were spawned later in the spawning season or that had initially recruited out of our sampling area may have immigrated into the sampling region. A similar observation was made by Dey (1981) in 1976, a year in which the striped bass spawning season appeared protracted.

However, protracted spawning and late recruitment do not explain how bluefish consumed more striped bass than were present during a given time interval in 1992 (Table 5). This discrepancy could result from either an underestimate of striped density or an overestimate of bluefish consumption, but more likely the former. Striped bass may have occurred in habitats missed by the beach seine in 1992 (e.g., offshore), or peak recruitment in 1992 may have occurred between sampling intervals. Although bluefish consumption estimates are likely not exact (see Potential sources of error section), our estimates show that bluefish consume an amount of striped bass that is greater than or equal to the quantity of striped bass present in early summer. At the very least, this suggests that bluefish are the major source of mortality for juvenile striped bass.

In 1993 the highest density of juvenile striped bass was measured in late June immediately after initial recruitment. Striped bass CPUE declined throughout July and August, allowing estimates of total striped bass loss to be calculated. Our estimate of striped bass loss from June 30 to August 10, 1993, was 4.1%·day^{-1}. This mortality rate estimate is similar to the June 25 – July 26, 1975, Hudson River striped bass late larval and early juvenile mortality rate estimate of 5.1%·day^{-1} (Dey 1981). The three mean bluefish predation mortality estimates during the late June to early August time period explained from half to all of the total striped bass mortality.

Much of the bluefish predation on striped bass occurred during the first few weeks following the appearance of juvenile striped bass in the lower Hudson. From June 30 to July 13, 1993, predation mortality induced by bluefish averaged 5.3%·day^{-1} (± 1 SE, 3.7–6.9) and accounted for 129% (89–

168%) of the total striped bass loss from the system. In both 1992 and 1993, over 70% of the total number of striped bass consumed by bluefish throughout the entire summer were consumed by July 14. The declining predation on striped bass after mid-July is due to the lowered incidence of striped bass in bluefish diet. It is not due to declining consumption of prey biomass by bluefish. Total consumption did not decline until August in both 1992 and 1993.

The availability of bay anchovy and Atlantic silverside appears to indirectly affect striped bass survival. Bluefish showed positive selection for striped bass based on the early collections in 1992 and 1993 and then either fed randomly or avoided striped bass during later collections. The low relative abundance of bay anchovy and Atlantic silverside during these early collections likely resulted in higher striped bass predation mortality. For example, the number of striped bass consumed during late July to early August would be 3–3.5 times higher if the proportion of striped bass in bluefish diets stayed at late June to early July levels throughout the summer in both years.

Few studies have examined the influence of estuarine piscivores on the mortality of estuarine fish populations. Wright et al. (1993) measured mortality in spot (*Leiostomus xanthurus*) resulting from southern flounder (*Paralichthys lethostigma*) predation in estuarine ponds. They found that their experimental measurements of spot mortality were similar to field estimates of spot mortality, suggesting that southern flounder predation was significant. Gleason and Bengtson (1996a) showed that bluefish feed on inland silverside (*Menidia beryllina*) in Narragansett Bay, R.I., and that this predation was size selective. Larger inland silverside were selected over smaller inland silverside in mesocosm experiments. They went on to examine size-selective mortality in cohorts of inland silverside in the field using back-calculated lengths from otolith–size relationships. Gleason and Bengtson (1996b) concluded that size-selective predation throughout the summer months was strong enough to significantly affect the size distribution of inland silverside. They attributed this size-dependent loss to bluefish predation.

Hartman and Brandt (1995) developed bioenergetic models for three estuarine piscivores in Chesapeake Bay: bluefish, weakfish (*Cynoscion regalis*), and striped bass. Although they modeled the cumulative consumption of these fish, the influence of this prey loss on prey populations within Chesapeake Bay was not measured. Their modeling efforts support our findings. Of the three piscivores they examined, bluefish were the most likely to affect prey populations (Hartman and Brandt 1995).

The effect of shrimp predation on recently settled flatfish provides the most conclusive proof of predation affecting the population dynamics of coastal prey populations. van der Veer (1986) showed that variability in abundance of plaice (*Pleuronectes platessa*) declined from the larval to the juvenile stage, indicating that density-dependent mortality reduced variability in year-class strength. Mortality estimates of recently settled plaice can be high (up to 6%·day^{-1}). Shrimp (*Crangon crangon*) predation causes density-dependent mortality in age-0 plaice shortly after settlement, resulting from both the functional and numerical responses

284

Can. J. Fish. Aquat. Sci. Vol. 56, 1999

Table 5. Geometric mean striped bass density, striped bass loss resulting from bluefish predation (see the text for calculation description), predation mortality, and percentage of striped bass mortality due to juvenile bluefish predation.

Date	Geometric mean density (no.·100 m^{-2})	Mean estimated predation loss during time period (no.·100 m^{-2}) (±1 SE)	Predation mortality M_{pred} (%·day^{-1}) (±1 SE)	% of total loss (Z + emigration) (±1 SE)
1992				
June 26 – July 7	4.7	15.4 (5.5–25.4)	25.9 (10.1–39.0)	na
July 7–22	6.6	13.1 (5.5–22.4)	13.2 (5.4–20.4)	na
July 22 – August 5	10	3.3 (0.9–6.5)	2.6 (0.6–4.6)	na
1993				
June 30 – July 13	48.2	36.8 (25.2–48.4)	5.3 (3.7–6.9)	128.5 (88.9–167.5)
July 13–28	27.6	14.0 (7.8–20.2)	3.3 (1.9–4.8)	80.6 (45.2–115.6)
July 28 – August 10	14.8	4.4 (1.1–7.8)	2.1 (0.5–3.7)	51.4 (12.9–89.2)

Note: Total loss (mortality plus emigration) was estimated as $Z = 4.1\%\cdot day^{-1}$ for 1993; no estimate of Z could be made in 1992. na, not applicable.

of shrimp to changes in the density of plaice (van der Veer and Bergman 1987).

Potential sources of error

The potential sources of error in our analyses include estimates of relative abundance, consumption rate, and diet of bluefish. Of these potential sources of error, beach seine estimates of relative abundance are the most likely to be biased. Although beach seines have limitations, Pierce et al. (1990) found that capture efficiencies on pelagic fish were relatively high. Additionally, McBride et al. (1995) found that bluefish abundances were underestimated only in beach seines <50–60 m long.

Estimates of striped bass density could have been influenced by seine capture efficiencies during early collections. The numbers of striped bass may have been underestimated due to fish not being retained by the seine mesh. This would lead to underestimates of striped bass total mortality rates and overestimates of bluefish selectivity for striped bass in early collections. Other biases in the calculation of striped bass mortality include fish emigration and immigration. Fish can also escape when the seine hits snags or rolls up on macrophytes (Pierce et al. 1990). The NYDEC beach seine survey monitors these factors during seine sets; the occurrence of these problems was rare in both 1992 and 1993.

The remaining potential sources of error were probably not important in this study. Our field estimates of bluefish daily ration in the Hudson River (Buckel and Conover 1997) are likely robust given their similarity to laboratory (Juanes and Conover 1994, Buckel et al. 1995), bioenergetic modeling (Steinberg 1994), and past field (Juanes and Conover 1994) measurements of bluefish feeding rates. However, point estimates of consumption rate in the field do not account for day-to-day variability in feeding rates. The estimates of bluefish diet are robust given that bluefish were sampled from 25 different beach seining stations covering a large area of the river throughout the summer. This section of the river contains the majority of the juvenile striped bass population (see Materials and methods).

Very few other studies of predation mortality have estimated the variability around predation mortality estimates. Using primarily the delta method (Seber 1973), standard error estimates of bluefish density, weight, daily ration, diet, and prey sizes were used to calculate an estimate of error

around the mean numbers of striped bass consumed by bluefish; for example, the mean (± SE) loss of striped bass to bluefish predation was 36.8 (± 11.6) fish·100 m^{-2} from June 30 to July 13, 1993 (Table 5). Given that confidence limits are roughly equal to ± 2 SE of the mean (Sokal and Rohlf 1981), the confidence limits for this estimate would range from 13.6 to 60 fish·100 m^{-2}. These large confidence limits point out the uncertainty of our estimate and the difficulty in quantifying predatory impacts in large systems. Field sampling should be designed to aid in reducing variability around estimates of diet, daily ration, predator and prey density, and other required data.

Bluefish predation explained a large amount of striped bass mortality in a year when bluefish density was relatively low. Therefore, the ability of bluefish to affect striped bass or other estuarine prey populations at high bluefish density years may be larger than estimated in this study in 1993.

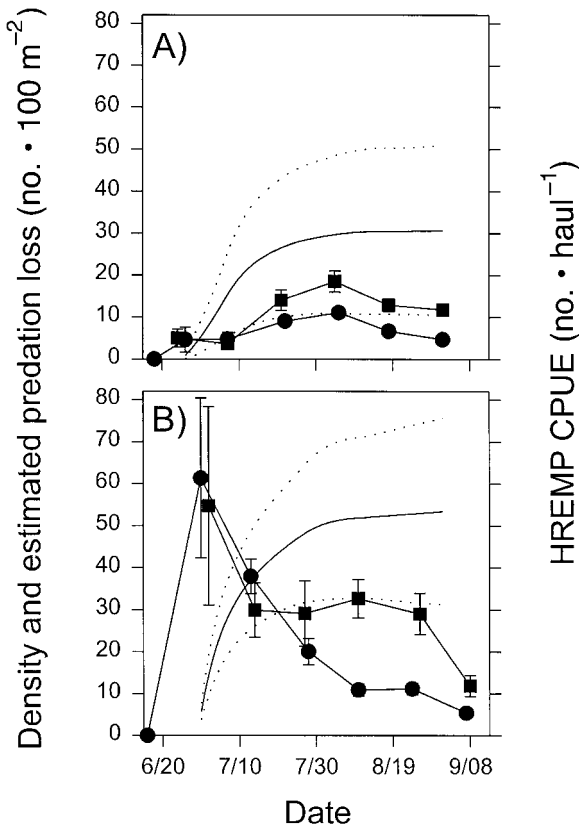### Relationship between bluefish and striped bass abundance

The NYDEC juvenile striped bass abundance index and HREMP's PYSL index for striped bass were uncorrelated. Years with a large PYSL abundance do not correspond to a large juvenile striped bass year-class. Pace et al. (1993) also examined the relationship between PYSL abundance and juvenile striped bass abundance but used HREMP data for both PYSL and juvenile striped bass. They also found no relationship between these factors and concluded that either (*i*) recruitment to the juvenile stage is not dependent on larval abundance or (*ii*) the juvenile striped bass abundance estimates are in error.

Bluefish abundance explained a significant amount of the variation ($r = -0.61$, $p = 0.022$) in juvenile striped bass recruitment. Therefore, bluefish predation may account, in part, for the lack of a relationship between PYSL abundance and recruitment of juvenile striped bass in the lower Hudson River. Further studies into the mortality at metamorphosis and the early juvenile stage are needed to better understand the early life history of the Hudson River striped bass stock.

Management implications

Since the early 1960's, there has been a large effort to assess the impact of Hudson River powerplant entrainment on the abundance of the early life history stages of striped bass

Fig. 3. Estimated Hudson River striped bass density ± 1 SE (circles, from EF/NYDEC beach seining) and cumulative loss to bluefish predation (solid line) for (A) 1992 and (B) 1993. Broken lines represent the cumulative consumption of ± 1 SE of the daily numbers of striped bass consumed by bluefish per 100 m^{-2}. CPUE of striped bass from HREMP beach seine sampling is also shown (squares).
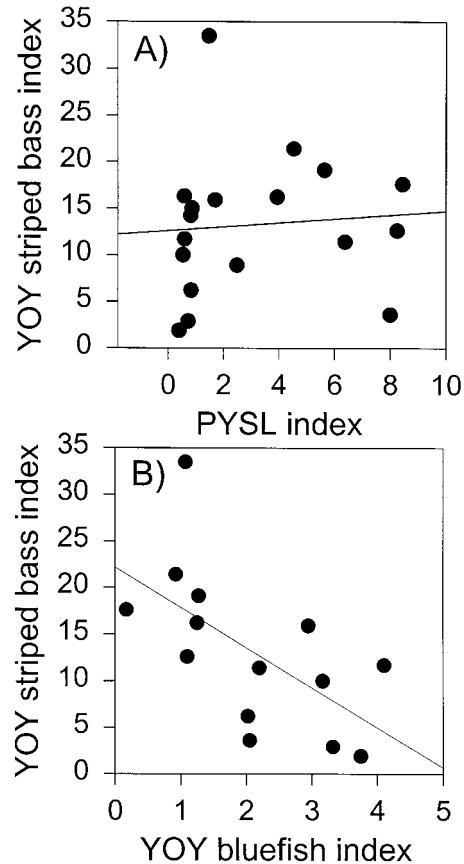
Fig. 4. Annual geometric mean Hudson River juvenile striped bass index from the NYDEC seine survey as a function of (A) the HREMP PYSL index ($r = 0.08$, $p = 0.746$) and (B) the annual bluefish index ($r = -0.61$, $p = 0.022$) developed from the mean CPUE of YOY bluefish from HREMP sampling during the month of July.

(Barnthouse et al. 1988). It is still unknown if powerplant entrainment affects striped bass population dynamics. However, it is known that the entrainment mortality of the early life stages of bay anchovy is exceedingly high (35–79% of the standing stock; Boreman and Goodyear 1988). Powerplant entrainment of bluefish forage species, such as bay anchovy, may indirectly affect striped bass mortality. Bluefish preference for striped bass prey increased as a function of striped bass relative abundance. Hence, a reduction in bay anchovy abundance due to powerplant entrainment may lead to an increase in bluefish predation on striped bass. Management of powerplant entrainment should not be concerned only with direct entrainment of striped bass (see Barnthouse et al. 1988) but also with the consequences of the removal of bluefish forage (e.g., bay anchovy early life history stages) on striped bass survival.

Acknowledgments

References

Bailey, K.M. 1994. Predation on juvenile flatfish and recruitment variability. Neth. J. Sea Res. **32**: 175–189.

Baird, S.F. 1873. The bluefish. *In* Part I. Report on the condition of the sea fisheries of the south coast of New England in 1871 and 1872. U.S. Commission of Fish and Fisheries, Washington, D.C. pp. 235–252.

Barnthouse, L.W., Klauda, R.J., Vaughan, D.S., and Kendall, R.L.

1988. Science, law, and Hudson River power plants: a case study in environmental assessment. Am. Fish. Soc. Monogr. **4**.

Beebe, C.A., and Savidge, I.R. 1988. Historical perspective on fish species composition and distribution in the Hudson River estuary. Am. Fish. Soc. Monogr. **4**: 25–36.

Boreman, J., and Goodyear, C.P. 1988. Estimates of entrainment mortality for striped bass and other fish species inhabiting the Hudson River estuary. Am. Fish. Soc. Monogr. **4**: 152–160.

Buckel, J.A. 1997. Impact of bluefish (*Pomatomus saltatrix*) predation on estuarine and continental shelf fishes. Ph.D. dissertation, State University of New York, Stony Brook, N.Y.

Buckel, J.A., and Conover, D.O. 1997. Movements, feeding periods, and daily ration of piscivorous young-of-the-year bluefish (*Pomatomus saltatrix*) in the Hudson River estuary. Fish. Bull. U.S. **95**: 665–679.

Buckel, J.A., Steinberg, N.D., and Conover, D.O. 1995. Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish. J. Fish Biol. **47**: 696–706.

Campbell, K.P. 1979. Predation principles in large rivers: a review. *In* Predator–prey systems in fisheries management. *Edited by* H. Clepper. Sport Fishing Institute, Washington, D.C.

Chesson, J. 1978. Measuring preference in selective predation. Ecology, **59**: 211–215.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology, **64**: 1297–1304.

Cochran, W.G. 1977. Sampling techniques. Wiley, New York.

Dey, W.P. 1981. Mortality and growth of young-of-the-year striped bass in the Hudson River estuary. Trans. Am. Fish. Soc. **110**: 151–157.

Fogarty, M.J., Sissenwine, M.P., and Cohen, E.B. 1991. Recruitment variability and the dynamics of exploited marine populations. Trends Ecol. Evol. **6**: 241–246.

Friedland, K.D., Garman, G.C., Bejda, A.J., Studholme, A.L., and Olla, B. 1988. Interannual variation in diet and condition in juvenile bluefish during estuarine residency. Trans. Am. Fish. Soc. **117**: 474–479.

Fritzsche, R.A., and Johnson, G.D. 1980. Early osteological development of white perch and striped bass with emphasis on identification of their larvae. Trans. Am. Fish. Soc. **109**: 387–406.

Gleason, T.R., and Bengtson, D.A. 1996a. Growth, survival and size-selective predation mortality of larval and juvenile inland silversides, *Menidia beryllina* (Pisces: Atherinidae). J. Exp. Mar. Biol. Ecol. **199**: 165–177.

Gleason, T.R., and Bengtson, D.A. 1996b. Size-selective mortality of inland silversides: evidence from otolith microstructure. Trans. Am. Fish. Soc. **125**: 860–873.

Hare, J.A., and Cowen, R.K. 1996. Transport mechanisms of larval and pelagic juvenile bluefish (*Pomatomus saltatrix*) from South Atlantic Bight spawning grounds to Middle Atlantic Bight nursery habitats. Limnol. Oceanogr. **41**: 1264–1280.

Hartman, K.J., and Brandt, S.B. 1995. 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.

He, X., and Wright, R.A. 1992. An experimental study of piscivore–planktivore interactions: population and community responses to predation. Can. J. Fish. Aquat. Sci. **49**: 1176–1183.

Hixon, M.A. 1991. Predation as a process structuring coral reef fish communities. *In* The ecology of fishes on coral reefs. *Edited by* P.F. Sale. Academic Press, Inc., San Diego, Calif. pp. 475–508.

Hogg, R.V., and Craig, A.T. 1970. Introduction to mathematical statistics. Macmillan Publishing Co. Inc., New York.

Juanes, F., and Conover, D.O. 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.

Juanes, F., Marks, R.E., McKown, K.A., and Conover, D.O. 1993. Predation by age-0 bluefish on age-0 anadromous fishes in the Hudson River Estuary. Trans. Am. Fish. Soc. **122**: 348–356.

Juanes, F., Hare, J.A., and Miskiewicz, A.G. 1996. Comparing early life history strategies of *Pomatomus saltatrix*: a global approach. Mar. Freshwater Res. **47**: 365–379.

Kendall, A.W., Jr., and Walford, L.A. 1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull. U.S. **77**: 213–227.

Kerfoot, W.C., and Sih, A. 1987. Predation:direct and indirect impacts on aquatic communities. University Press of New England, Hanover, N.H.

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, N.C.

Leggett, W.C., and DeBlois, E. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Neth. J. Sea Res. **32**: 119–134.

Marks, R.E., and Conover, D.O. 1993. Ontogenetic shift in the diet of young-of-year bluefish *Pomatomus saltatrix* during the oceanic phase of the early life history. Fish. Bull. U.S. **91**: 97–106.

McBride, R.S., and Conover, D.O. 1991. Recruitment of young-of-the-year bluefish *Pomatomus saltatrix* to the New York Bight: variation in abundance and growth of spring- and summer-spawned cohorts. Mar. Ecol. Prog. Ser. **78**: 205–216.

McBride, R.S., Scherer, M.D., and Powell, J.C. 1995. Correlated variations in abundance, size, growth, and loss rates of age-0 bluefish in a southern New England estuary. Trans. Am. Fish. Soc. **124**: 898–910.

Murdoch, W.W., Avery, S., and Smyth, M.E.B. 1975. Switching in predatory fish. Ecology, **56**: 1094–1105.

Nielsen, L.A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Can. J. Fish. Aquat. Sci. **37**: 11–19.

Nyman, R.M., and Conover, D.O. 1988. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fish. Bull. U.S. **86**: 237–250.

Pace, M.L., Baines, S.B., Cyr, H., and Downing, J.A. 1993. Relationships among early life stages of *Morone americana* and *Morone saxatilis* from long-term monitoring of the Hudson River estuary. Can. J. Fish. Aquat. Sci. **50**: 1976–1985.

Pierce, C.L., Rasmussen, J.B., and Leggett, W.C. 1990. Sampling littoral fish with a seine: corrections for variable capture efficiency. Can. J. Fish. Aquat. Sci. **47**: 1004–1010.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Rieman, B.E., Beamesderfer, R.C., Vigg, S., and Poe, T.P. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day reservoir, Columbia River. Trans. Am. Fish. Soc. **120**: 448–458.

Scharf, F.S., Buckel, J.A., Juanes, F., and Conover, D.O. 1997. Estimating piscine prey sizes from partial remains: testing for shifts in foraging mode by juvenile bluefish. Environ. Biol. Fishes, **49**:377–388.

Scharf, F.S., Buckel, J.A., Juanes, F., and Conover, D.O. 1998. Predation by juvenile piscivorous bluefish: the influence of prey: predator size ratio and prey type on predator capture success and prey profitability. Can. J. Fish. Aquat. Sci. **55**: 1695–1703.

Seber, G.A.F. 1973. The estimation of animal abundance, and related parameters. Hafner Press, New York.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman and Company, New York.

Steinberg, N.S. 1994. Young-of-the-year bluefish (*Pomatomus saltatrix*) consumption in the Hudson River estuary: a bioenergetics modeling approach. M.S. thesis, State University of New York, Stony Brook, N.Y.

Sykes, J.E., and Manooch, C.S. 1979. Estuarine predator–prey relations. *In* Predator–prey systems in fisheries mangement. *Edited by* H. Clepper. Sport Fishing Institute, Wahington, D.C.

Texas Instruments Inc. 1976. Predation by bluefish in the lower Hudson River. Consolidated Edison Company, New York.

Tonn, W.M., Paszkowski, C.A., and Holopainen, I.J. 1992. Piscivory and recruitment: mechanisms structuring prey populations in small lakes. Ecology, **73**: 951–958.

Townsend, C.R., Winfield, I.J., Peirson, G., and Cryer, M. 1986. The response of young roach *Rutilus rutilus* to seasonal changes in abundance of microcrustacean prey: a field demonstration of switching. Oikos, **46**: 372–378.

van der Veer, H.W. 1986. Immigration, settlement, and density-dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. **29**: 223–236.

van der Veer, H.W., and Bergman, M.J.N. 1987. Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. Mar. Ecol. Prog. Ser. **35**: 203–215.

Versar, Inc. 1988. Evaluation of Hudson River beach seine programs conducted by the New York Utilities and the New York State Department of Environmental Conservation. Versar, Inc., Columbia, Md.

Waldman, J.R. 1986. Diagnostic value of *Morone* dentition. Trans. Am. Fish. Soc. **115**: 900–907.

Walters, C.J., and Juanes, F. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can. J. Fish. Aquat. Sci. **50**: 2058–2070.

Wright, R.A., Crowder, L.B., and Martin, T.H. 1993. The effects of predation on the survival and size-distribution of estuarine fishes: an experimental approach. Environ. Biol. Fishes, **36**: 291–300.