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.


**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...
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 oreognomus)) 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 1996a), 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 (en- graulid 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 Runsey 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 conger ners 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 (Fk) was calculated as

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\[ F_k = \frac{\sum_{i=1}^{n} M_i p_{ik}}{\sum M_i} \]

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

\[ \nu(F_k) = \frac{1}{nM^2} \sum_{i=1}^{n} M_i^2 (p_{ik} - F_k)^2 \]

where \( M \) 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

\[ W_k = \frac{\sum_{i=1}^{n} M_i q_{ik}}{\sum M_i} \]

where

\[ q_{ik} = \frac{w_{ik}}{w_j} \]

and where \( w_j \) 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

\[ \nu(W_k) = \frac{1}{nM^2} \sum_{i=1}^{n} M_i^2 (q_{ik} - W_k)^2 \]

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

\[ \alpha_i = \frac{n_i/p_i}{\sum_{j=1}^{m} n_j/p_j}, \text{ } i = 1, \ldots, m \]

where \( \alpha_i \) 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 \( \alpha_i \) were calculated for each beach seine haul. The mean \( \alpha_i \) 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 \( \alpha_i \) on a given date — an identical value of \( p_i \) was used for each beach seine haul estimate of \( \alpha_i \). For statistical purposes, a unique value of \( p_i \) for each seine haul estimate of \( \alpha_i \) 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 \( \alpha_i \) 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 \( \alpha_i \) 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, \( D \leq SE \)), weight (grams, \( W \leq SE \)), daily ration (grams per gram per day, \( R \leq SE \)), and striped fish sizes eaten by bluefish (grams, \( S \leq SE \)), and striped bass sizes eaten by bluefish (grams, \( S \leq SE \)). 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, \( r^2 \geq 0.70 \), \( n = 66 \); 1993: striped bass TL eaten (millimetres) = 0.965·(day) – 9.081, \( r^2 = 0.70 \), \( n = 135 \); 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 \( (S \text{ grams}) = 7.0 \times 10^{-6} \text{TL}^{3.06}, \text{ } r^2 = 0.99 \), \( n = 246 \). 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 \( D, W, (\log \text{ transformed to linearize), } C, \) 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 (±SE) of the

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nearshore per day was calculated in three steps. First, nearshore bluefish biomass \((B \pm SE)\) was calculated as 
\[
B = D \times W,
\]
where \(D\) is the number of fish per 100 m² per day (SBC ± SE) was calculated as 
\[
SBC = B \times C \times P.
\]
where \(C\) is the geometric mean number of striped bass per 100 m² (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 ±1 SE of \(N_i\). 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>
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<th>Date</th>
<th>Survey</th>
<th>Weight (g)</th>
<th>Mean (SD)</th>
<th>CPUE</th>
<th>Mean (SD)</th>
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<tr>
<td></td>
<td></td>
<td>No. of fish</td>
<td></td>
<td>No. of hauls</td>
<td></td>
</tr>
<tr>
<td>1992</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>2.25 (1.83)</td>
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<td>8</td>
<td>6.57 (5.35)</td>
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<td>179</td>
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<td>3.76 (3.77)</td>
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<td>25</td>
<td>2.00 (1.94)</td>
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<tr>
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<td>25</td>
<td>1.92 (2.45)</td>
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<tr>
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<td>September 1–2</td>
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<td>25</td>
<td>0.52 (1.12)</td>
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<tr>
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<td>na</td>
<td>8</td>
<td>0</td>
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<tr>
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<td>8.14 (1.86)</td>
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<tr>
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<td>na</td>
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<td>25</td>
<td>5.26 (8.48)</td>
</tr>
<tr>
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</tr>
<tr>
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<td>na</td>
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<tr>
<td>August 24–25</td>
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<td>23</td>
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<td>1.64 (1.98)</td>
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<td>34</td>
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<td>2.00 (4.80)</td>
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<tr>
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<td>NYDEC</td>
<td>2</td>
<td>119.66 (7.25)</td>
<td>25</td>
<td>0.20 (0.41)</td>
</tr>
</tbody>
</table>

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.
catch curve analysis; the instantaneous mortality rate (Z, per day) was calculated as the slope of the linear regression of log(CPUE) against day (Ricker 1975). Daily conditional mortality rates (percent per day) were calculated as 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; Barnhouse 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 larval (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-Harmonstraw 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 Rhiithropanopus harisi) 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 pseudoharengus), 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. harisi), unidentified copepods, unidentified isopods, unidentified amphipods, blue crab (Callinectes sapidus), sand shrimp (Cragon 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, χ² = 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.

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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 –
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 feeding 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
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 (Chesson’s α, see text for calculations) in spring-spawned bluefish collected in the Hudson River estuary.

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

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.

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 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%·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 the summer.
Fig. 2. Relationship between bluefish selectivity (Chesson’s $\alpha$) 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 $4.1\text{-day}^{-1}$. 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 $5.1\text{-day}^{-1}$ (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 $5.3\text{-day}^{-1}$ ($\pm 1$ 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 $6\%\text{-day}^{-1}$). Shrimp (Crangon crangon) predation causes density-dependent mortality in age-0 plaice shortly after settlement, resulting from both the functional and numerical responses
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.

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**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.

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

**Note:** Total loss (mortality plus emigration) was estimated as $Z = 4.1$ · day−1 for 1993; no estimate of Z could be made in 1992. na, not applicable.
Buckel et al.

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.

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