Functional response and switching behavior of young-of-the-year piscivorous bluefish

Jeffrey A. Buckel*, Allan W. Stoner

NOAA National Marine Fisheries Service, James J. Howard Marine Sciences Laboratory, 74 Magruder Road, Highlands, NJ 07732, USA

Abstract

Young-of-the-year (YOY) bluefish, *Pomatomus saltatrix* (L.) impose significant mortality on recently metamorphosed striped bass, *Morone saxatilis* (W.) in the Hudson River estuary. Field observations indicate that bluefish selectivity on striped bass increases with increasing striped bass density suggesting a density-dependent feeding response. Functional response and switching experiments were conducted to aid in determining the mechanism for this response. The type of functional response exhibited by bluefish under several prey treatments was examined. These were striped bass alone, Atlantic silversides, *Menidia menidia* (L.) alone, striped bass with a background density of alternative prey, and striped bass in the presence of eelgrass *Zostera marina* (L.). The functional response of bluefish to increasing prey density was more similar to a type I or II model than a type III model under all treatments. Switching was examined by providing bluefish both striped bass and silversides at five different ratios with and without a prey refuge, eelgrass. Bluefish did not exhibit a type III functional response or switching behavior suggesting that these mechanisms do not explain the observed density-dependent selectivity pattern in the field. Switching experiments did suggest that the presence of prey refuge can determine selectivity by YOY bluefish in the field. The abundance of submerged aquatic vegetation and other prey refuge may be important in controlling the predatory impact of bluefish on striped bass in the Hudson River. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Density-dependent; Functional response; *Morone saxatilis*; *Pomatomus saltatrix*; Seagrass; Switching

*Corresponding author. Present address: Department of Biology, University of West Florida, 11000 University Parkway, Pensacola, FL 32514, USA. Tel.: +1-850-474-2014; fax: +1-850-474-2749.
E-mail address: buckel@uwf.edu (J.A. Buckel)

1. Introduction

The importance of density-dependent mortality to the maintenance of population stability is widely recognized (Murdoch and Oaten, 1975; Hassell, 1978). Several field studies provide evidence for density-dependent mortality in marine fishes (Van der Veer, 1986; Myers and Cadigan, 1993; Forrester, 1995; Hixon and Carr, 1997). However, identifying mechanisms that generate density-dependent mortality has been elusive (Bailey, 1994). One mechanism that can induce density-dependent mortality is the type III functional response (Holling, 1965; Hassell, 1978).

The functional response refers to the number of prey eaten per predator per unit time as a function of prey density. In the type III functional response (sigmoid), the risk of being preyed upon is small at low prey densities but increases up to a certain point as prey density increases. This is referred to as positive density-dependent or stabilizing mortality (Holling, 1965; Hassell, 1978). Several factors can lead to a type III functional response such as predator learning, prey refuge, and the presence of alternative prey (Holling, 1965). The presence of a prey refuge has been hypothesized to be a factor leading to positive density-dependent mortality in several predator/prey systems (Hassell, 1978; Bailey, 1994; Hixon and Carr, 1997). Alternative prey can lead to a type III functional response through switching behavior (Murdoch, 1969; Murdoch and Marks, 1973; Murdoch et al., 1975). Prey switching occurs when the prey type with the highest relative abundance is included disproportionately more in the predator's diet than would be expected from random feeding.

After being spawned in offshore oceanic waters, young-of-the-year (YOY) bluefish *Pomatomus saltatrix* (Linnaeus) move into the Hudson River estuary in late June becoming piscivorous upon arrival (Juanes et al., 1993). During their first summer, YOY bluefish growth is rapid with fish growing from ~ 60 to 150–200 mm before leaving the estuary in early fall (Nyman and Conover, 1988; McBride and Conover, 1991). This rapid growth results from high feeding rates (Juanes and Conover, 1994a; Buckel and Conover, 1997). In the Hudson River estuary, predation by YOY bluefish is a significant source of mortality in YOY striped bass *Morone saxatilis* (Walbaum) (Buckel et al., 1999). However, the presence of alternative prey, such as Atlantic silversides *Menidia menidia* (Linnaeus) and bay anchovy *Anchoa mitchilli* (Valenciennes), appears to reduce the predation pressure of bluefish on striped bass. Bluefish selectivity for striped bass increases with increasing striped bass abundance suggesting a type III functional response resulting from density-dependent switching behavior (Buckel et al., 1999). Additionally, the Hudson River estuary has areas of submerged aquatic vegetation (e.g. freshwater eelgrass, *Vallisneria americanna*) which may provide refuge for striped bass.

Here, we attempt to identify the mechanism that leads to a density-dependent response of YOY bluefish preying on YOY striped bass using laboratory experiments. First, we determine if YOY bluefish exhibit a type III functional response under several prey treatments. These were striped bass alone, Atlantic silversides alone, and striped bass with a background density of alternative prey. These experiments were conducted on small and large bluefish resembling bluefish sizes from early and late summer. Second, the effect of eelgrass on the functional response of bluefish preying on striped bass was examined. Third, we tested for switching behavior in bluefish using striped bass and

Atlantic silversides as prey. The last experiment was conducted with and without eelgrass.

2. Methods

2.1. Fish collection and acclimation

Young-of-the-year bluefish, Atlantic silversides (AS), and killifish (*Fundulus* sp.) were collected in Sandy Hook Bay, NJ (40° 27′ N, 74° 00′ W) and YOY striped bass (SB) were collected in the Haverstraw Bay region of the lower Hudson River estuary, NY (41° 10′ N, 73° 10′ W) using beach seines. Fish were immediately transported to the James J. Howard Marine Sciences Laboratory at Sandy Hook and acclimated in round tanks (1.8 m diameter, 0.6 m deep) with flow-through seawater. Striped bass collected in the Hudson River were brought from low salinity (~ 5 ppt) to Sandy Hook Bay salinities (~ 25 ppt) over 24 h. Fish held for experiments were maintained in water temperatures of 19–21°C and a 12-h light/dark photoperiod; lighting was programmed for 30-min 'sunrise' and 'sunset' periods. Temperature was controlled by a mixture of ambient and chilled seawater. Fish were held for at least 48 h before being used in an experiment. All bluefish were fed cut fish and live killifish. Striped bass, AS, and killifish were fed a commercial fish food, previously frozen adult brine shrimp, and brine shrimp nauplii.

2.2. Functional response

2.2.1. Effects of bluefish body size, prey type, and alternative prey

Functional response experiments were performed with small YOY bluefish during mid-summer (8–17 July, 1997) and large YOY bluefish during late-summer (20–29 August, 1997). A group of 30 bluefish was used for each 10-day series of trials. At the start of each series of trials, bluefish were measured (total length (TL); ±1 mm), weighed (±0.01 g), and randomly assigned to ten round tanks (2.3 m diameter × 0.6 m deep) with flow-through sea water and lined with a 2–3-cm layer of coarse sand. Each tank received three bluefish. These fish were allowed to acclimate for 24 h before experiments were conducted. Bluefish were not measured daily because of the short duration of trials within each size group. Initial (day 0; small bluefish mean TL = 81 mm, range = 72–90; large bluefish mean TL = 155 mm, range = 148–164) and final measurements of bluefish sizes (day 10; small bluefish mean TL = 94 mm, range = 82–103; large bluefish mean TL = 166 mm, range = 155–175) were made (Table 1). Growth rates of bluefish within each tank were calculated from the initial and final sizes and used to estimate the size of bluefish for any given trial date. Temperature was maintained at 20–21°C throughout all experiments.

Three functional response experiments were conducted with small and large bluefish (Table 1): Atlantic silversides (AS) alone, striped bass (SB) alone, and SB with five AS as alternative prey. The third experiment was conducted to determine the effect of a constant background density of an alternative prey on the shape of the bluefish functional response. Five AS were chosen so that at low SB densities, bluefish had

Table 1
Mean bluefish and prey sizes, and mean prey:predator length ratios for each functional response experiment[a]

Bluefish size	Treatment	n	Mean bluefish size (mm) (S.E.)	Mean prey size (mm) (S.E.)	Mean prey:predator length ratio (S.E.)
S	AS	24	83.7 (0.5)	30.4 (0.4)	0.363 (0.005)
S	SB	18	88.6 (0.9)	29.0 (0.2)	0.327 (0.004)
S	SB + AS	18	90.3 (0.8)	29.5 (0.5)	0.328 (0.006)
L	AS	15	163.1 (0.8)	57.6 (0.4)	0.353 (0.002)
L	SB	12	161.4 (0.7)	58.2 (0.4)	0.361 (0.002)
L	SB + AS	12	160.4 (1.0)	58.5 (0.5)	0.365 (0.003)
NA	SB + eelgrass	23	126.0 (0.3)	50.3 (0.2)	0.399 (0.001)

[a] Treatments are: AS, Atlantic silversides; SB, striped bass; SB + AS, striped bass + five Atlantic silversides for both small (S) and large (L) bluefish. SB + eelgrass refers to the eelgrass (*Zostera marina*) treatment conducted using striped bass as prey. NA, not applicable. n = number of trials.

nearly equal choice of prey types and at high SB densities the AS would represent an uncommon prey at 20–25% of the total available prey.

For the small bluefish treatment, the initial prey densities within each of the prey type experiments were 4, 6, 8, 12, 16, and 20 prey replicated at least three times. Because AS were easy to obtain, additional trials with 1, 2, and 3 prey were completed for this prey species. These extra densities were added to aid in determining the shape of the functional response near the origin. Initial prey densities for the large bluefish trials were 4, 8, 12, and 16 prey replicated three times. The AS prey treatment for large bluefish required one extra density (20 prey) for the function to reach an asymptote.

We could not conduct each prey type experiment sequentially because bluefish and their prey grow rapidly (e.g. if we began with prey type 'a' and ended with prey type 'b', the bluefish sizes used for the prey type 'b' experiment would be larger than those used for the prey type 'a' experiment). Therefore, the three experiments were conducted simultaneously over 10 days. On an experimental trial day, ten different prey type × prey density trials were selected and assigned randomly to the ten tanks of three bluefish each. Prey sizes were matched to bluefish sizes to control for prey length:predator length ratios (Table 1).

Bluefish were fed live killifish to satiation on the day prior to an experiment. Small bluefish were starved for at least 12 h prior to an experiment and large bluefish required a starvation of at least 24 h to insure feeding during the experimental trial. At the start of an experiment, prey were held within a clear tube near the center of the tank. The tube allowed prey to acclimate to the presence of predators (e.g. begin schooling). Bluefish often struck the tube while attempting attacks on prey. After 5–10 min of acclimation, the tube was removed to allow bluefish access to the prey. After 1 h, (sufficient time for bluefish to become sated), uneaten prey were removed and counted. For each initial prey density, the number of prey consumed per bluefish per h was calculated. Also, the sand was closely examined for buried fish and the percentage of the initial prey density that buried was calculated.

2.2.2. Effects of eelgrass

The effect of eelgrass *Zostera marina* (Linnaeus) on the functional response of YOY bluefish to YOY striped bass was determined from 20–23 July 1998. These trials were

conducted identically to those described above with a 24-h starvation period. Additionally, the experimental tanks were planted with eelgrass in bunches that covered half of the tank bottom (mean bunch per tank = 17 and mean shoots per tank = 449 (225 shoots m^{-2}; mean of three randomly chosen tanks)). As above, initial (day 0; bluefish mean TL = 124 mm, range = 114–132) and final sizes (day 3; bluefish mean TL = 128 mm, range = 120–134; see Table 1) were used to estimate growth rates of bluefish within each tank; estimates of growth rate were used to calculate the size of bluefish for any given trial date. The initial prey densities were 2, 4, 6, 8, 12, and 16. These densities were replicated at least four times with the exception of 16 prey for which there was one observation.

2.2.3. Analysis

The type of functional response curve (e.g. type I, II, or III) that provided the best fit to the data was determined using logit analysis (Trexler et al., 1988; Juliano, 1993). This analysis was performed on proportion of prey eaten verse initial prey density using a second order logit model for all functional response experiments. If bluefish exhibit a type III functional response, the linear term of the logit model is significantly positive and the second order term of the model is significantly negative (Juliano, 1993). A type II functional response is appropriate if the first order term is significantly negative (proportion prey eaten declines with increasing initial prey density) (Juliano, 1993). If the linear term of the logit model is non-significant (proportion prey eaten constant over increasing initial prey density), then a type I functional response model best describes the original data.

Based on the logit analysis results (see below), YOY bluefish did not exhibit a type III response in six out of seven functional response experiments. In five out of seven trials, the logit analysis suggested a type I functional response but our experimental design may have limited our ability to detect the type II model (see below). Therefore, both type I and II functional response models were used on our data. To model the type I functional response, piecewise regression analysis was used to estimate the attack constant (initial slope, Hassell, 1978) and determine the breakpoint. The following piecewise regression model was fitted with a non-linear estimation procedure:

$$N_e = aNT + b(N - BREAK)*(N > BREAK)$$

where, N_e = number of prey eaten.bluefish^{-1} h^{-1}, N = initial prey density, a = attack constant (or instantaneous search rate), T = total time available (1 h), b = change in slope after the breakpoint, and $BREAK$ = the estimated breakpoint ($N > BREAK$ is a conditional statement that returns a value of 0 if false and a value of 1 if true). The constant b was ignored as the breakpoint was considered the asymptote of the type I functional response. The type II model based on the Holling (1965) disc equation (see Hassell, 1978) was fitted using non-linear regression analysis:

$$N_e = \frac{aNT}{1 + aNT_h}$$

where terms are as above and T_h = handling time.

2.3. Prey switching

We tested for prey switching in bluefish provided with striped bass and Atlantic silverside prey. These trials were conducted with and without eelgrass. Striped bass and Atlantic silversides were presented in five different ratio treatments: 12% SB:88% AS, 25% SB:75% AS, 50% SB:50% AS, 75% SB:25% AS and 88% SB:12% AS. The total prey number was 40 for the 25% SB:75% AS, 50% SB:50% AS, 75% SB:25% AS ratios and 100 for the 12% SB:88% AS and 88% SB:12% AS ratios. The total prey number was increased to 100 for the extreme ratios because the rare prey could have been too easily depleted if only 40 prey were used (e.g. 10% of 40 equals only four prey). Each treatment was replicated three times.

Each ratio treatment was performed in two identical glass fronted tanks (1900 l; 2.48 m length×0.88 m width×0.96 m depth) with and without eelgrass. Bunches of eelgrass were planted in a grid-like pattern in half of the eelgrass tank (total of 20 clumps in a 1-m^2 area). Of five randomly chosen bunches there was a mean of 45 shoots per bunch and 3.7 blades per shoot. Temperature was maintained at 19–21°C and the photoperiod was 12-h light/dark.

Prey length, bluefish length, and prey length/predator length ratios were measured and means were calculated for each trial. The mean of these means was calculated for each treatment (Table 2). The total length of AS was not statistically different from SB TL at any of the ratio×refuge treatments (*t*-test, all *p*>0.05).

At least 3 h before the start of the experiment, three bluefish were stocked into each of the two tanks. It was necessary to satiate bluefish before prey were added so that bluefish did not make immediate indiscriminate attacks where potential predator choice and prey behavior would have no influence on selectivity patterns. After bluefish were satiated with killifish experimental prey were introduced into each tank.

Each trial began in early afternoon and ran for 20 h. In this design, bluefish experienced 'sunset' and 'sunrise' periods. Bluefish feeding activity is often highest near these crepuscular periods (Juanes and Conover, 1994a; Buckel and Conover, 1997). Bluefish and prey behavior were quantified in the 12% SB:88% AS and 88% SB:12% AS ratio treatments approximately 30 min before sunset and 30 min after sunrise for the three replicates. The observation periods lasted 10 min and predator and prey locations in the tank were recorded every minute. For each observation period, the percent minutes that prey spent at the surface was calculated.

At the end of the trial, both tanks were drained and bluefish and prey removed. Prey were identified and counted. The proportion of striped bass taken out of the total number of prey consumed was calculated for each ratio×refuge treatment. The proportion of striped bass eaten was compared to proportion of striped bass offered to test for switching. Bluefish preference for striped bass was estimated for the 15 trials with eelgrass and for the 15 trials conducted without eelgrass. Chesson's Index (1978) under conditions of prey depletion was used to calculate values of selectivity. The mean values of selectivity for striped bass in these two eelgrass treatments were compared to a constant value of 0.50 representing random feeding for a two prey type situation (Chesson, 1978).

Table 2
Mean bluefish and prey sizes, and mean prey:predator length ratios for the switching experiment[a]

Treatment	Ratio treatment (% SB:AS)	Mean bluefish size (mm) (S.E.)	Mean SB size (mm) (S.E.)	Mean AS size (mm) (S.E.)	Mean SB:predator length (S.E.)	Mean AS:predator length (S.E.)
Eelgrass	12:88	110.7 (2.3)	45.1 (1.3)	45.0 (1.2)	0.407 (0.004)	0.407 (0.002)
Eelgrass	25:75	138.9 (4.0)	49.5 (1.5)	48.1 (1.5)	0.357 (0.007)	0.346 (0.001)
Eelgrass	50:50	140.4 (1.8)	50.8 (0.9)	49.9 (1.1)	0.362 (0.001)	0.355 (0.003)
Eelgrass	75:25	142.6 (5.3)	51.6 (2.0)	50.8 (2.2)	0.362 (0.002)	0.356 (0.003)
Eelgrass	88:12	115.1 (4.3)	47.2 (2.0)	47.2 (1.8)	0.410 (0.002)	0.410 (0.003)
No eelgrass	12:88	110.2 (2.3)	45.2 (1.4)	44.7 (1.0)	0.410 (0.004)	0.406 (0.001)
No eelgrass	25:75	138.0 (3.7)	50.0 (1.2)	48.3 (1.4)	0.362 (0.005)	0.350 (0.001)
No eelgrass	50:50	140.0 (1.5)	50.4 (1.0)	50.3 (1.4)	0.360 (0.003)	0.359 (0.006)
No eelgrass	75:25	142.7 (5.3)	51.3 (2.2)	50.9 (2.7)	0.359 (0.003)	0.357 (0.006)
No eelgrass	88:12	115.2 (4.1)	47.6 (1.6)	47.6 (1.7)	0.414 (0.003)	0.413 (0.002)

[a] Treatments are eelgrass and no eelgrass. Prey ratio treatments are: 12% SB:88% AS, 25% SB:75% AS, 50% SB:50% AS, 75% SB:25% AS and 88% SB:12% AS. The total prey number for the 25% SB:75% AS, 50% SB:50% AS, and 75% SB:25% AS ratios was 40. The total prey number was 100 for the 12% SB:88% AS and 88% SB:12% AS treatments. Each treatment was replicated three times.

3. Results

3.1. Functional response

3.1.1. Effects of bluefish body size, prey type, and alternative prey

Bluefish feeding rate increased with increasing initial prey density in all functional response experiments (Fig. 1). The logit regression analysis describing the proportion mortality verse initial mean prey density indicates that bluefish did not exhibit a type III density-dependent feeding response. The first order term from the logit regressions was significantly positive ($p < 0.05$) in only one out of six experiments (Table 3). Although the analysis of the large bluefish SB experiment suggests a type III response (Table 3) the shape of the raw data indicates a type I or II response.

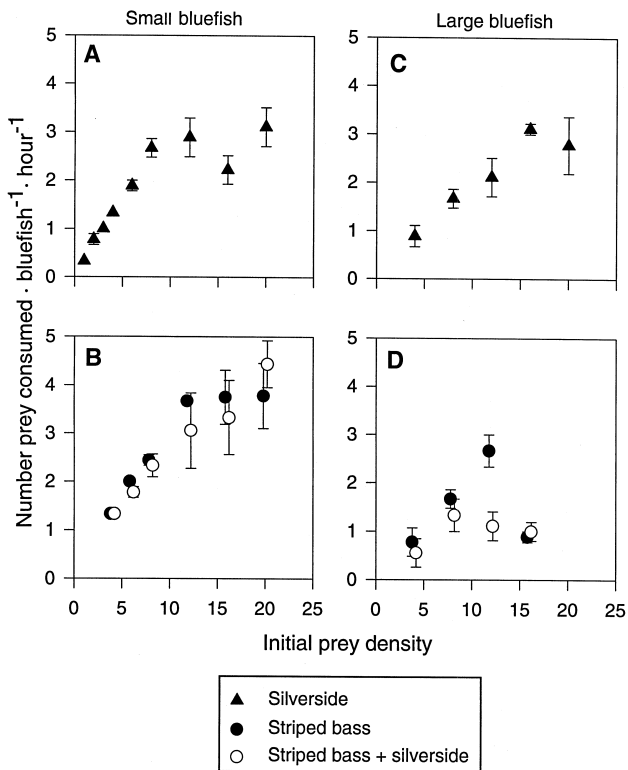Small bluefish had maximum feeding rates of 3.1 AS and 3.8 SB per hour for single

Fig. 1. Number of prey consumed.bluefish^{-1}.h^{-1} for small (A and B) and large (C and D) bluefish with increasing initial prey density at three prey treatments. Prey treatments are Atlantic silverside (A,C: closed triangles), striped bass (B,D: closed circles) and striped bass + Atlantic silverside prey (B,D: open circles). Bars are ($\pm$) standard error.

Table 3

Parameter estimates (and significance levels) from second-order logit analyses of proportion of prey killed verse initial prey density[a]

Bluefish size	Prey type	Intercept (p-level)	N_o (p-level)	N_o^2 (p-level)	Interpretation (Type)
S	AS	8.3426 (0.0006)	−0.9505 (0.0039)	0.0262 (0.0154)	II
S	SB	6.4053 (0.0223)	−0.4571 (0.2101)	0.0075 (0.5261)	I
S	SB + AS	4.8178 (0.0074)	−0.4405 (0.0917)	0.0116 (0.2033)	I
L	AS	0.5160 (0.6299)	0.0246 (0.8869)	−0.0032 (0.6211)	I
L	SB	−2.1780 (0.1325)	0.7384 (0.0172)	−0.0435 (0.0039)	III
L	SB + AS	−0.3686 (0.7957)	0.0968 (0.7399)	−0.0106 (0.4386)	I
NA	SB + eelgrass	0.2945 (0.7039)	−0.0237 (0.9016)	−0.0048 (0.6531)	I

[a] The functional response type (I, II, or III) interpreted from the analysis is listed (see text for explanation). Treatments are: AS, Atlantic silversides; SB, striped bass; SB + AS, striped bass + five Atlantic silversides for both small (S) and large (L) bluefish. SB + eelgrass refers to the eelgrass (*Zostera marina*) treatment conducted using striped bass as prey. NA, not applicable.

prey species experiments (Fig. 1A,B). Maximum feeding rates on AS and SB in the large bluefish functional response experiments were 3.1 and 2.7 prey per hour, respectively (Fig. 1C,D). The addition of five AS in the SB + AS treatments did not affect the shape of the functional response of bluefish to increasing initial SB density (Tables 3, 4, Fig. 1B,D); however, the feeding rates of both small and large bluefish on SB were reduced in the SB + AS treatments at most prey densities (Fig. 1B,D).

Striped bass prey in the large bluefish functional response experiment were not completely available to bluefish. Striped bass buried in the sediment and by doing so avoided predation by bluefish. There was a significant negative relationship between the

Table 4

Parameter estimates for type I and type II functional response models fitted to numbers of prey killed per bluefish verse initial prey density[a]

Bluefish size	Prey type	Type I			Type II		
		a	Asymptote (*BREAK*)	r^2	a	T_h	r^2
S	AS	0.3268	7.9999	83.44	0.5947	0.2487	78.93
S	SB	0.3173	11.5733	68.87	0.5096	0.1487	64.28
S	SB + AS	0.3048	7.0597	63.56	0.3612	0.0985	62.95
L	AS	0.1917	16.0150	70.54	0.2835	0.1532	65.79
L	SB	0.2163	12.1456	81.62	0.5831	0.4592	12.57
L	SB + AS	0.1600	8.0000	32.23	0.3983	0.6975	13.87
NA	SB + eelgrass	0.1571	10.2065	54.41	0.2753	0.4555	49.68

[a] See text for model descriptions and parameter definitions. Treatments are: AS, Atlantic silversides; SB, striped bass; SB + AS, striped bass + five Atlantic silversides for both small (S) and large (L) bluefish. SB + eelgrass refers to the eelgrass (*Zostera marina*) treatment conducted using striped bass as prey. NA, not applicable.
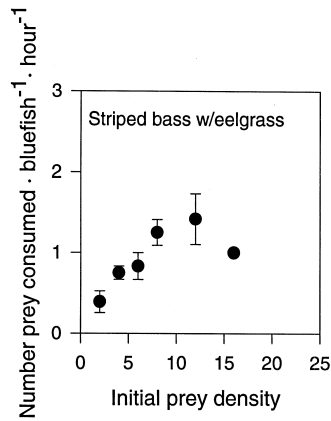
Fig. 2. Number of striped bass.consumed.bluefish^{-1} h^{-1} with increasing striped bass density in the presence of eelgrass (*Zostera marina*). Note differences in *y*-axis scale compared to Fig. 1. Bars are ($\pm$) standard error.

proportion of buried striped bass and initial striped bass density for the combined SB and SB + AS experiment ($r = -0.422$, $p = 0.040$). Therefore, striped bass that occurred in larger schools in the experimental tanks appear to have less propensity to bury in response to bluefish predation.

3.1.2. Effects of eelgrass

Bluefish feeding rate increased with increasing initial striped bass density in the presence of eelgrass (Fig. 2). The logit regression analysis indicated that the functional response of bluefish to striped bass with eelgrass was not a type III functional response (Tables 3, 4). However, in two out of five trials conducted at the lowest density of striped bass there was zero mortality; this was never seen in the trials with no eelgrass. Additionally, the maximum number of prey consumed was reduced compared to the small and large bluefish trials feeding on striped bass without eelgrass (Fig. 1).

3.2. Prey switching

In the eelgrass and no eelgrass trials, the mean proportion of SB consumed was not statistically different than the proportion of SB offered at any of the treatment ratios (*t*-test, all $p > 0.005$, adjustment for multiple *t*-tests: $p = 0.05/10$; Fig. 3). Switching behavior was not observed. However, mean estimates of Chesson's selectivity index show that bluefish selected for striped bass in the no eelgrass treatment (*t*-test of Chesson's index vs. 0.50, $t = 3.79$, df $= 14$, $p = 0.002$) but preyed randomly with respect to relative abundance of striped bass in the eelgrass treatment (*t*-test of Chesson's index vs. 0.50, $t = 0.41$, df $= 14$, $p = 0.690$; Fig. 4).

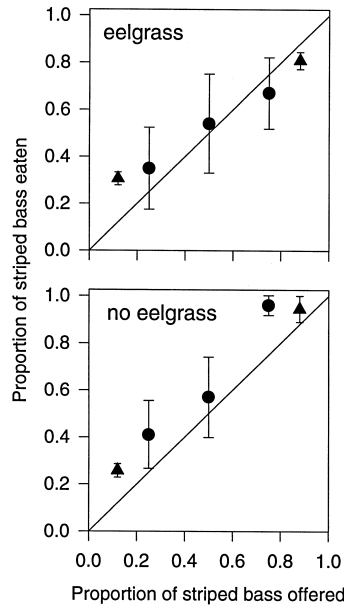The use of the water surface by Atlantic silversides differed between the eelgrass and

Fig. 3. Mean ($\pm$S.E.) proportion of striped bass consumed vs. proportion of striped bass offered for (a) eelgrass (*Zostera marina*) and (b) no eelgrass treatments. The alternative prey was Atlantic silverside. Percentages of the total prey that are striped bass out of a total of 40 prey are shown as squares and those out of 100 prey are shown as triangles. Random feeding is represented by diagonal line.

no-eelgrass treatments. In the absence of eelgrass, silversides spent a significantly larger amount of time (92%) at the water surface compared to the eelgrass treatment (37% of time at surface; $t = 3.39$, df $= 22$, $p = 0.003$; Fig. 5). There was no difference in time spent at the water surface by striped bass in the eelgrass and no eelgrass treatments (25 vs. 25%; $t = 1.9 \times 10^{-16}$, df $= 22$, $p = 1.0$).
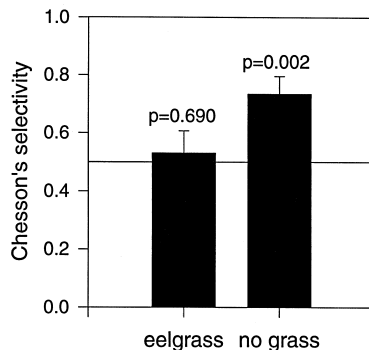

Fig. 4. Mean ($\pm$S.E.) Chesson's selectivity index for striped bass in eelgrass (*Zostera marina*) and no eelgrass treatments. All ratio treatment trials are pooled.
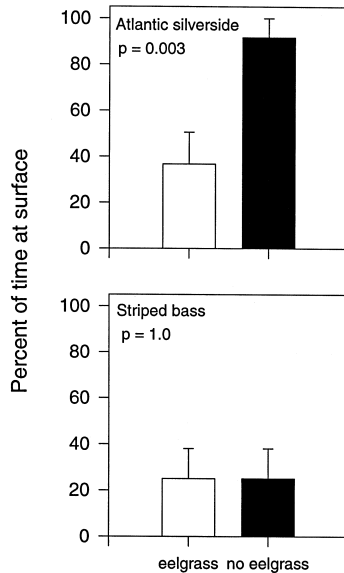
Fig. 5. Mean (±S.E.) percent time spent at surface out of 10-min observation periods during crepuscular periods for striped bass and Atlantic silverside prey in (a) eelgrass (*Zostera marina*) and (b) no eelgrass treatments.

4. Discussion

4.1. Functional response

There was no evidence for a type III response indicative of positive density-dependence in any of the functional response experiments. The lack of a type III response was expected for the single prey type experiments because bluefish are known to consume prey readily at low densities in experimental tanks. The single prey type treatments provided a laboratory baseline for comparison with more complex treatments. Based on previous empirical findings (Holling, 1965), we hypothesized that an alternative prey would affect the shape of the functional response of bluefish with striped bass as prey. Bluefish predation on striped bass was lowered in the presence of the alternative prey but the shape of the functional response curve did not differ between the SB alone or SB + AS treatment at either bluefish size. Similar to our findings, Chesson (1989) found that the plateau of the functional response of an aquatic predator on mosquito prey declined with increases in alternative prey with no apparent influence on the shape of the functional response. One potential criticism of our experimental design is that we used a low density of alternative prey. However, given that switching behavior was not observed in subsequent laboratory experiments it appears unlikely that a type III response would have been observed with a large number of alternative prey.

The striped bass fed to large bluefish buried. To our knowledge this is the first documentation of striped bass burial. This behavior could be an artifact of laboratory

confinement; however, it is equally plausible that burial is a natural defense mechanism. The proportion of striped bass that buried decreased with increasing initial striped bass density suggesting that schooling became a sufficient anti-predator behavior at larger school sizes.

Given the ability of striped bass to avoid predation by burial we provided striped bass with eelgrass as refuge to investigate its effect on bluefish functional response. Although several studies have examined the effect of submerged aquatic vegetation on piscivorous fishes (Savino and Stein, 1982; Eklov and Diehl, 1994; Rooker et al., 1998), none to our knowledge have examined the effect of submerged vegetation on their functional response. The type III functional response was not observed in the striped bass trials with eelgrass. However, striped bass mortality was zero in two of the five replicates at the lowest initial density of striped bass. This total absence of predation was never seen in trials without eelgrass; typically, prey were consumed immediately. That the presence of eelgrass provided a complete refuge for a 1-h trial is striking. Young-of-the-year bluefish are known to avoid submerged vegetation (Lascara, 1981; McCollum, 1996; pers. obs.) and striped bass selected for refuge in some trials. Further studies into the effect of habitat complexity on striped bass survival are warranted.

Although we were able to reject the type III functional response model we could not discriminate between the type I and II models. The logit analysis suggests that YOY bluefish have a type I functional response, but our experimental design precludes this conclusion. Prey were not replaced and initial densities dropped during the 1-h experiment. Predators often consumed 100% of the available prey at low prey densities; higher predation rates would have been recorded if prey were replaced. Additionally, trials lasted only 1 h and post-consumptive factors like digestion time, which can affect handling time (Lankford and Targett, 1997) could not influence the shape of the functional response. Future functional response experiments with YOY bluefish should employ longer trials and prey replacement to test between these possibilities.

4.2. Prey switching

Switching was not observed in YOY bluefish in our experiment. However, field selectivity data suggests that YOY bluefish do exhibit switching behavior (Buckel et al., 1999). An examination of switching mechanisms helps to interpret the apparent discrepancy between our laboratory and field findings. Murdoch et al. (1975) found that switching could result from several different mechanisms including when (1) the predator develops a search image for the prey type with the highest relative abundance, (2) capture success on a prey type increases with increases in its relative abundance (learning), and (3) when the predator's habitat contains sub-habitats that are occupied by different prey types. In the latter mechanism switching occurs when the predator spends more time in the sub-habitat that contains the prey with the higher relative abundance. An important distinction between these mechanisms is that the prey may be encountered simultaneously in cases one and two, whereas the predator has to travel between sub-habitats to encounter different prey in the third situation.

Mechanisms one and two appear unlikely for bluefish. Previous experiments on size- (Juanes and Conover, 1994b) and prey-selection (Bell et al., 1999) indicate that bluefish

attack any prey encountered. The second mechanism involves predator learning. This mechanism has been observed in invertebrate predators feeding on drastically different prey (Lawton et al., 1974). Bluefish may learn and become more proficient at capturing specific piscine prey types with more experience; however, given that both prey types in our experiments were fish, capture techniques are not likely to be excessively different.

The third mechanism, habitat effect, may explain the difference between our laboratory and field results. This mechanism explained switching behavior by guppies in the laboratory (Murdoch et al., 1975) and by roach in a small lake (Townsend et al., 1986). In nature, predators may aggregate on the prey type that occurs in the highest relative abundance in the system but is spatially separated from the habitat occupied by rare prey. The numerical response refers to the way predator number responds to increasing prey density. For example, Van der Veer (1986) found that shrimp (predators) aggregated in habitats where newly metamorphosed juvenile plaice were abundant; this numerical response combined with a type II functional response led to positive density-dependent mortality. For a pelagic predator such as bluefish, the numerical response may not be constant because the 'feeding frenzy' behavior of bluefish (Safina and Burger, 1989) is an aggregative response. Spatial separation of two prey types is difficult to duplicate in the laboratory. Murdoch et al. (1975) documented switching in guppies between surface and bottom prey with a vertical divider in the tank that forced the guppies to spend more time moving around the aquarium. Our attempt to create different sub-habitats and separate the two prey types with eelgrass was not consistently successful and switching did not occur. The lack of spatial separation between striped bass and Atlantic silverside and the inability of bluefish to 'aggregate' on one prey type may explain the differences between our laboratory and field data. The manner in which bluefish respond numerically to relative striped bass density may result in switching behavior and an overall density-dependent response. Field and laboratory research designed to measure this response is needed.

Bluefish showed positive selection for striped bass in treatments without eelgrass and fed randomly when eelgrass was present. Behavioral differences between Atlantic silverside and striped bass appear to explain these results. In single-prey trials with no refuge bluefish had higher capture success when preying on Atlantic silverside than on striped bass (Scharf et al., 1998). With this information alone we would predict a priori that bluefish would select Atlantic silversides over striped bass. Given that bluefish did not show positive selection for Atlantic silversides in either treatment, we conclude that prey behavior influenced encounter rate. The number of attacks must, necessarily, have been higher on striped bass than Atlantic silverside. Without eelgrass, Atlantic silverside may be better at refuging in an open water column than striped bass. During our observations, Atlantic silverside spent a significantly higher percent of time at the water surface in the no eelgrass treatment than in the eelgrass treatment. The use of the water surface by striped bass did not differ between these treatments. The differences in prey behavior correspond to what is known about the behaviour of juvenile striped bass and Atlantic silversides in the field. When eelgrass was present, relative encounter rates of striped bass and bluefish likely declined in comparison to encounters in the no eelgrass treatments because, at times, striped bass used the eelgrass as refuge. Prey behavior influences encounter rate, which can ultimately affect prey selectivity patterns (reviewed

in Sih, 1993). We have shown that habitat complexity can have a significant effect on predator/prey interactions and conclude that predator/prey experiments that ignore habitat complexity may be suspect.

4.3. Summary and implications

Bluefish did not exhibit a type III functional response or switching behavior suggesting that these mechanisms do not explain the density-dependent selectivity pattern observed in the Hudson River. Although not observed in our laboratory experiments, switching cannot be ruled out as the mechanism that causes positive density-dependent selection for striped bass. Our inability to detect this behavior in a laboratory setting may be due to tank confinement. Experiments are needed that examine prey switching in a larger and deeper experimental arena that could potentially provide a larger spatial separation between the more benthic striped bass and more pelagic Atlantic silverside.

Bluefish showed strong selection for striped bass when eelgrass was absent. The abundance of submerged aquatic vegetation and other refugia may be important in controlling the recruitment dynamics of striped bass in the Hudson River estuary. Buckley (1992) argues that the abundance of submerged aquatic vegetation in the Hudson River estuary has declined leading to a decrease in nursery habitat for juvenile fish. It is currently unknown how declines in submerged aquatic vegetation or the use of alternative refugia have affected estuarine fish production (Ruiz et al., 1993).

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