Journal of Experimental Marine Biology and Ecology 368 (2009) 129–137

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Interactions between bluefish and striped bass: Behavior of bluefish under size- and number-impaired conditions and overlap in resource use

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ARTICLE INFO

Article history:
Received 1 June 2008
Received in revised form 9 September 2008
Accepted 10 September 2008

Keywords:
Bluefish
Striped bass
Competition
Diet overlap
Habitat overlap

ABSTRACT

A decline in bluefish (*Pomatomus saltatrix* L.) recreational landings during the 1990s and the early 2000s led to multiple theories on the ultimate cause. One theory was that a large portion of the bluefish population moved offshore and was unavailable to nearshore recreational fishers; one reason given for the movement offshore was increased competition with striped bass (*Morone saxatilis* W.). We conducted laboratory experiments (feeding and non-feeding) to examine behavioral interactions between adult bluefish and sub-adult striped bass in a large (121,000 L) research aquarium. Additionally, we examined diet and habitat overlap of bluefish and striped bass from the fall and spring bottom trawl surveys conducted by the National Marine Fisheries Service. Observations of feeding trials for the following treatments were made: non-impaired (i.e., same number and size of bluefish and striped bass), size-impaired (i.e., large striped bass/small bluefish), number-impaired (i.e.,10 striped bass/3bluefish), and single-species controls. Within a species, there was no difference in a variety of behavioral measures (e.g., attack rate, capture success, ingestion rate, and activity) between mixed- and control treatments under non-impaired or size-impaired conditions. However, behavior of number-impaired bluefish differed from control and size-impaired fish suggesting that striped bass may have a negative influence on bluefish foraging when bluefish are "out-numbered". Feeding had a strong effect on swimming speeds for both species. Diet and habitat overlap between bluefish and striped bass in continental shelf waters was low. Overall, foraging behavior in mixed-species treatments and field observations suggest no competitive interactions between adult bluefish and sub-adult striped bass.

1. Introduction

There is much interest in collecting data that facilitate an ecosystem-based approach to fisheries management (Gislason et al., 2000; Browman and Stergiou, 2004). Besides information on socioeconomic and habitat related issues, it is necessary to understand the interactions among species or functional groups for this approach. Often, the biotic interactions most discussed are predator-prey interactions (Whipple et al., 2000; Link, 2002). However, competitive interactions are known to influence distribution and abundance of marine fishes (Hixon and Jones, 2005) and may be important to include in models of multispecies interactions (e.g., Collie and DeLong, 1999).

Competition occurs when one organism causes a common resource to be limiting to another. Exploitative and interference competition can be important in determining the foraging behavior of fish (see Sih, 1993 for review). Exploitative (or scramble) competition refers to a dominant having a superior edge in obtaining a limited prey resource- the subordinate gets less to eat because the dominant obtains it first. Interference competitive behavior (e.g., fights, territoriality) between a dominant and subordinate can influence both foraging behavior and habitat use of the subordinate.

Much of what we know about competition in marine fishes comes from reef fish examples. For example, controlled experiments on reef fishes have shown that competition can be important in determining numbers of surviving settlers and community structure if observed over long time scales (Hixon and Jones, 2005). For pelagic fishes, the importance of competition on growth, habitat use, and survival rate is less understood because of the mobility of such species. Typically, these studies do not get beyond inferring the potential for interaction from diet overlap (Hartman and Brandt, 1995a; Bethea et al., 2004).

In the northeast U.S., two pelagic piscivores for which large recreational and commercial fisheries exist are striped bass *Morone saxatilis* W. and bluefish *Pomatomus saltatrix* L. (see Buckel and McKown, 2002 for landings data). Adult landings and juvenile recruitment indices indicate that the population of bluefish in this area declined during the 1990s and into the 2000s (Munch, 1997; Anonymous, 1998; Conover et al., 2003) and historical records indicate dramatic variations in abundance (Baird, 1873). One proposed theory for the decline in bluefish was that competition with striped bass led to displacement of bluefish

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doi:10.1016/j.jembe.2008.09.002

offshore. Wilson and Degnbol (2002) studied the debate over bluefish management in a sociological study of the stock assessment process and use of anecdotal data; they described the displacement hypothesis as one of the possibilities considered during a mid-1990s stock assessment as an explanation for declines in bluefish landings. Crecco (1996) (cited in Salerno et al., 2001) provided evidence from commercial landings and effort data that adult bluefish had been displaced further offshore where they were not as available to recreational fishers as they were in the past. One of the arguments put forward for the "displacement hypothesis" was the influence of increased numbers of striped bass in the early 1990s (Wilson and Degnbol, 2002).

There is little information on competitive interactions between bluefish and striped bass. Buckel and McKown (2002) examined habitat and diet overlap to investigate the potential for competition between age-0 bluefish and age-0 and age-1 striped bass. Juvenile bluefish and striped bass had little overlap in habitat (at a fine scale; i.e., 10's to 100's of m) or diet. Age-0 bluefish and age-1 striped bass were also found to have little diet overlap in Chesapeake Bay (Hartman and Brandt, 1995a). The presence of interference competition between these two species at the juvenile stage was assessed in a 60-d growth experiment (Buckel and McKown, 2002). Bluefish grew significantly faster than striped bass; however, within a species, there were no significant differences in growth between fish held in mixed vs. single species treatments (i.e., bluefish held alone grew similarly to bluefish held with striped bass). Competition does not appear to be important in the juvenile stage. The diet of juvenile and sub-adult striped bass is dominated by invertebrates while bluefish become piscivorous at very small sizes (Marks and Conover, 1993; Hartman and Brandt, 1995a). Competition may not occur until bluefish and striped bass are of sizes that allow both species to be piscivorous.

Here, we examine the potential for competition between larger, older bluefish and striped bass when bluefish groups are size-impaired, number-impaired, and non-impaired (terminology usage after Sabo and Pauley (1997)). Our objectives were to determine the behavior and foraging habits of (1) large striped bass (~60 cm) and small bluefish (~30 cm) when held at equal densities (*size-impaired*), (2) striped bass and bluefish of equal size (30-40 cm) at a ratio of 10 striped bass to 3 bluefish (*number-impaired*), and (3) striped bass and bluefish of equal sizes (30-40 cm) when held at equal densities (*non-impaired*). Equal density treatments had a ratio of three striped bass to three bluefish. In the number- and size-impaired treatments bluefish were the "focal species" and striped bass were the "associate species" (terminology usage after Goldberg and Scheiner (2001)) because of the specific hypothesis that bluefish were being displaced by striped bass. We also examined diet and spatial overlap between these two species in continental shelf waters of the U.S. east coast using data from the National Marine Fisheries Service groundfish trawl surveys.

2. Methods

2.1. Laboratory

2.1.1. Fish collection and acclimation

Age-1+ bluefish and age-2+ striped bass were angled during fall months on both the bay and ocean side of Sandy Hook, NJ (40º28, 74º06). Mummichog killifish (*Fundulus heteroclitus* L.) prey were collected by traps on the bay side of Sandy Hook, NJ; this prey type was used because it was readily available and is a common prey of bluefish and striped bass within salt marsh habitats (Tupper and Able, 2000; D. Fox & K. Able, Rutgers University, pers. comm.). Fish were immediately transported to the James J. Howard Marine Laboratory at Sandy Hook, New Jersey, USA and acclimated in round 'holding' tanks (2 m diameter, 30 cm deep) with flow-through seawater (mean temperature = 18 °C). Bluefish and striped bass were kept in holding tanks for at least 10 days prior to being transferred to the experimental research aquarium. Bluefish and striped bass were fed cut fish and live mummichog during this acclimation period. Because of the predator's large size and problems with obtaining fish of identical size consistently throughout the year, predators were re-used. However, striped bass and bluefish were given at least three weeks between trials with the exception of one treatment (3 bluefish: 3 large striped bass) in which the same group was used consecutively with a five day rest period.

2.1.2. Experimental arena and treatment description

Pelagic marine fishes such as striped bass and bluefish require a large holding tank (Olla et al., 1967). Experimental trials were conducted in the James J. Howard Marine Sciences Laboratory's large (121,000 L) research aquarium (see Stoner et al. (1999) for detailed description). The aquarium is an oval-shaped tank (10.6 m × 4.5 m × 3 m deep) containing eight 1.2 m high × 0.7 m wide observation windows (one on each end and three on each side). Bottom substrate was coarse sand. Water temperature (mean = 19 °C) and photoperiod (12 h light:12 h dark) were kept constant throughout all experimental trials to avoid seasonal changes in swimming speed (Olla and Studholme, 1972). Fish were removed from holding tanks, measured for TL (mm) and weight (g), and transferred to the research aquarium; fish were allowed to acclimate to the research aquarium at least 14 days before a trial was conducted. This length of time was necessary because predators would not begin to feed on live fish prey immediately after transfer; fish were first fed cut fish and then gradually switched to live fish prey only. During trials, at least two observers and three video cameras were used to record fish behaviors. Two cameras filmed from each end of the oval tank (looking through the end windows) while the third camera filmed through a window on the tank side.

There were a total of seven single- and mixed-species experimental treatments. Mixed-species treatments were non-impaired

Table 1
Mean sizes (total length, mm (L) and weight, g (W)) of bluefish (BF), striped bass (SB), and mummichog for single- and mixed-species treatments

Bluefish				Striped Bass			
Experimental treatments	Mean bluefish L (SD)	Mean bluefish W (SD)	Mean mummichog L (SD)	Experimental treatments	Mean striped bass L (SD)	Mean striped bass W (SD)	Mean mummichog L (SD)
Single species	454	951	73	Single species	451	926	73
3 BF	(17.3)	(150.4)	(0.4)	3 SB	(2.2)	(10.7)	(0.5)
Single species	446	867	74	Single species	463	1005	74
6 BF	(11.7)	(107.4)	(0.1)	6 SB	(22.2)	(166.5)	(0.4)
Mixed non-impaired	442	858	73	Mixed non-impaired	449	920	73
3BF: 3SB	(10.4)	(114.1)	(0.7)	3BF: 3SB	(5.8)	(85.0)	(0.7)
Mixed size-impaired	443	955	72	Mixed size-impaired	818	5111	72
3BF: 3LG SB	(4.8)	(38.5)	(1.2)	3BF: 3LG SB	(15.4)	(38.1)	(1.2)
Mixed numb.-impaired	506	1233	71	Mixed numb.-impaired	599	1973	71
3BF: 10SB	(93.8)	(581.2)	(1.3)	3BF: 10SB	(8.1)	(73.7)	(1.3)

SD = standard deviation. Treatments were three striped bass (3 SB), six striped bass (6SB), three bluefish (3BF), six bluefish (6BF), mixed non-impaired (3BF:3SB), mixed size-impaired (3BF: 3LG SB), and mixed number-impaired (3BF: 10SB).

(three bluefish and three striped bass), size-impaired (three bluefish and three large striped bass), and number- impaired (three bluefish and 10 striped bass). Single-species treatments (which served as controls) were three bluefish, three striped bass, six bluefish and six striped bass. Two group sizes of predators were used in the single-species treatments because it was unknown if mixed groups would behave as a single group (e.g., bluefish and striped bass schooling together) or two separate groups. These treatments represent a combination of two common designs used in competition experiments; they are substitutive and additive designs (Fausch, 1998; Goldberg and Scheiner, 2001). Substitutive designs keep density constant across treatments; this design was represented by the six bluefish, six striped bass, and mixed non-impaired treatments. Additive designs keep the numbers of focal species constant and adjust the numbers of associate species; our three bluefish, mixed non-impaired, and mixed number-impaired treatments follow this design. The latter design confounds density with effects from interspecific competition (Fausch, 1998).

Each treatment was performed with three independent groups of fish (with one exception described above); two feeding trials were done with each group of fish giving two non-independent trials for each replicate. For all dependent variables, the mean of these two non-independent trials was taken which gave three independent estimates of a given dependent variable for each treatment. Additionally, one non-feeding trial (see below) was done with each fish group. These observations were used to compare feeding and non-feeding behaviors for single- and mixed-species treatments.

Prior to a feeding trial, 30 prey fish (mummichog) were measured (mm), weighed (g), and placed in a partially submerged cage at least one hour prior to the start of a trial to allow prey to acclimate to the presence of predators (see Table 1 for prey size information). The prey cage (0.9 × 1.1 × 1.0 m deep) was constructed of a polyvinylchloride pipe frame and plastic mesh walls (0.64 cm). A hinged trap door at the bottom of the cage allowed prey to be introduced into the tank. To begin a trial, the trap door was opened to allow prey to escape as a cohesive group. The cage was then removed from the tank. All trials began at ~1300 hours and were terminated after all prey were consumed, after two hours, or after a non-attack period of 30 minutes (whichever came first).

2.1.3. Dependent variables and data analysis

We measured several dependent variables. These can be broken down into foraging and "other" behaviors. Foraging behaviors included per capita attack rate (number attacks • predator^{-1}), capture success (# successful captures/total number of attacks), and per capita ingestion rate (number prey eaten • predator^{-1}). Any behavioral interactions indicative of competitive interactions between the two species (e.g., nipping, chasing) were recorded.

To better understand behaviors of bluefish and striped bass in mixed-species treatments, we compared "other" behaviors (swimming speeds and vertical location) for all treatments. "Other" behaviors were obtained from video records from the side camera that recorded behaviors of fish occurring on the opposite tank wall; behavior in the video foreground was ignored. These behaviors were recorded for bluefish and striped bass during three feeding trials and one two-hour non-feeding trial for each treatment. The view opposite the middle camera was a wall (between two windows) with a known width (142 cm). Swimming speed was calculated from the time it took a fish to cross this distance. The vertical location in the tank at which a fish, or school of fish, crossed was recorded; the tank was divided into thirds with 1 = bottom, 2 = middle, and 3 = top. Vertical location was only determined on fish that were close enough to estimate swimming speed. Determining if the fish was close enough to the wall in order to get an accurate swimming speed was not always clear so the swimming speed was only determined for those fish that were close enough to the wall to produce a shadow (during the complete pass) and that swam in a straight line. If these criteria were not met, no swimming speed measurement was made.

The foraging behaviors (attack rate, capture success, and ingestion rate) were compared among four treatments containing bluefish and three treatments containing striped bass using one-way ANOVA; the number-impaired treatment was not included in this analysis because of the lack of control (see below). Bluefish and striped bass attack rate, capture success, and ingestion rate were compared using t-tests. Two-way ANOVAs were used to examine the effect of experimental treatment and feeding on swimming speed and vertical location in the water column for bluefish; a two-way ANOVA for striped bass swimming speed was not possible due to a lack of swimming speed estimates for striped bass. Tukey HSD tests were used for post-hoc comparisons.

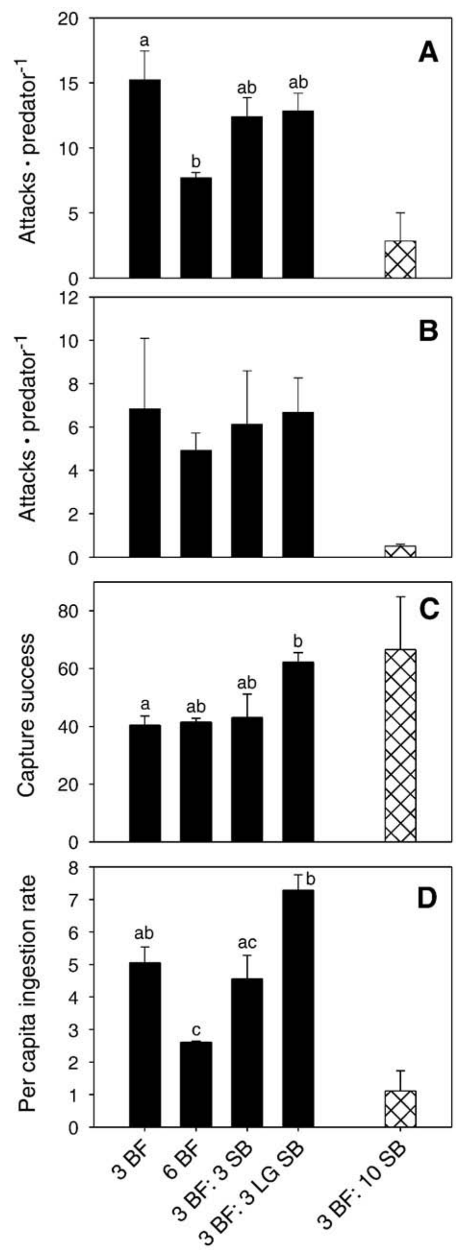

Fig. 1. Attack rate (A), attack rate during first 15 minutes of trial (B), capture success (C) and ingestion rate (D) of bluefish in five experimental treatments. Treatments were three bluefish (3BF), six bluefish (6BF), three bluefish and three striped bass of equal size (non-impaired, 3BF:3SB), and three bluefish and three large striped bass (size-impaired, 3BF:3LG SB). Like letters indicate no significant difference between mean values as determined by Tukey HSD. Data for an additional treatment (number-impaired, 3BF:10SB) that were not included in the ANOVA analyses are presented in the hatched bars. Error bars are SE.

2.2. Field

2.2.1. Diet overlap and spatial distribution of striped bass and bluefish

Diet and spatial overlap of bluefish and striped bass were examined using data collected during National Marine Fisheries Services (NMFS) groundfish surveys. Detailed descriptions of the survey design and methodologies (Azarovitz, 1981; Reid et al., 1999) and food habits sampling protocols (Link and Almeida, 2000) are described elsewhere. Schoener's (1970) overlap index was calculated using diet data from three different size groups of striped bass and bluefish collected from 1973 to 2005. The sizes were small <30 cm, medium =30-70 cm, and large >70 cm. Diet overlap was examined from all trawls combined (pooling across years, seasons, and regions) and in specific regional locations where striped bass and bluefish overlapped closely in space and time (i.e., caught in a specific region within same season). These regional locations were Southern New England, Georges Bank, and Middle Atlantic Bight and the time period was >1990 to 2005; this shorter time period was chosen because of larger samples sizes of stomach contents. An estimate of spatial overlap between bluefish and striped bass was determined using pooled trawl data from 1968 to 2006; a qualitative examination of their spatial overlap was accomplished by plotting numbers caught and cumulative numbers caught against depth for both species from spring and fall NMFS groundfish surveys.

3. Results

3.1. Laboratory

3.1.1. Attack, capture, and ingestion rates

Attacks per bluefish were lowest when bluefish were outnumbered by striped bass (Fig. 1A). However, we did not have a proper control (i.e., 13 bluefish) to compare with this treatment (i.e., could not rule out density-dependent over interspecific competition; see Fausch (1998)) and it was not included in ANOVA analyses. For the remaining four treatments, striped bass had no negative influence on bluefish attack rates; although there were significant differences in the per capita attack rates between these treatments (ANOVA, p=0.043; Table 2; Fig. 1A), this was a result of individual bluefish in the six bluefish treatment making a significantly lower number of attacks compared to the three bluefish treatment (Tukey HSD, p=0.03; no other comparisons were significant). Reductions in the number of available prey over the course of the experiment led to this result. We attempted to reduce this bias by examining attack rates during the first 15 minutes of the trial when there were large numbers of prey remaining; using these data, there were no significant differences in attack rates between the four treatments (ANOVA, p=0.926; Table 2; Fig. 1B). However, bluefish within the number-impaired treatment still had a relatively low per capita attack rate (Fig. 1B).

There was no evidence for a negative effect of striped bass on bluefish capture success; although capture success varied significantly among

Table 2
Results of one-way ANOVAs examining the effect of experimental treatments on per capita attack rate, capture success, and ingestion rate in bluefish

Effect	df	MS	F	P-value
Attack rate				
Treatment	3	29.761	4.361	0.043
Error	8	6.825		
Attack rate – first 15 minute				
Treatment	3	2.255	0.151	0.926
Error	8	14.903		
Capture success				
Treatment	3	320.29	4.854	0.033
Error	8	65.59		
Ingestion rate				
Treatment	3	11.033	14.977	0.001
Error	8	0.737		

Treatments were three bluefish, six bluefish, mixed non-impaired, and mixed size-impaired. Results of multiple contrasts are presented in text and on Fig. 1.

Table 3
Results of one-way ANOVAs examining the effect of experimental treatments on per capita attack rate, capture success, and ingestion rate in striped bass

Effect	df	MS	F	P-value
Attack rate				
Treatment	2	27.204	0.800	0.492
Error	6	34.016		
Capture success				
Treatment	2	67.276	1.947	0.223
Error	6	34.551		
Ingestion rate				
Treatment	2	1.195	0.569	0.594
Error	6	2.102		

Treatments were three striped bass, six striped bass, and the mixed non-impaired treatment.

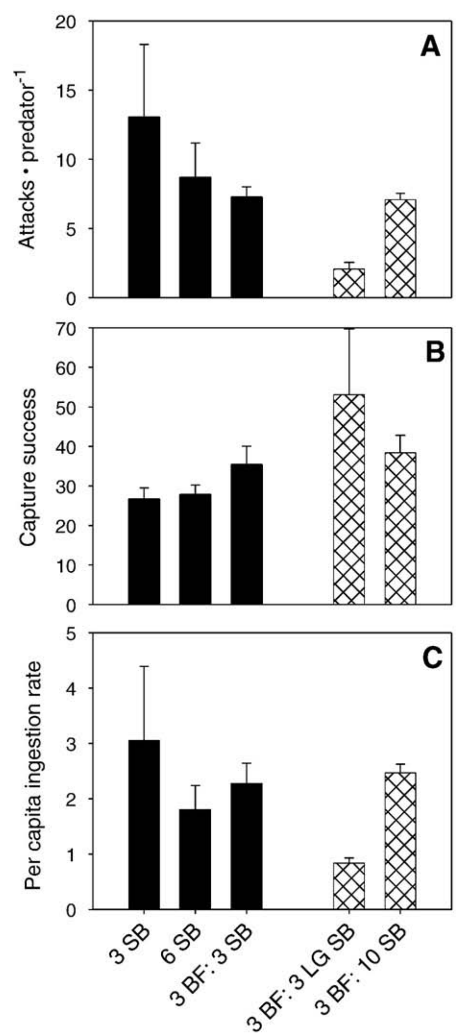

Fig. 2. Attack rate (A), capture success (B), and ingestion rate (C) of striped bass in five experimental treatments. Treatments were three striped bass (3SB), six striped bass (6SB), three bluefish and three striped bass of equal size (non-impaired, 3BF:3SB). Data for additional treatments (size-impaired, 3BF:3LG SB; number-impaired, 3BF:10SB) that were not included in the ANOVA analyses are presented in the hatched bars. Error bars are SE.

Table 4
Results of two-way ANOVAs examining the effect of experimental and feeding treatments on swimming speed and vertical location of bluefish

Effect	df	MS	F	P-value
Swimming speed				
Exp. Treatment	4	1060.541	15.938	<0.0001
Feeding	1	3714.971	55.829	<0.0001
Interaction	4	218.386	3.282	0.032
Error	20	66.542		
Vertical location				
Exp. Treatment	4	0.675	10.196	<0.0001
Feeding	1	0.388	5.854	0.025
Interaction	4	0.138	2.090	0.120
Error	20	0.066		

Experimental treatments were three bluefish, six bluefish, mixed non-impaired, mixed size-impaired, and mixed number-impaired. Feeding treatments were feeding and no feeding. Results of multiple contrasts are presented in text.

the four experimental treatments (ANOVA, p = 0.033; Table 2; Fig. 1C), capture success of bluefish in the size-impaired treatment was higher compared to bluefish in the three bluefish treatment (Tukey HSD, p = 0.045; no other comparisons were significant). There was a significant difference in per capita bluefish ingestion rates among the four experimental treatments (ANOVA, p = 0.001; Table 2, Fig. 1D); bluefish held with striped bass had similar (Tukey HSD, $p > 0.05$) or significantly higher (Tukey HSD, $p < 0.05$) ingestion rates indicating no adverse effects on bluefish feeding from presence of striped bass. Qualitatively, bluefish in the number-impaired treatment had capture success values similar to those in the size-impaired treatment (Fig. 1C) while ingestion rate per bluefish was lowest in the number-impaired treatment (Fig. 1D).

There was no significant effect of experimental treatment (three striped bass, six striped bass, and non-impaired) on attack rate, capture success, or ingestion rate of striped bass (ANOVA, $p > 0.05$ for all dependent variables; Table 3; Fig. 2A–C). Thus, the presence of bluefish did not influence striped bass foraging behaviors under non-impaired conditions. The data on attack rate, capture success, and ingestion rate for striped bass in the size-impaired and number-impaired trials were not included in the ANOVA analysis because those treatments were designed to look at effects of striped bass on bluefish; qualitatively, rates from the number-impaired treatments were similar to the three treatments examined above but large striped bass from the size-impaired treatment had the lowest attack and ingestion rates (Fig. 2A-C).

3.1.2. Swimming speeds and vertical location

During feeding, bluefish swam significantly faster than when non-feeding but this was not true across all experimental treatments (significant interaction in 2-way ANOVA, Table 4, Fig. 3A). In particular, swimming speeds of bluefish were not elevated during feeding trials when bluefish were outnumbered suggesting bluefish were inhibited (Tukey HSD, p = 0.999; Fig. 3A). Swimming speeds of bluefish differed significantly among experimental treatments (Table 4); we interpret this effect separately for feeding and non-feeding treatments due to interaction. Swimming speeds of bluefish in the size-impaired treatment were significantly faster than the three bluefish and non-impaired treatment (Tukey HSD, $p < 0.05$) when feeding; no other feeding trial comparisons were significant. In non-feeding trials, bluefish from the non-impaired treatment had significantly lower swimming speeds than bluefish from the six bluefish, size-impaired, and number-impaired treatment; the swimming speeds in the latter two treatments were also significantly higher than the three bluefish treatment (Tukey HSD, $p < 0.05$) with no other comparisons significant. Thus, there was no consistent influence of striped bass on swimming speeds of bluefish within non-feeding or feeding trials.

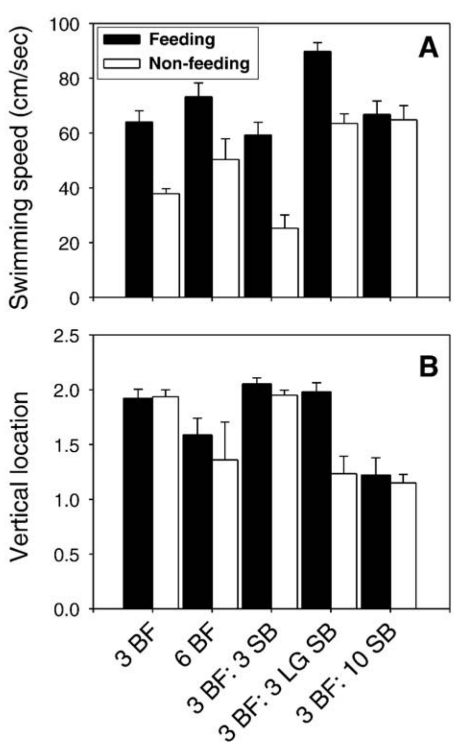

Fig. 3. Swimming speed (cm/s; A) and vertical location off bottom (i.e., one = bottom third; B) of bluefish. Treatments were three bluefish (3BF), six bluefish (6BF), three bluefish and three striped bass of equal size (non-impaired, 3BF:3SB), three bluefish and three large striped bass (size-impaired, 3BF:3LG SB), and three bluefish and ten striped bass of equal size (number-impaired, 3BF:10SB). Measurements of swimming speed and vertical location were made during feeding (closed bars) and non-feeding (open bars) trials. Error bars are SE.

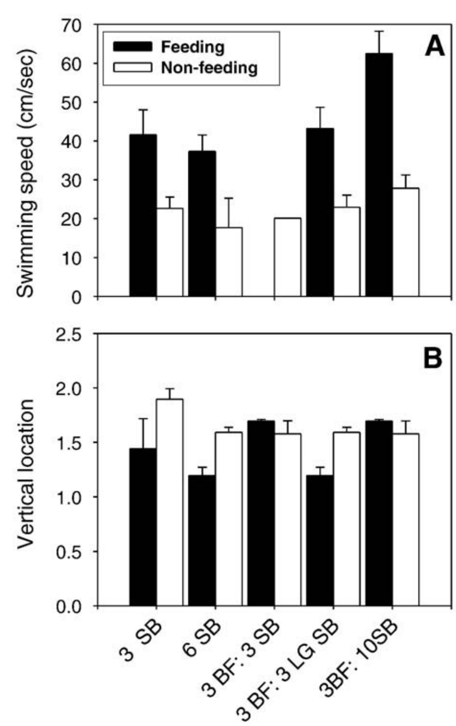

Fig. 4. Swimming speed (A) and vertical location off bottom (i.e., one = bottom third; B) of striped bass. Treatments were three striped bass (3SB), six striped bass (6SB), three bluefish and three striped bass of equal size (non-impaired, 3BF:3SB), three bluefish and three large striped bass (size-impaired, 3BF:3LG SB), and three bluefish and ten striped bass of equal size (number-impaired, 3BF:10SB). Measurements of swimming speed and vertical location were made during feeding (closed bars) and non-feeding (open bars) trials. Error bars are SE.

Table 5
Results of two-way ANOVA examining the effect of experimental and feeding treatments on vertical location of striped bass

Effect	df	MS	F	P-value
Vertical location				
Exp. treatment	4	0.102	1.603	0.213
Feeding	1	0.269	4.212	0.053
Interaction	4	0.085	1.341	0.290
Error	20	0.064		

Experimental treatments were three striped bass, six striped bass, and mixed non-impaired. Feeding treatments were feeding and no feeding.

Similarly, the vertical location differed significantly between experimental treatments but there was no evidence for a strong effect of striped bass (Table 4; Fig. 3B). Bluefish in the number-impaired treatment swam lowest in the water column of all treatments; this value was significantly lower than the three bluefish and non-impaired treatments ($p<0.001$, Tukey HSD) but not the size-impaired ($p=0.068$, Tukey HSD) or six bluefish ($p=0.332$, Tukey HSD) treatments. Additionally, bluefish in the six bluefish treatment swam lower in the water column than bluefish in the three bluefish and the non-impaired treatments ($p<0.05$, Tukey HSD). Bluefish swam significantly higher in the water column when feeding compared to not feeding and the interaction between experimental and feeding treatments was not significant (Table 4; Fig. 3B).

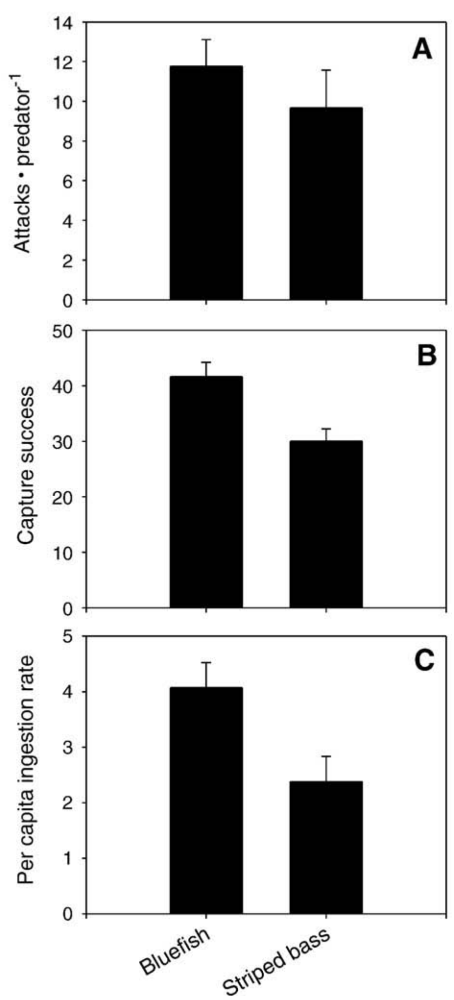

Fig. 5. Attack rate (A), capture success (B), and ingestion rate (C) of bluefish and striped bass pooled over the single-species and non-impaired treatments. Error bars are SE.

No swimming speed observations were made of striped bass during feeding trials with the non-impaired treatment because fish did not swim close enough to tank wall (Fig. 4A). Therefore, a two-way ANOVA to examine for effects of experimental and feeding treatments simultaneously (as done with bluefish above) was not possible. There was no effect of experimental treatments on swimming speeds of striped bass in the non-feeding trials (one-way ANOVA, $F=1.213$, $df=4,7$, $p=0.385$); however, swimming speeds of feeding striped bass were significantly higher than non-feeding fish (t-test, $t=5.699$, $df=22$, $p<0.0001$). The vertical location of striped bass was not influenced by experimental or feeding treatment (Table 5; Fig. 4B).

3.1.3. Comparisons between striped bass and bluefish

The comparison of foraging behaviors of striped bass and bluefish was limited to pooled data from the single-species and non-impaired treatments. Although bluefish and striped bass attacked mummichog at similar rates, bluefish were better at capturing prey. The per capita attacks by bluefish were slightly higher than per capita attack rate by striped bass, though not significant (Fig. 5A; $t=0.901$, $df=16$, $p=0.381$). Capture success of bluefish feeding on mummichog was significantly higher than that of striped bass (Fig. 5B; $t=3.457$, $df=16$, $p=0.003$). The slight differences in attack rates and the differences in capture success of bluefish compared to striped bass led to significantly higher ingestion rates for bluefish compared to striped bass (Fig. 5C; $t=2.645$, $df=16$, $p=0.018$). During feeding, mean swimming speed of bluefish (69 cm/sec) was significantly higher than that of striped bass (39 cm/sec) in the single-species treatments ($t=5.776$, $df=10$, $p=0.0002$).

3.2. Field

3.2.1. Diet overlap and spatial distribution of striped bass and bluefish

Diet overlap between bluefish and striped bass was low; values of overlap were less than 0.40 in 21 out of 24 comparisons (Table 6). Others have considered values >0.60 to be “biologically significant” (Wallace 1981). Low diet overlap occurred at both coarse (all years, all seasons, and all regions) and fine (Fall, Southern New England; Fall, Georges Bank; Spring, Middle Atlantic Bight) temporal and spatial scales and across all size combinations (Table 6). Spatial overlap of bluefish and striped bass was very low; in all surveys, seasons, and regions, the spatial overlap between striped bass and bluefish was

Table 6
Diet overlap values for bluefish and striped bass collected during spring and fall bottom trawl surveys by the National Marine Fisheries Service

		All tows, all years, all seasons, all regions	
	Small SB, n=48	Medium SB, n=501	Large SB, n=385
Small BF, n=2,523	0.225	0.246	0.266
Medium BF, n=1,864	0.179	0.353	0.361
Large BF, n=305	0.185	0.269	0.297
		>**1990, Fall, Southern New England**	
	Small SB, n=0	Medium SB, n=58	Large SB, n=53
Small BF, n=301	nd	0.431	0.324
Medium BF, n=296	nd	0.277	0.224
Large BF, n=13	nd	0.047	0.087
		>**1990, Fall, Georges Bank**	
	Small SB, n=0	Medium SB, n=10	Large SB, n=76
Small BF, n=0	nd	nd	nd
Medium BF, n=51	nd	0.288	0.337
Large BF, n=20	nd	0.413	0.478
		>**1990, Spring, Middle Atlantic Bight**	
	Small SB, n=0	Medium SB, n=11	Large SB, n=53
Small BF, n=3	nd	0.172	0.104
Medium BF, n=3	nd	0.084	0.036
Large BF, n=0	nd	nd	nd

Sizes of bluefish and striped bass were small=<30 cm, medium=30-70 cm, and large=>70 cm. Values represent Schoener's (1970) overlap index. nd=no data.

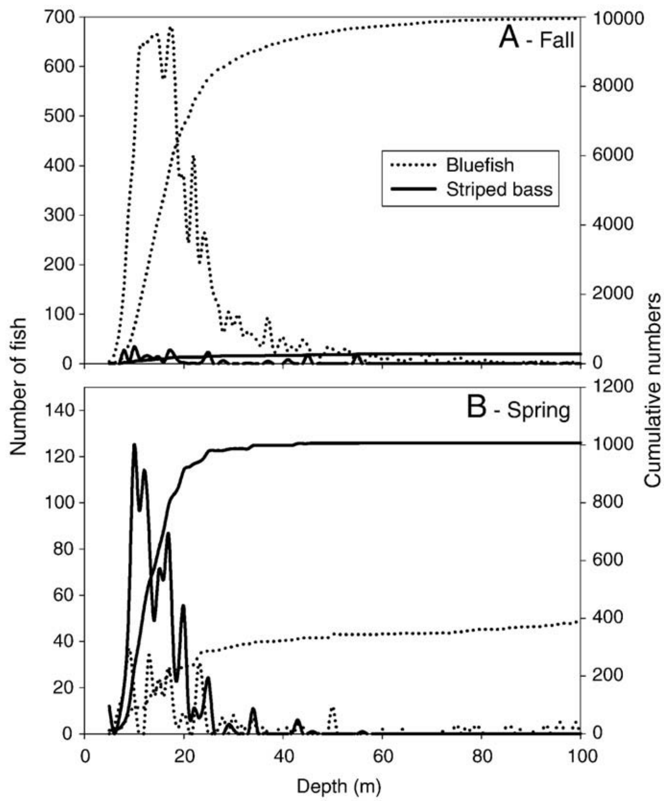

Fig. 6. Numbers and cumulative catch of striped bass and bluefish caught in bottom trawl surveys conducted by the National Marine Fisheries Service from Cape Hatteras, NC to Gulf of Maine during A- Fall and B-Spring by depth in meters.

~0.07. Bluefish and striped bass use the nearshore shelf at different times of the year. The largest catches of bluefish occurred in fall when striped bass catches were low (Fig. 6A); in spring, this was reversed and striped bass had higher catches than bluefish (Fig. 6B).

4. Discussion

We found no strong evidence for competition between adult bluefish and striped bass in laboratory experiments or field observations. The behaviors of bluefish and striped bass were not influenced by the presence of their heterospecific under non-impaired conditions. However, there was limited evidence for negative effects when bluefish were outnumbered by striped bass. Based on spatial and diet overlap data from field collected bluefish and striped bass, the potential for exploitative and interference competition during spring and fall on the continental shelf of the U.S. east coast is low. Our results are consistent with findings from work done on juveniles. Buckel and McKown (2002) similarly found no support for competition between juvenile bluefish and striped bass using a combination of laboratory and field approaches.

We were interested in addressing the question of whether or not striped bass have a deleterious effect on bluefish (Crecco, 1996). Therefore, two of the three mixed-species treatments examined for competitive interactions when bluefish were size- and number-impaired. Future experiments should test effects of bluefish on striped bass in size- and number-impaired treatments. The size-impaired treatment was not part of the substitutive or additive designs. We added this treatment because size has been found to be as important as species type in determining competitive dominance in a variety of fishes (Sabo and Pauley, 1997; Webster, 2004; Young, 2004).

Large striped bass did not have a negative effect on foraging or non-foraging behaviors in bluefish; although the highest swimming rates of bluefish were observed in this feeding treatment they were not significantly higher than swimming speeds in the six bluefish feeding treatment. Large striped bass made few attacks resulting in mean ingestion rates by bluefish in this treatment being no different than when three bluefish were held alone. Weight-dependent consumption rates of these large striped bass is about half that of the smaller bluefish (Hartman and Brandt, 1995b); however, the differences in biomass between the two species in this treatment means that striped bass had almost a 3-fold higher predatory demand. The lowered attack and ingestion rates by large striped bass relative to bluefish could be due to the presence of bluefish but we did not have a proper control (three large striped bass alone) to test this.

The presence of a relatively large group of striped bass (10) inhibited bluefish activity; swimming speeds were lowered, vertical movement was limited, and attack and feeding rates were reduced. These attack and feeding rate data have to be interpreted with caution given the larger number of predators and the lowered number of prey per predator in the number-impaired treatment. This additive portion of our experimental design allowed us to examine effects of striped bass when intraspecific competition within bluefish was held constant ($n=3$ bluefish for all three treatments). A drawback of the design is that it allows for differences in total density between treatments; therefore, our results could simply represent density-dependence rather than interspecific competition (Fausch, 1998). However, the non-foraging behaviors also support inhibition. Although we have identified a negative influence of striped bass on bluefish behavior that provides evidence in favor of Crecco's (1996) hypothesis, analysis of bluefish and striped bass spatial and temporal distribution patterns in the wild do not support offshore displacement.

There was minimal spatial overlap between the two species on the continental shelf between Gulf of Maine and Cape Hatteras, NC during fall and spring; this resulted from the two species occupying this area of the shelf during different seasons. Additionally, Salerno et al. (2001) found no support for Crecco's (1996) displacement hypothesis when examining this same fall bottom trawl survey data by year from 1985 to 1996; they reported that older bluefish (age 3+) consistently occurred offshore during this time period with no shift in spatial distribution during the decline in bluefish landings.

The differing thermal preferences of striped bass and bluefish are likely the major determinant of the timing of shelf use. Demers et al. (2000) determined growth rate potential of striped bass and bluefish in two mid-Atlantic estuaries using prey density and temperature profile data; they speculated that competitive overlap between bluefish and striped bass would be limited, even though they consumed the same prey, due to lack of habitat overlap given different thermally based growth rate potentials. One limitation of our spatial overlap analysis is that it could only be done during fall and spring when fishery-independent trawl data exist. However, overlap in this area during winter is low given more southerly and offshore winter habitats of bluefish compared to striped bass (Shepherd et al., 2006; Welsh et al., 2007). Spatial overlap during summer months is possible but given different thermal preferences appears unlikely (Demers et al., 2000).

Diet overlap between bluefish and striped bass collected on the continental shelf was minimal across a range of sizes. Similarly, diet overlap values between age-0 bluefish and age-0 and age-1 striped bass in New York and New Jersey estuaries were low (Buckel and McKown, 2002). Given that diet is the realization of a suite of factors: e.g., prey selectivity (size and type); predator morphology (e.g. gape width); ontogenetic shifts; predator behavior (swimming, feeding, reaction to threats, etc.); predator and prey spatio-temporal overlap; prey abundance (relative to the rest of the prey field); detection, capture, attack, and ingestion success; etc., it is then not surprising that bluefish and striped bass have low diet overlaps. For instance, even subtle differences in distribution of these species can result in these fish experiencing a different prey field. This coupled with the differential behaviors noted above can then result in distinct diets between these species.

We found that bluefish were better than striped bass at capturing fish prey. Scharf (2001) also found this for juvenile stages of these two species and argued that differences in attack velocity and tooth morphology allowed bluefish to achieve higher capture success. Bluefish have higher critical swimming speeds (Freadman, 1979), routine swimming speeds (this study), and attack velocities (Scharf, 2001) when compared to striped bass. Our findings suggest that under equal conditions, bluefish will be able to exploit a limited prey resource more quickly than striped bass. Scharf (2001) confirmed this in a mixed treatment of juvenile bluefish and striped bass. In Chesapeake Bay, Hartman and Brandt (1995c) concluded that bluefish were better able to achieve their maximum consumption rates relative to striped bass across several age groups. This would imply that both juvenile and older bluefish are not competitive (exploitative) inferiors to striped bass.

There were dramatic differences in behavior between feeding and non-feeding fish. Bluefish (excluding number-impaired treatment) and striped bass swam on average 1.7 and 2.0 times as fast, respectively, in feeding trials compared to non-feeding periods. Some bioenergetic models require information on the differences in metabolic requirements between non-feeding and feeding fish (e.g, Scharf et al., 2006). Using Freadman's (1979) data on metabolic rate as a function of swimming speed for bluefish and striped bass, the activity multiplier for metabolic differences between routine and feeding metabolism is ~1.4 for both bluefish and striped bass. This value is similar to multiplier estimates between feeding and routine metabolism found in other fishes (Brett and Groves, 1979).

There are caveats with the inferences we made from laboratory experiments and field observations. The response variables we measured in the laboratory were behavioral and addressed effects at the individual level. Ultimately, we want to know if competition is important at the population level; however, we were limited to short term and small spatial scale experiments because of logistical constraints. Field experiments that take advantage of natural contrasts in density of striped bass and bluefish and measure biological responses (e.g., growth) that have a direct influence on population dynamics may be useful (Fausch, 1998). Our approach was to use both laboratory experiments and field observations to gain a more complete understanding of striped bass and bluefish interactions. However, our field observations may have missed an important habitat that both species use as a feeding area. Given depth constraints of the NOAA research vessel, the surf zone and immediately adjacent shelf habitats were not sampled; the seasonal patterns in spatial and diet overlap and prey supply in this habitat awaits further study.

Overall, results from our laboratory experiments did not demonstrate interference competition between age-1+ bluefish and age-2+ striped bass. If fish prey and foraging times were ever limited, bluefish would out-compete striped bass given the differences we observed in foraging efficiency between these two species (at equal sizes). However, diet and spatial overlap of striped bass and bluefish on the continental shelf were low suggesting resource partitioning and low chance for competitive displacement (e.g. Crecco, 1996) due to shared resources. This information, combined with previous investigations on juveniles of these species (Buckel and McKown, 2002), indicates that competition between bluefish and striped bass is not likely a major force that influences their population dynamics.

Acknowledgements

We thank personnel of the Behavioral Ecology Branch at the James J. Howard Marine Sciences Laboratory (NOAA/NMFS) for assistance with fish collections and laboratory experiments especially Mike Temple for analysis of video recordings and Allan Stoner for discussions on experimental design; comments from Kevin Craig and Kyle Hartman greatly improved the manuscript. This work was supported by a National Research Council-National Oceanic and Atmospheric Administration (NOAA) Research Associateship (to J.A.B.) and a grant from the NOAA/National Marine Fisheries Service-Institute of Marine and Coastal Sciences at Rutgers University Bluefish/Striped Bass Dynamics program (to J.A.B.). **[SS]**

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