006/98A ✓

Bluefish and striped bass predation on juvenile bay anchovy in the Hudson River

A Final Report submitted to the Hudson River Foundation

by

Frederick S. Scharf

Abstract

This report details the results of a series of laboratory experiments conducted to examine the influence of predator and prey behavior on the outcome of size-structured species interactions between piscivorous fishes and their prey. A primary focus was to evaluate the relative susceptibility of bay anchovy to predation and identify potential mechanisms responsible for differences among bay anchovy and other common forage species.

Bay anchovy were highly susceptible to capture by bluefish and required minimal handling time. Bay anchovy greater than 40% of bluefish body size were highly profitable prey, which is not typical for most piscivore-prey interactions. Bluefish selected large bay anchovy when given a choice of prey sizes. High attack proportions on larger bay anchovy may have been influenced by size-related differences in antipredator behaviors. Results indicate that bay anchovy probably never achieve a size refuge from predation.

Compared to other common forage species, bay anchovy were the easiest prey to capture, required low handling times, and were generally the most profitable prey for piscivores. Short reaction distances to approaching predators may have contributed to disparate susceptibilities to capture among forage species. Findings highlight the potential importance of life history strategy and phylogeny in determining the effectiveness of the antipredator behaviors expressed by prey.

Piscivores consistently selected bay anchovy over several alternative forage species. Attack proportions were highly skewed toward bay anchovy prey. Forage species differed considerably in the expression of antipredator behaviors related to use of refuge, tank positioning, activity levels, schooling aggregation, and the frequency of stragglers. Piscivores displayed several attack strategies, but mostly attacked solitary prey individuals. Differences in antipredator behavior appeared to directly influence predator attacks, suggesting that differential attack proportions among prey may not necessarily represent active choice by piscivores.

Piscivores differed in their patterns of resource utilization, with bluefish achieving piscivory earlier and consuming larger prey sizes compared to striped bass. Behavioral foraging abilities differed markedly between piscivores, with bluefish foraging efficiency reaching levels nearly four times those reached by striped bass. When prey resources were limited, bluefish grew faster than expected and were able to exploit prey at the expense of striped bass. Findings indicate the importance of available forage fish of appropriate size to the onset of piscivory in striped bass.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

SIZE-DEPENDENT VULNERABILITY OF JUVENILE BAY ANCHOVY (*Anchoa mitchilli*) TO BLUEFISH PREDATION: DOES LARGE BODY SIZE ALWAYS PROVIDE A REFUGE?

Introduction

The bay anchovy (*Anchoa mitchilli*) is one of the most abundant marine fishes in the western Atlantic and Gulf of Mexico (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953). Bay anchovy are small, schooling planktivores that occupy pelagic waters in habitats ranging from low salinity estuaries to the continental shelf. Along the U.S. east coast, spawning generally occurs in the estuary and extends from approximately May to September (Vouglitois et al. 1987; Luo and Musick 1991; Zastrow et al. 1991) with peak spawning activity typically occurring in mid-summer that may be closely associated with peaks in food abundance (Castro and Cowen 1991). In estuaries, high densities of bay anchovy during summer and early fall are due primarily to large numbers of young-of-the-year fish, which make up the majority of estuarine population biomass (Vouglitois et al. 1987; Newberger and Houde 1995). Relatively high abundances of juveniles are usually present in east coast estuaries into October before fish migrate to continental shelf waters to overwinter.

Bay anchovy are considered to be an important trophic link in estuarine food webs as they are preyed upon by several species of piscivorous fishes, including bluefish (*Pomatomus saltatrix*), striped bass (*Morone saxatilis*), weakfish (*Cynoscion regalis*), and summer flounder (*Paralichthys dentatus*) (Poole 1964; Schaefer 1970; Manooch 1973; Merriner 1975; Friedland et al. 1988; Juanes et al. 1993; Hartman and Brandt 1995; Juanes and Conover 1995; Buckel et al. 1999a, 1999b; Buckel and McKown in review).

In fact, Baird and Ulanowicz (1989) proposed that bay anchovy may contribute up to 60-90% of the diets of piscivorous fishes in Chesapeake Bay. Because of their importance in transferring energy through the food web (Luo and Brandt 1993; Wang and Houde 1995), bay anchovy have been the focus of several studies attempting to identify mechanisms associated with high and variable natural mortality rates. Natural mortality rates for early life stages of bay anchovy are among the highest reported among teleost fishes, with conditional rates at 80-90% d^{-1} for eggs and yolk-sac larvae and 20-30% d^{-1} for older larvae (Leak and Houde 1987; Castro and Cowen 1991; Dorsey et al. 1996; Rilling and Houde 1999). Predation by both fish and invertebrate predators has been identified as a considerable source of mortality for egg and larval stages of bay anchovy (Cowan and Houde 1992, 1993; Houde et al. 1994; Purcell et al. 1994). For example, Purcell et al. (1994) concluded that scyphomedusae predators were responsible for an average of 41% of the total estimated mortality for larval bay anchovy in Chesapeake Bay.

Although recent efforts have generated considerable insight as to the potential mechanisms responsible for high mortality in egg and larval stages of bay anchovy, very little is known about the processes that operate during the juvenile stage, especially with regard to the size-dependence of mortality in older individuals. In fact, Cowan and Rose (1999) used fixed size-independent rates of mortality for juveniles and adults in a bay anchovy population model in Chesapeake Bay due to lack of empirical evidence for a size-based mortality relationship in older life stages. Mortality rates for juveniles are estimated to remain high based on annual mortality rates for entire cohorts as high as 95% yr^{-1} (Newberger and Houde 1995). In the Chesapeake Bay, Baird and Ulanowicz (1989) speculated that bay anchovy (mainly age-0 juveniles and age-1+ adults) could make up more than half of the biomass consumed by piscivorous fishes during some seasons. Age-0 juvenile bluefish, in particular, can represent a significant source of mortality for juvenile bay anchovy in estuarine and marine systems. In the estuarine portion of the Hudson River, juvenile bay anchovy were the most consistently recovered prey from the stomachs of spring-spawned age-0 bluefish during summer and early fall of 1989-93 (Juanes et al. 1993; Buckel et al. 1999a). Diets of spring-spawned age-0 bluefish on the continental shelf during fall are also dominated by juvenile bay anchovy, as percent composition by weight generally ranged between 40-50% across shelf regions during 1994 and 1995 (Buckel et al. 1999b). Summer-spawned age-0 bluefish are even further dependent upon young bay anchovy as a source of food. In Great South Bay, NY, Juanes and Conover (1995) reported that bay anchovy accounted for 58-86% by weight of summer-spawned age-0 bluefish diets during 1988 and 1989. Similarly, Buckel et al. (1999b) found that juvenile bay anchovy contributed up to 90% composition by weight to diets of summer-spawned bluefish in continental shelf waters during fall.

The consistent occurrence of juvenile bay anchovy in the diets of estuarine and marine piscivores is probably due in some part to their high abundance levels relative to other forage species, which result in high rates of encounter with potential predators. However, no information exists on their relative susceptibility to predators once they are encountered, which may have significant influence in determining their contribution to the diets of predatory fishes. For instance, interannual variations of up to an order of magnitude in bay anchovy abundance have been demonstrated in Chesapeake Bay and Barnegat Bay estuaries (Vouglitois 1987; Newberger and Houde 1995). Despite large interannual fluctuations in abundance that may generate considerable variability in encounter rates with predators, juvenile bay anchovy remain a consistent prey included in piscivore diets both within and across years in systems that have been studied (Manooch 1973; Friedland et al. 1988; Juanes and Conover 1995; Buckel et al. 1999a, 1999b). A more thorough understanding of size-structured predator-prey relations among juvenile bay anchovy and their piscivorous predators will help to determine the relative importance of bay anchovy availability (encounter rate) and/or susceptibility to attack and capture towards their overall vulnerability to predation.

Here, I evaluate the size-dependent vulnerability of juvenile bay anchovy to predation by age-0 juvenile bluefish through a series of laboratory experiments and analysis of predator diets in the field. Video recorded feeding trials are conducted across a range of anchovy and bluefish body sizes to determine predator capture success, handling time, and feeding rates as functions of relative prey size (prey length/predator length ratio). Anchovy mass ingested is combined with capture success and handling time relationships to generate size-dependent profitability curves. To determine predator size-selection, I presented bluefish predators with different sizes of bay anchovy simultaneously in large laboratory mesocosms and quantified size-specific patterns of prey mortality. Mesocosm experiments were recorded on video to estimate predator attack proportions on different sized anchovy and evaluate potential behavioral mechanisms of observed feeding patterns. Absolute and relative sizes of bay anchovy eaten in the field by bluefish are examined and compared to laboratory predicted vulnerabilities.

Methods

Field collections and laboratory maintenance

Age-0 bluefish (60-80mm TL at capture) were collected during June of 1999 and 2000 in Jamaica, Little Neck, and Manhasset bays, which are estuaries in western Long Island, New York (40°40'N, 73°45'W). Additional bluefish were captured throughout summer months in Sandy Hook Bay located in the mid-Atlantic Bight in central New Jersey (40°24'N, 74°00'W). All bluefish were captured by using 30.5m × 2m and 61m × 3m beach seines and promptly taken to the James J. Howard Marine Laboratory (National Marine Fisheries Service, Northeast Fisheries Science Center) Highlands, New Jersey, USA. Fish were transported in aerated coolers (approx. 100 liters) containing ambient seawater and transferred to 1500 liter circular flow-through seawater tanks (1.8m diameter × 0.6m depth) for acclimation of at least 1 week prior to use in feeding experiments. Bluefish were fed a combination of live and frozen fish prey twice daily and were maintained throughout the experimental period at ambient water temperatures (19-21 °C), salinities (22-27ppt), and light conditions (14:10 light:dark cycle) consistent with conditions during summer in Sandy Hook Bay.

Juvenile bay anchovy (25-45mm TL at capture) were captured primarily in the Navesink River estuary immediately adjacent to Sandy Hook Bay during July-September of 1999 and 2000. Additional bay anchovy were captured along ocean beaches within 30 kilometers south of Sandy Hook Bay during early fall of each year. Both 9.1m beach seines and 4.9m otter trawls were used to capture juvenile bay anchovy. During beach seine collections, seines were never retrieved to the beach, but rather were pursed in the water column after seining for 1-2 minutes by bringing the ends of the seine together and lifting the lead line as each end of the seine was retrieved. Once most of the seine had been retrieved, this pursing technique resulted in a pocket of water containing the captured fish, which were subsequently dipped out using a plastic scoop and placed into aerated coolers or buckets (19-38 liters) containing ambient estuarine water for transport to the laboratory. By pursing the seine and dipping out live fishes, any bay anchovy that were captured were never removed from the water and direct contact with the mesh walls of the seine was minimized.

During summer 2000, otter trawls were used in the Navesink River estuary in an attempt to increase catch rates. In order to reduce bay anchovy mortality suffered during trawling, the cod end of a single otter trawl was fitted with a rectangular frame (1.0m × 0.5m × 0.5m) constructed of 2.5cm diameter PVC tubing. The insertion of a rigid frame was intended to modify the cod end into a live box and reduce direct contact between bay anchovy and the cod end mesh liner. Trawls were either fished just off the bottom or in mid water for short durations (1-2 minutes) at slow speeds (1-2 knots). Trawls were retrieved by hand and the live box was positioned on the side of the vessel and kept submerged continuously. The cod end of the trawl was cinched closed just anterior to the live box and then untied and opened just posterior to the live box to retrieve captured fish. Juvenile bay anchovy were dipped out using a plastic scoop and placed into aerated coolers or buckets containing ambient estuarine water for transport to the laboratory. Although trawling caused higher mortality rates of captured bay anchovy, trawl catch rates were considerably higher compared to seining, resulting in higher numbers of surviving bay anchovy per sampling effort.

Once returned to the laboratory, juvenile bay anchovy were acclimated over a 6-8 hour period from ambient Navesink River estuary water (22-24 °C water temperature; 5-10ppt salinity) to ambient Sandy Hook Bay water (19-21 °C water temperature; 22-27ppt salinity) and then transferred to 1500 liter circular, flow-through tanks for at least 2 weeks of acclimation time prior to use in feeding experiments. Bay anchovy were fed twice daily and were maintained on a diet consisting of a combination of live cultured artemia, frozen brine shrimp, and a commercial feed (710μm particle size) throughout the summer.

Experimental design

All feeding experiments were completed during summers of 1999 and 2000 at the James J. Howard Marine Laboratory. Experiments were completed using individual fish predators randomly sampled with replacement from laboratory populations of bluefish (n = 50-60 individuals per summer). If predator sampling was completely random, each individual predator would be expected to be used in 2-3 experimental trials feeding on bay anchovy throughout the summer. Juvenile bay anchovy used in foraging trials were supplied from laboratory populations consisting of 1000-1500 individuals each summer.

Foraging trials to determine size-dependent capture success, handling times, and feeding rates were conducted in 475 liter rectangular flow-through tanks (1.05m x 0.76m x 0.60m depth) equipped with a clear, plexiglass viewing window and maintained at water depths of 0.50m using standpipes positioned outside of the tanks. The bottom of each tank was covered with a thin layer (10mm) of course sand and lighting was provided by two 150-watt halogen bulbs positioned 1.0m above each tank. All experimental feeding trials were video recorded using either Hi-8 or digital video cameras placed approximately 1.0m directly in front of each tank.

For each feeding trial, a group of three size-matched (10mm TL range) bluefish was starved for at least 12 hours and acclimated to experimental arenas (475 liter glass front tanks) for 6-8 hours prior to the start of the experiment. A group of ten size-matched (5mm TL range) juvenile bay anchovy were then added to the experimental arena and allowed to acclimate for 10-15 minutes within a clear, plexiglass holding chamber before the chamber was removed and the predators had access to the prey. All feeding trials were video recorded and lasted for 15 minutes, at which time remaining prey and predators were removed and prey were counted. Feeding experiments were completed using a range of sizes of bluefish (90-180mm TL), and bay anchovy (30-65mm TL) that closely resembled the natural range for each species occurring in estuarine waters during summer months. The size ranges of predator and prey used in the feeding experiments allowed predation components for juvenile bay anchovy prey to be estimated across a wide range of relative prey sizes (0.20-0.65 prey length/predator length ratio). During summer 1999 and 2000, 47 separate feeding trials were completed using age-0 bluefish as predators to estimate predator capture success, handling time, and profitability.

Bluefish capture success and handling time when feeding on bay anchovy were estimated from video analysis of feeding experiments. Capture success was measured separately for each feeding trial as the number of successful attacks (strikes) divided by the total number of attacks. Successful attacks were those resulting in consumption of the prey. Handling time was measured for each prey consumed within a feeding trial beginning with the time of initial contact with the prey until opercular movements ceased and normal schooling behavior resumed. Within each feeding trial, handling times for each prey consumed were averaged to obtain a mean handling time for that trial. In addition, bluefish feeding rates were calculated for each feeding trial as the number of prey eaten per predator per unit time (# prey eaten × # predators^{-1} × hours^{-1}).

Feeding trials to determine size-selective feeding by bluefish on juvenile bay anchovy were conducted in 1800 liter rectangular flow-through tanks (2.4m x 0.80 m x 0.80m) equipped with a plexiglass viewing window along the entire tank length. Tanks were separated into two chambers with an opaque plexiglass divider; one predator holding chamber (approximately 40% of tank volume) and one experimental feeding arena (approximately 60% of tank volume). The two chambers were connected by a door within the opaque plexiglass divider that was operated remotely to allow predators access to the feeding arena. Tank bottoms were covered with a 10mm layer of coarse sand and one corner of the tank contained a patch (0.5m × 0.4m) of simulated eelgrass with a shoot density (240 shoots per m^2) within the density range observed in eelgrass patches in local estuarine waters. Tanks were illuminated using two 150 watt halogen bulbs positioned 1m above each tank. Experiments were video recorded using a digital video camera positioned approximately 1.5m from the front of the tank.

Each size-selection trial involved a group of three size-matched (10mm TL range) bluefish being offered two size groups (small and large, each size group had a 5mm TL range) of 15 juvenile bay anchovy. Small bay anchovy sizes ranged from 35-47mm TL and were approximately 20-25% of predator length, whereas large bay anchovy sizes ranged from 55-70mm TL and were approximately 35-40% of predator length. The average difference in TL between small and large bay anchovy across feeding trials was 22.1mm ±1.0mm, with average differences in prey length/predator length ratio of 0.125±0.006. Each group of bluefish was starved prior to each feeding trial to standardize hunger levels. Starvation periods needed to be sufficiently long in order to produce feeding activity by predators during the first 1.5 hours of each trial (video recorded period), while also avoiding long starvation periods that may produce frenzied non-selective feeding behavior when prey are initially available to predators. Such frenzied feeding activity may not represent natural feeding behavior, being caused only by deprivation of food for long time periods (24 hours), and therefore may bias any true selective feeding. For this study, trials were conducted using 4-6 hour starvation periods, estimated as the time required to empty 50-70% of the gut of juvenile bluefish at 21-24°C (Buckel and Conover 1996).

For each feeding trial, a group of three bluefish was placed within the experimental tank and contained within the predator holding chamber for a 24 hour acclimation period. Prey were also added to the feeding arena at this time and allowed to disperse and acclimate for 24 hours. Bluefish were fed live prey until the designated starvation period began immediately preceding each feeding trial, at which time all remaining food was removed from the predator holding chamber. Bay anchovy prey were fed a commercial feed 1-2 hours prior to each feeding trial. Active, normal feeding behavior by bay anchovy served as an indicator of health prior to the start of a feeding trial. If prey did not feed normally, the trial was postponed until normal behavior was observed. At the start of each feeding trial, the door separating the predator holding chamber and the feeding arena was lifted and bluefish had access to prey. Each feeding trial was video recorded for 1.5 hours, after which the numbers of remaining prey of each size were estimated visually, the experimental lighting was turned off and an opaque curtain was pulled in front of the tank for the remainder of the trial to minimize disturbance. Video recording during the initial 1.5 hours of each feeding trial allowed determination of the proportion of predator attacks on small and large bay anchovy. Each feeding trial had a duration of approximately 16-18 hours, beginning in late afternoon and ending sometime after sunrise the following day. Therefore, bluefish fed during both dusk and dawn crepuscular periods, times when feeding activity is generally heightened in the field (Buckel and Conover 1997). At the end of each trial, all remaining prey and predators were removed, and prey were counted and remeasured. A priori power analyses indicated that with alpha (α) set at 0.05, at least five (5) replicates were needed to detect a 5% difference in mean number consumed while achieving a power ($1-\beta$) of 95%. Therefore, during summer 1999 and 2000, a total of 10 separate feeding trials were conducted to examine bluefish size-selection when feeding on juvenile bay anchovy. Power analyses were completed using estimates of variance from previous work on relative proportions of prey sizes eaten by bluefish feeding on three different sizes of Atlantic silversides (Juanes and Conover 1994).

An additional four size-selection experiments were performed in small aquaria with low water depths and no eelgrass refuge in order to limit antipredator behavior of prey and evaluate the potential influence of differential prey behavior on size-selectivity of predators. Experiments were conducted in 475 liter tanks, with lighting and substrate as used above, with water depths limited to 25cm using a standpipe positioned outside each tank. Each tank was partitioned in half using a single section of opaque plexiglass.

Three size-matched bluefish were added to one side and 12 bay anchovy (6 small and 6 large) were added to the other side and allowed to acclimate for 30 minutes. Feeding trials commenced when the plexiglass was removed, lasted for 1.5 hours, and were video recorded for the entire duration. Remaining prey were counted and measured upon completion of each feeding trial. Absolute and relative bay anchovy and bluefish sizes were similar to those used in size-selection experiments outlined above.

Juvenile bay anchovy needed to be handled for size measurements prior to use in all feeding experiments. Due to the sensitivity of small bay anchovy to handling stress, care was taken to minimize disturbance during handling by measuring individuals within a compartment containing a sufficient amount of seawater to keep individual fish at least partially submerged. In order to determine if handling bay anchovy for measurement purposes imparted significant stress that may have increased their susceptibility to predators, a separate experiment was performed to compare behavior and survival of measured vs. unmeasured fish. Four groups of ten individual bay anchovy (2 groups measured and 2 groups unmeasured) of approximately equal sizes (35-40mm TL) were placed in separate tanks and maintained at ambient conditions while behavior and survival were monitored for 10 days. Only one bay anchovy failed to survive (1 unmeasured fish died on day 2) and no behavioral differences between the treatments could be detected. Fish in both treatments fed normally within 4-6 hours after being transferred to experimental tanks.

Linear regressions were fit to express bluefish capture success on juvenile bay anchovy as a function of relative prey size (prey length/predator length ratio). Mean handling times were linearized (Log_e transformed) before regressions were fit to determine handling time as a function of relative prey size. Regressions were fit to feeding rate data after adding 1 and taking log transformations ($Log_e (y + 1)$). Size-dependent profitability as a function of relative prey size was calculated as prey mass ingested × predator mass^{-1} × handling time^{-1} × capture success.

Both sets of size-selective feeding trials were analyzed using an ANOVA design to test for differences in the mean number of each prey size group consumed. In addition, the mean proportion of attacks on each size group were compared to an expected proportion of attacks on each size group. The probability of an attack on a small or large bay anchovy was calculated for each individual attack based on the number of individuals of each size group remaining alive immediately prior to each attack (i.e., attacks are random). The expected proportion of attacks on small and large bay anchovy for the entire feeding trial was calculated as the mean of attack probabilities for all individual attacks. For each feeding trial, the actual and expected attack proportions on each size group were arcsine square-root transformed, to prevent the functional dependence of the variance upon the mean, and were then compared across replicate feeding trials using ANOVA.

Predator size-prey size relationships in the field

Diet composition data for bluefish collected in local estuarine waters were used to analyze predator size-prey size relationships in the field. Sizes of bay anchovy consumed by bluefish in the lower Hudson River during 1990-1993 were examined. Scatterplots of bay anchovy size vs. bluefish size were constructed and variation in minimum, mean, and maximum bay anchovy size were determined as a function of predator size using regression quantiles (Scharf et al. 1998; Cade et al. 1999). Sizes of bay anchovy eaten and predator sizes were combined to construct histograms of relative prey sizes eaten. Absolute and relative bay anchovy sizes consumed most frequently in the field were compared to laboratory data on size-dependent predator capture success, bay anchovy profitability, and predator selective behaviors to evaluate whether laboratory derived predictions matched field observations.

Results

Capture success of age-0 bluefish preying on juvenile bay anchovy declined linearly with increasing relative prey size (Fig. 1.1). Bluefish capture efficiency was as high as 70-80% at relative prey sizes less than 0.30 and decreased linearly to 40-50% at relative prey sizes greater than 0.50 ($y = 1.01 - 0.98x$; $p < 0.0001$; $r^2 = 0.50$). Bluefish handling time when feeding on juvenile bay anchovy increased exponentially as a function of relative prey size (Fig. 1.2). Handling time was less than 10 seconds for relative prey sizes under 0.30 and rose to over 30 seconds at relative prey sizes above 0.50 ($y = 2.81e^{4.23x}$; $p < 0.0001$; $r^2 = 0.86$). Bluefish feeding rates on juvenile bay anchovy declined exponentially with increasing relative prey size (Fig. 1.3). Juvenile bay anchovy were consumed at a rate of 8-10 per hour at relative prey sizes less then 0.30, and at a rate of about 3 prey per hour at relative prey sizes greater than 0.40 ($y + 1 = 19.87e^{-3.18x}$; $p < 0.0001$; $r^2 = 0.51$).

Profitability of juvenile bay anchovy as a forage species for bluefish was a dome-shaped function of relative prey size (Fig. 1.4). Bluefish profitability rose steeply with increasing relative size of bay anchovy prey and peaked at a relative prey size near 0.50.

Relative bay anchovy sizes between 0.45 and 0.60 were about twice as profitable to bluefish predators compared to relative bay anchovy sizes around 0.30. The range of relative prey sizes tested in predation experiments for this study was sufficient to quantify the shape of the profitability function at the peak for age-0 bluefish feeding on bay anchovy.

When offered different sizes of bay anchovy simultaneously in large aquaria, age-0 bluefish consumed significantly higher numbers of large prey (12.0±0.8) compared to small prey (7.9±1.3) (Fig. 1.5). Based on video analysis of the initial 1.5 hours of each feeding trial, bluefish attacked significantly higher proportions of large prey than would be expected if attacks were randomly distributed among both prey size groups (observed 85.2% large:14.8% small; expected 48.7% large:51.3% small) (Fig. 1.5). In contrast to results obtained in large aquaria, experiments performed in small aquaria, with low water depths and no structural refuge, did not produce a strong pattern of size-selection by bluefish. Mean numbers eaten of large (4.0±0.7) and small (3.5±1.3) bay anchovy were not significantly different (Fig. 1.6). In addition, attack proportions were closer to random (observed 58.8% large:41.2% small; expected 49.9% large:50.1% small) and were not statistically different from expected proportions (Fig. 1.6).

Video observations of bay anchovy behavior made prior to the introduction of predators indicated that large and small bay anchovy grouped together in tight schools and that individuals did not stray more than 1-2 body lengths from adjacent individuals. Schools were located in the mid to upper water column in the open area of the tank and anchovy did not use the eelgrass refuge. Upon introduction of bluefish at the onset of size-selection experiments, bay anchovy schools dispersed briefly before quickly reforming into a cohesive group (usually within 1-2 minutes). Similar to predator free situations, large and small anchovy schooled together in the presence of bluefish, however schools were located in areas of the tank opposite to those occupied by bluefish. Bluefish generally maintained positions in mid to upper regions of the water column near the front of the tank and did not swim into eelgrass patches, thus bay anchovy schools were located in the lower, rear areas of the tank. Contrary to predator free situations, bay anchovy made extensive use of eelgrass patches during 4 of the size-selection trials.

A total of 57 bluefish attacks on bay anchovy were observed during the initial 1.5 hours of size-selection experiments. Bluefish attacks could be broadly categorized into one of three types of attack behavior: 1) a single bluefish would approach the bay anchovy school and attack an individual prey that did not respond rapidly by fleeing, but rather remained stationary and non-reactive as the predator approached; 2) a single bluefish would approach and cause a rapid dispersal of the bay anchovy school, resulting in the isolation of several prey individuals (4-5 body lengths from the nearest neighbor), one of which would be subsequently attacked; or 3) bluefish would attack an individual prey that had strayed from the school, causing it to become isolated and generally in closer proximity to predators. The majority of observed bluefish attacks (39) fell under the third type of attack behavior, attacking individual prey that had isolated themselves by straying from the school.

The use of eelgrass patches appeared to provide a refuge for bay anchovy. The mean total number of prey eaten for the entire trial (17.8 when using grass vs. 20.2 when not using grass), the mean number of prey eaten during the initial 1.5 hours of each trial (1.3 when using grass vs. 4.4 when not using grass), and the mean number of attacks observed (2.3 when using grass vs. 9.2 when not using grass) were all lower during trials when bay anchovy made extensive use of the eelgrass, although only the difference in mean number eaten during the initial 1.5 hours of each trial was statistically significant ($p < 0.05$). Further, only 2 of 59 observed bluefish attacks took place within the eelgrass patches.

During size-selection experiments conducted in small aquaria, with low water depths and no structural refuge, bay anchovy had difficulty maintaining cohesive schools, instead forming loose aggregations in opposite areas of the tank from those occupied by bluefish. Groups of bay anchovy were routinely caused to disperse by approaching and attacking bluefish. At any given time, several individual prey were isolated due to the small arena and the frequency of bluefish approaches and attacks that occurred often enough as to not allow sufficient time for groups of bay anchovy to reform. All 34 attacks that occurred during these experiments were made on individual bay anchovy that were relatively isolated (3-4 body lengths from nearest neighbor).

Field diet data demonstrated that a wider range of bay anchovy sizes was consumed as bluefish size increased (Fig. 1.7a, Table 1.1). Mean bay anchovy sizes eaten increased from about 20 to 45 mm TL as bluefish size increased from 60 to 200 mm TL, where as maximum bay anchovy sizes eaten increased more rapidly from 25 to 80mm TL with increasing bluefish size. Minimum bay anchovy sizes eaten remained relatively constant with increasing bluefish size, as even the largest bluefish consumed small (15-20mm TL) bay anchovy. Diet data indicated that bluefish are capable of eating large bay anchovy relative to their own size, as bluefish between 100-125mm TL were often found with bay anchovy as large as 60mm TL in their stomachs, and 150mm TL bluefish had