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Effects of temperature and prey size on predator–prey interactions between bluefish and bay anchovy

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ABSTRACT

Little is known about the behavioral responses of fishes at low temperatures. Of particular interest are predator–prey interactions because feeding at low temperature is necessary for the overwinter survival of many species. This experiment examined how low temperatures affect behavioral interactions between bluefish (*Pomatomus saltatrix* L.) and two sizes of bay anchovy (*Anchoa mitchilli* V.) prey. Temperature had an effect on multiple responses of predator–prey encounters including the approach distance of bluefish towards prey, attack and escape speeds, and prey handling time. The reaction distance of prey was important in determining the outcome of an attack; anchovy reacting at a greater distance from an attacking bluefish escaped more often. However, temperature did not have an effect on either reaction distance or bluefish capture success. The influence of prey size depended on how capture success was defined. Bluefish ability at catching prey was not affected by anchovy size, but larger prey were ingested less frequently due to a greater incidence of prey being dropped in trials with large anchovy. Further, bluefish had greater difficulty handling and ingesting prey at lower temperatures, especially for larger prey. At the lowest temperature treatment small anchovy were readily consumed, but no attacks were made on larger prey. This shows that bluefish modify prey size-selectivity behavior based on temperature, which probably results from a perceived inability to handle and ingest large prey at low temperatures. These results suggest that at low winter temperatures bluefish are restricted to smaller prey.

1. Introduction

The importance of feeding to offset starvation during winter is often overlooked for temperate fishes (Hurst, 2007). Previously, starvation was considered the primary source of mortality during winter, but there is limited field evidence that conclusively shows that starvation mortality occurs in the wild (but see Lambert and Dutil, 1997). Many laboratory studies show that the availability of food is critical for winter survival (Biro et al., 2004; Bystrom et al., 2006; Thompson et al., 1991). Further, field studies show that many temperate fishes feed during winter (Eckmann, 2004; Hurst and Conover, 2001; Morley et al., 2007) and some are capable of winter growth (Bell, 2012; Bystrom et al., 2006). Therefore, feeding at low winter temperatures is probably essential for many species. While much information exists about how temperature limits the physiological maximum consumption of fish, relatively little is known about how ecological processes affect feeding at low temperatures (Hurst, 2007). Of particular interest are behavioral studies on responses of predator and prey to low temperatures.

Bluefish *Pomatomus saltatrix* L. are a migratory pelagic piscivore found in temperate and subtropical waters in many areas of the world. They exhibit one of the highest consumption and growth rates among temperate species (Hartman and Brandt, 1995; Juanes and Conover, 1994). For the United States Atlantic population, winter has been hypothesized to be critical for juvenile survival (Wiedenmann and Essington, 2006). Juvenile bluefish from this population exhibit a bimodal length distribution during winter, consisting of summer- and spring-spawned cohorts (Morley et al., 2007, 2013). The spring cohort consists of larger fish, which are capable of greater energy storage during fall, and they are resilient to starvation (Morley, 2013; Morley et al., 2007; Slater et al., 2007). Conversely, the summer cohort maintains relatively low energy reserves, and winter feeding is critical (Morley, 2013; Morley et al., 2007). In the lab when consuming thawed food, bluefish are capable of feeding and maintaining body weight at typical winter temperatures (Morley et al., 2013). However, it is unknown if low temperatures negatively affect bluefish ability to catch and consume live prey. Further, it is unknown if low temperatures affect bluefish foraging mode. For example, during summer and fall, bluefish feed on a large range of prey sizes (Scharf et al., 2000); larger prey are first severed into two pieces and then ingested (Scharf et al., 1997). If low temperatures affect bluefish ability to consume larger prey, then bluefish may not have as broad a range of prey available to them during winter.

We conducted a laboratory experiment to examine the effect of temperature on behavioral interactions between bluefish and bay anchovy *Anchoa mitchilli* V., which are common prey of bluefish (Buckel et al., 1999; Gartland et al., 2006). Speed and distances were estimated by

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using two video cameras arranged perpendicularly, which allowed the estimation of fish location in three dimensions. Predation trials were filmed at a range of temperatures that encompass environmental conditions bluefish experience from fall through spring (Morley et al., 2007, 2013). Two sizes of bay anchovy were used to determine if the effect of temperature on behavioral responses of bluefish depends on prey size.

2. Methods

2.1. Laboratory

Bluefish and bay anchovy were collected from estuaries in Morehead City, North Carolina with a 30 m beach seine. Fish were transported to the University of North Carolina Fisheries Research Laboratory. Bluefish and anchovy were held in separate 540 L circular holding tanks that received flow-through seawater from Bogue Sound and were maintained at 20 °C. Throughout the experiment bluefish were fed daily to satiation with either thawed anchovy *Anchoa* spp. or live anchovy and Atlantic silversides *Menidia menidia*. Bay anchovy that were used in experimental trials were fed twice daily with formulated fish feed. Natural light was provided throughout the experiment.

The experiment was conducted during summer to ensure that feeding motivation was high because bluefish consumption is influenced by season (Morley et al., 2013). Feeding trials occurred from late June through August in 2009, and mid July through September 2010. Sampling for bluefish and bay anchovy was done periodically throughout the experiment. Predators and prey were acclimated for at least one week prior to use in trials. Two 740 L experimental tanks were used for the feeding trials (180 cm length × 72 cm width × 57 cm deep), each fit with a window encompassing one side. Three bluefish between 131 and 140 mm fork length were used for all trials, and were randomly sampled with replacement from holding tanks. However, individuals were not used in consecutive trials. Trials were conducted with eight bay anchovy from either a small (36–40 mm total length) or a large (61–65 mm total length) size group that was randomly sampled without replacement. Anchovy were not handled directly and were kept submerged during measurements. During acclimation in experimental tanks (2–7 d), predators and prey were kept separate with a two-layer partition. One layer of the partition was clear and the other opaque, and mesh panels allowed for water circulation. Bluefish were fed mostly live prey while acclimating and were starved 48 h before trials. The partition was positioned so the bluefish had access to 75% of the tank.

The bluefish and anchovy in the experimental tanks were adjusted from 20 °C at 2 °C d^{-1} to one of five randomly selected test temperatures: 10, 11, 13, 16, and 20 °C. The lowest temperature treatment is the minimum at which juvenile bluefish are caught in trawl surveys (Morley et al., 2007; Wiedenmann and Essington, 2006; Wuenschel et al., 2012); bluefish are not capable of maintaining body mass at this temperature (Hartman and Brandt, 1995; Morley et al., 2013). The highest temperature is an intermediate value for juvenile bluefish consumption and growth (Buckel et al., 1995; Hartman and Brandt, 1995). Three replicate trials were conducted at each temperature using the smaller prey, but for large prey three replicate trials were conducted only at the 10, 13, and 20 °C treatments. Fish were held at the designated treatment temperature for 24 h prior to trials. Two fluorescent lights (17 W), were positioned 0.25 m above the experimental tanks during acclimation and trials.

Feeding trials were conducted between 0800 and 1000 h. The opaque layer of the partition was removed 5 min before the transparent partition, to allow prey to acclimate to the presence of predators. During this acclimation time, the bluefish and anchovy were clearly aware of each other; the bluefish would occasionally swim aggressively towards the partition and the anchovy would school against the far wall. Trials were recorded with two video cameras (30 frames s^{-1}) positioned perpendicularly, one 1.2 m in front of the window, and the other facing down from 1.04 m above the tank.

2.2. Data analysis

Nine variables characterizing predator–prey encounters were measured during video analysis (Table 1). Distances were determined by using the estimated three-dimensional coordinates of predator and prey (see below for coordinate estimation). Speed was estimated using coordinates from sequential video frames; when fish moved in a straight line, coordinates from start and end points were used. Swimming speeds were measured to approximate maximum values by not including any periods of gliding or deceleration at the end of a response. Based on qualitative observations of experimental trials, the anti-predatory behavior of anchovy (e.g., locations occupied within tanks and schooling) was not influenced by temperature or prey size. Therefore, we concluded that there was no bias in comparing bluefish behavioral responses across temperatures and prey sizes.

The initial goal of the experiment was to determine the best functional relationship of each response variable with temperature, and examine how these relationships differed between the two prey sizes. However, bluefish made no attacks on the larger prey at 10 °C, and we were not logistically able to conduct trials with large anchovy at all five temperatures. This prevented the examination of functional relationships with larger prey. Therefore, we took a two-step analysis for each response variable. First, 2-factor ANOVA was used to examine the effects of temperature and prey size at the two temperatures used with both anchovy sizes (13 and 20 °C). Log_{10} transformations were used on four response variables to normalize residual distributions. A Bonferroni adjusted significance value of $p = 0.006$ was used for ANOVA tests. The second step of the analysis was fitting functional relationships across the full temperature range examined for each response variable. If no effect of prey size was found with the ANOVA in step 1, then replicates from both prey sizes were used to estimate functional relationships. However, if prey size had a significant effect (p-value conservatively set at 0.1), then only trials with small prey were used. A variety of functions were fit between each response variable and temperature, including linear, asymptotic, exponential, saturation, maximum, and sigmoidal curves. A null model containing only an intercept value was also fit. To determine the most suitable functional relationship we used standard residual analysis and AIC_c (Burnham and Anderson, 2002). The analysis of attack rate differed from the above in

Table 1
Definition of response variables estimated during feeding trials with bluefish and bay anchovy.

Variable	Description
Attack rate	Bluefish attacks per minute during the first 20 min of trials or until all prey were consumed. Trials began when the first attack was made.
Approach distance	Distance between predator and prey at initiation of movement towards prey.
Approach angle	From prey perspective, 0° (anterior) to 180° (posterior); e.g., at 180° bluefish approached from behind.
Attack distance	Distance between predator and prey at initiation of predator movement from an S-start position or the beginning of continued aggressive swimming.
Reaction distance	Distance between predator and prey at initiation of prey movement in response to bluefish approach or attack.
Attack speed	Bluefish speed from initiation of attack until prey is captured or escapes.
Escape speed	Prey speed during successful escapes, from initiation of startle response when attacked until prey stopped swimming.
Capture success	Proportion of attacks resulting in prey ingestion (or prey caught, see text). Attacks made on anchovy that were against the tank wall were excluded.
Handling time	From capture until rapid opercular movement ceases.