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

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A B S T R A C T

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.

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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.

that we were able to use three temperature treatments for the ANOVA (10, 13, and 20 °C).

2.3. Estimating fish coordinates with two video cameras

A clear 5 cm-scale grid was affixed to the back and bottom of each experimental tank. During video analysis, cameras were first synchronized using LED lights that flashed before each trial. The *apparent location* of a fish on a given video frame could be estimated in three-dimensions by recording the coordinates of the fish as a point on the grid. The *apparent location* could be determined in the x (left to right) and y (bottom to surface) dimensions using the front camera, and the z (front to back) and x dimensions using the overhead camera. The units on the grid were further refined into quarters by eye (e.g. of fish *apparent location*: $x = 6.25$, $y = 4.0$, $z = 2.75$). For bluefish, the snout (area anterior to the eyes) was used to estimate *apparent location*, and for anchovy the center of the body mass was used.

Due to the cone-shaped video field of the cameras, the *apparent location* of a fish is biased depending on its location in the field of view. To correct for this bias, a three-dimensional matrix of coordinate correction factors was developed for both camera angles. To develop this matrix, a rod was positioned across the top of the tank at $x = 1$, and a series of eight weights were hung from the rod to $y = 1$ at designated points along the z-axis. While filming, the rod was repositioned at different co-ordinates along the x-axis. Then the weights were adjusted to the next y coordinate and the procedure was repeated. In this fashion, we recorded the difference between the *apparent location* as seen on the video frame and the *actual location* of the suspended weights for 25% of the three-dimensional coordinates in the tank.

As an example of how the three-dimensional matrix of coordinate correction factors was used, consider a video frame where a bluefish has an *actual location* of $x = 25$, $y = 5$, and $z = 11$, which is initially unknown to the observer. The video frame from the overhead camera, used to estimate the x and z coordinates, shows the fish to have an *apparent location* of $x = 26$ and $z = 11.75$ due to camera bias. At this point, the true correction factor is unknown because the *actual location* is unknown, and so must be approximated by using the value from the *apparent location*. The correction factor for the *apparent location* would lead to an *estimated location*$_1$ of $x = 25$ and $z = 10.75$. In this example, the *estimated location*$_1$ is not accurate in the z coordinate because the correction factor for the *apparent location* differs slightly from the correction factor of the *estimated location*$_1$. To adjust for this error, the correction factor for *estimated location*$_1$ ($x = 25$, $z = 10.75$) was applied to the *apparent location* to obtain *estimated location*$_2$, which more closely approximates the *actual location* of the fish. For most estimates of fish location (~91%), the correction factors between the *apparent location* and the *estimated location*$_1$ did not differ and so a second iteration was not necessary.

To test the accuracy of this approach, we randomly generated twenty-five x, y, and z coordinates. While filming, a single weight was sequentially positioned at each random coordinate. The videos were then analyzed blind to estimate coordinates. To test for systematic bias in the estimation of each dimension, a t-test was used to see if the mean difference between the actual and estimated values was different from zero. We also calculated the distance between the estimated three-dimensional coordinates and the actual locations in the tank.

3. Results

When testing our approach for estimating location in the tanks using random points, we found no evidence for systematic bias with the x and z coordinates (t-test for x-value, $t = 0.47$, $p = 0.65$; z-value, $t = 1.36$, $p = 0.19$). Estimates for the y-value were biased towards greater than the actual values ($t = 2.87$, $p = 0.01$). However, this bias was not large, and the mean y-value estimates were only 0.4 cm greater than the actual values. Further, the average distance between the

estimated and actual three-dimensional point locations was only 1.2 cm (SD = 0.98). Therefore, we ignored this bias in response variable measurements.

Bluefish typically ate all available prey during trials with small anchovy at the warmest two treatments, and between two and eight prey (out of eight available) at the three coldest treatments. On average, fewer prey were consumed during trials with large anchovy; between two and eight at the highest temperature and between one and four at the 13 °C treatment. The effect of temperature on attack rate was not significant (Table 2), although a positive trend was evident (Fig. 1). The effect of prey size on attack rate was also not significant, but we did observe an important pattern. Larger anchovy were never attacked at the coldest treatment (10 °C), while up to eight anchovy were consumed during small-prey trials at this temperature. Thus, feeding motivation may be high at 10 °C, but feeding behavior suggests relatively large prey are effectively unavailable at this temperature.

Table 2
Analysis of variance tables for response variables measured during bluefish feeding trials at two temperatures (13 and 20 °C) and two size classes of bay anchovy prey (36–40 and 61–65 mm). Three temperature treatments (10, 13, and 20 °C) were used for attack rate.

| Effect	df	MS	F	P
Attack rate (log transformed)				
Prey size	1	0.069	2.754	0.12
Temperature	2	0.076	3.053	0.08
Prey size × temperature	2	0.023	0.905	0.43
Error	12	0.025		
Approach distance				
Prey size	1	2.190	0.046	0.84
Temperature	1	3.580	0.075	0.79
Prey size × temperature	1	4.750	0.100	0.76
Error	8	47.721		
Attack distance				
Prey size	1	0.496	0.092	0.77
Temperature	1	26.880	4.996	0.06
Prey size × temperature	1	0.389	0.072	0.80
Error	8	5.380		
Reaction distance				
Prey size	1	0.066	0.025	0.88
Temperature	1	1.880	0.703	0.43
Prey size × temperature	1	5.535	2.070	0.19
Error	8	2.674		
Attack speed (log transformed)				
Prey size	1	0.003	1.250	0.30
Temperature	1	0.044	16.490	<0.01
Prey size × temperature	1	0.011	4.180	0.08
Error	8	0.003		
Effect	df	MS	*F*	*P*
Escape speed (log transformed)				
Prey size	1	0.016	6.800	0.03
Temperature	1	0.044	19.210	<0.01
Prey size × temperature	1	0.001	0.430	0.53
Error	8	0.002		
Capture success (prey ingested)				
Prey size	1	0.118	6.189	0.04
Temperature	1	0.042	2.203	0.18
Prey size × temperature	1	0.040	2.081	0.19
Error	8	0.019		
Capture success (prey caught)				
Prey size	1	0.0002	0.004	0.95
Temperature	1	0.0024	0.051	0.83
Prey size × temperature	1	0.0030	0.064	0.81
Error	8	0.0470		
Handling time (log transformed)				
Prey size	1	0.208	4.150	0.08
Temperature	1	0.844	16.840	<0.01
Prey size × temperature	1	0.242	4.820	0.06
Error	8	0.050		
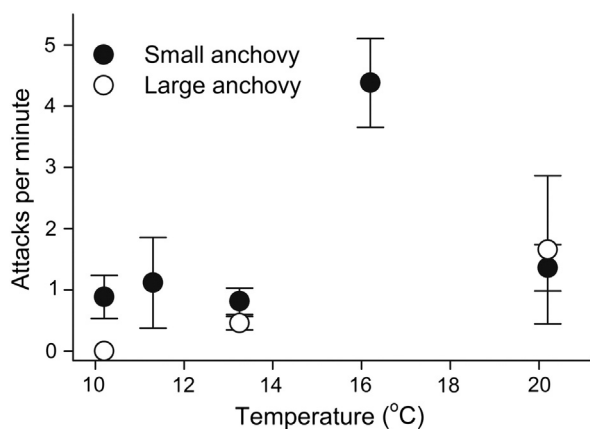
Fig. 1. Mean (±SE) number of attacks per minute between bluefish and bay anchovy prey of two sizes at different temperature treatments.

Bluefish typically attacked individual prey and would initiate an approach in response to anchovy movement. A majority of bluefish approaches and attacks came at a posterior or lateral angle to the anchovy (Fig. 2). The distance at which bluefish initiated an approach to prey was not influenced by anchovy size or temperature at 13 and 20 °C (Table 2). However, across all temperatures and prey sizes, the approach distance of bluefish exhibited a sigmoidal relationship with temperature (Table 3). At colder temperatures the bluefish initiated approaches when closer to prey (Fig. 3A).

The effect of temperature (13 vs. 20 °C) on the bluefish attack distance was marginally significant but there was no effect of prey size (Table 2; Fig. 3B). At most temperatures, the bluefish typically formed an S-start position while gliding towards prey, and then lunged with one tail flip. However, at the warmest treatment, the bluefish often would begin swimming aggressively towards prey from a greater distance. Functions that were fit to these data resulted in non-normal residual patterns, so the relationship of attack distance with temperature was not determined. The average attack distance for pooled successful attacks was 7.2 cm, compared to 8.0 cm for pooled missed attacks; this difference was not significant (t test, t = 0.92, p = 0.18).

Anchovy reaction distance was not influenced by size or temperature when comparing the 13 and 20 °C treatments (Table 2). However, at the lowest temperature the anchovy generally had low reaction distances (Fig. 3C). Functions that were fit to these data explained little variation ($r^2 < 0.18$) and residual patterns were not normal. The

reaction distance of anchovy had a strong impact on the outcome of predator–prey encounters (Fig. 4). When individual attacks from all trials were pooled, the anchovy reaction distances for successful bluefish attacks (including dropped or discarded prey) were significantly lower than for unsuccessful attacks (Mann–Whitney U test, n = 126, p < 0.01). Anchovy reaction distance has even greater importance considering that when prey reacted before a bluefish attacked, an approaching bluefish typically did not attack. Bluefish rarely pursued prey after a missed attack.

Bluefish attack speed increased significantly with temperature (from 13 to 20 °C), but was not affected by prey size (Table 2). Combining attack speed from both small and large prey trials across all temperatures, we found that multiple functions described the relationship with temperature well (Table 3). Based on the AIC_c weight scores (w), an exponential model was used for the functional relationship between bluefish attack speed and temperature (Fig. 5A). Anchovy escape speed increased with temperature (from 13 to 20 °C) and there was a trend of larger prey being faster, although the effect of prey size was not significant (Table 2). Using only small-prey trials, the relationship between escape speed and temperature was best explained by a saturation model (Table 3, Fig. 5B).

There was no effect of temperature on capture success at 13 and 20 °C, but bluefish exhibited a marginally significant trend of lower capture success rates with larger prey (Table 2, Fig. 6A). However, this prey-size effect was not due to bluefish having more difficulty catching larger anchovy, but from difficulty handling the larger prey. When a successful capture was redefined as a bluefish catching an anchovy and holding it in its jaws, there was no influence of prey size (Table 2, Fig. 6B). The effect of the full range of temperatures on capture success was examined using small-prey trials with linear regression and there was no significant temperature effect for either method of defining capture success (Fig. 6A and B, p > 0.33 for both). The difficulty bluefish had with handling larger prey was evident as larger anchovy were dropped more frequently (Fig. 6C). Further, temperature appeared to affect the frequency of bluefish dropping prey. For example, 24% of large prey were dropped after capture at 20 °C and 43% were dropped at 13 °C. No small prey were dropped at 20 °C and 11% were dropped at 13 °C (Fig. 6C). Anchovy condition after being dropped ranged from dead to exhibiting no sign of injury. On three out of nine occasions when anchovy were dead when dropped, a different bluefish intercepted and consumed the prey. However, dead prey were never picked up from the bottom of the tank.

At 13 and 20 °C, the interaction between prey size and temperature was marginally significant for handling time (Table 2) so we conducted a post hoc test. For small prey, handling time was significantly lower at 20 °C (Tukey HSD test, p = 0.01), but the temperature effect with large prey was not significant (p = 0.56). The effect of prey size at each temperature was not significant (p > 0.06 for both). Based on the AIC_c weight scores, a linear relationship best described how handling time decreases with increasing temperature for small prey (Table 3, Fig. 7A). Bluefish often severed prey in half before ingestion, which typically increased individual handling time. The proportion of ingested prey that were first severed was greater at lower temperatures and for larger prey (Fig. 7B). Of anchovy that were severed (n = 33), 91% were oriented so that the posterior section was consumed and the anterior section dropped; on 30% of occasions, a different bluefish intercepted and consumed the dropped half before it reached the tank bottom. Further, of the prey that were consumed whole that we were able to determine orientation for (n = 30), 87% were swallowed tail first.

4. Discussion

4.1. Effects of temperature and prey size on capture success and prey handling

It is generally assumed that temperature influences the ability of a piscivorous fish to capture and ingest prey, but this assumption has rarely been tested. In our experiment there was no effect of either
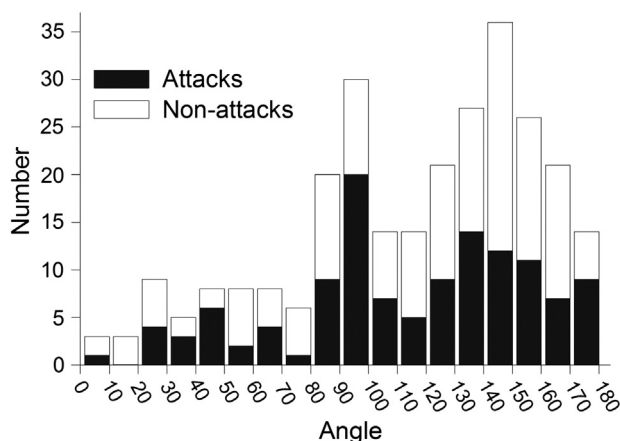

Fig. 2. Distribution of approach angles of bluefish towards bay anchovy prey. Approaches that resulted in both attacks and non-attacks are shown. Angle is from the anchovy perspective; 180° represents a bluefish approaching an anchovy from directly behind and 0° represents head on.

Table 3
Model selection for relationships between four different response variables and temperature (10–20 °C) from feeding trials with bluefish and bay anchovy. K = number of parameters, RSS = residual sum of squares, AIC_c = Akaike information criterion adjusted for small sample size, ΔAIC = difference in AIC_c value between each model and the best-fit model, w = AIC_c weight.

Function	Equation	K	r^2	RSS	AIC_c	ΔAIC	w
Approach distance							
Null	$y = 32.73$	1		1445.3	94.27	8.76	0.01
Linear	$y = 16.61 + 1.10x$	3	0.26	1066.1	92.71	7.20	0.02
Asymptote	$y = 65.93(x/14.42 + x)$	3	0.30	1005.5	91.42	5.91	0.04
Exponential	$y = 45.89(1 - e^{-0.09x})$	3	0.31	991.7	91.12	5.61	0.05
Maximum	$y = 0.005x^{4.94}e^{-0.29x}$	4	0.46	782.1	88.91	3.40	0.14
Sigmoid	$y = 36.91(x^{12.19} / (10.0^{12.19} + x^{12.19}))$	4	0.54	670.0	85.51	0	0.75
Attack speed							
Null	$y = 93.48$	1		9763.8	126.04	15.68	0
Linear	$y = 22.85 + 4.67x$	3	0.63	3578.6	111.24	0.88	0.20
Asymptote	$y = 361.2(x / 42.53 + x)$	3	0.65	3437.2	110.43	0.07	0.30
Exponential	$y = 213.8(1 - e^{-0.04x})$	3	0.65	3424.8	110.36	0	0.32
Saturation	$y = 147.0((x - 7.51) / (3.65 + x - 7.51))$	4	0.68	3096.8	111.51	1.15	0.18
Escape speed							
Null	$y = 98.34$	1		6796.0	94.05	23.45	0
Linear	$y = 25.73 + 5.12x$	3	0.77	1568.2	77.93	7.33	0.02
Asymptote	$y = 370.5(x / 38.49 + x)$	3	0.80	1382.3	76.03	5.43	0.06
Exponential	$y = 220.3(1 - e^{-0.04x})$	3	0.80	1363.0	75.82	5.22	0.06
Saturation	$y = 142.0((x - 8.54) / (1.81 + x - 8.54))$	4	0.89	745.8	70.60	0	0.86
Handling time							
Null	$y = 22.73$	1		3948.3	85.90	4.54	0.06
Linear	$y = 67.38 - 3.15x$	3	0.50	1971.6	81.36	0	0.59
Exponential	$y = 161.72e^{-0.15x}$	3	0.46	2115.6	82.42	1.06	0.35

temperature or prey size on the ability of bluefish to catch prey. However, prey handling and ingestion were inhibited at low temperatures, especially for larger anchovy. Further, while small anchovy were captured and consumed at 10 °C, no attacks were made on large prey at this temperature. We suggest that a perceived inability to handle and ingest relatively large prey was the reason bluefish made no attacks on large anchovy at the lowest temperature. This is an interesting prospect because it shows that temperature can modify predatory behavior in complex ways, in this case through prey size selectivity. Further, this may have important ecological consequences for bluefish because relatively large prey may be present in the environment, but effectively unavailable at the lower end of their thermal range.

The way a successful capture is defined has important consequences for interpreting our results. Typically, a successful capture is defined as prey being caught and ingested, and dropped prey are grouped with failed attacks. When defined this way, our results are consistent with previous research showing bluefish capture success to decline with increasing prey length (Scharf et al., 2003; Staudinger and Juanes, 2010). However, when we redefined a successful capture to include both ingested and dropped prey, there was no effect of either temperature or prey size. Therefore, prey handling was the mechanism behind significant prey size effects on the ability of bluefish to catch and ingest anchovy. Indeed, larger anchovy were dropped more frequently than small anchovy.

Bluefish exhibit two modes of ingestion; either prey are swallowed whole or they are first severed using rapid lateral movement of the anterior half of the body. We found that larger prey were more frequently severed, which is consistent with previous work on bluefish (Scharf et al., 1997). In addition to the effects of prey size, our experiment shows evidence for temperature effects on mode of ingestion. There was an increasing trend of prey being severed at lower temperatures. This contributed to a six fold increase in handling time at temperatures below 14 °C for small prey. Attempts at severing prey were not always successful and failed attempts would lead to prey either being consumed whole or dropped. Our data suggest that the success rate of prey severing was influenced by temperature. For example, when pooling trials with large and small anchovy at temperatures above 13 °C, seventeen out of twenty attempts to sever prey were successful. Whereas success rate

was only five out of sixteen in trials below 13 °C, which only includes small anchovy because large prey were not attacked at the coldest temperature. This decreased success rate is consistent with the increased frequency of dropped prey at low temperatures. It is interesting that bluefish attempt to sever prey more frequently at low temperatures, where they are less effective at doing so; the increased severing at low temperatures may result from a decreased ability to swallow prey whole or a temperature related constraint on meal size. The influence of temperature on the success rate of severing prey is probably due to the properties of skeletal muscle, which experiences a decrease in maximum contractile velocity as temperature declines (Bennett, 1984). It is clear that prey handling can be a constraining factor affecting the ability of a predator at low temperatures.

A limited number of studies have examined how temperature affects capture success with fishes, and results are varied. Some have suggested that the relationship may depend on the temperatures examined and how they overlap with the optimal temperature range of the predator and prey. For example, the ability of yellow perch *Perca flavescens* to capture lake whitefish *Coregonus clupeaformis* declines from 18 to 10 °C (Yocum and Edsall, 1974). In this case the predator had a higher optimal temperature than the prey. Conversely, Arctic grayling *Thymallus arcticus*, a cold-water species, exhibits higher capture success on the copepod *Heterocope septentrionalis* as temperature drops from 15 to 5 °C (Schmidt and O'Brien, 1982). Our experiment did not support the hypothesis that the more cold tolerant species will have an advantage as temperature declines. Available evidence suggests that bay anchovy are more cold tolerant than bluefish; bay anchovy overwinter throughout the northern half of the United States (Hartman and Nagy, 2006; Vouglitois et al., 1987), while juvenile bluefish are restricted to waters south of North Carolina during winter (Morley et al., 2007; Wuenschel et al., 2012). Despite this potential difference in thermal tolerance between predator and prey, the capture success of bluefish did not decline at low temperatures. Both bluefish and anchovy experienced a similar reduction in swimming speed as temperature declined, which may partly explain why capture success was not affected by temperature. Further, the reaction distance of anchovy was small at the lowest temperature, which probably enhanced bluefish capture success at this treatment and disrupted the relationship of capture success with temperature.
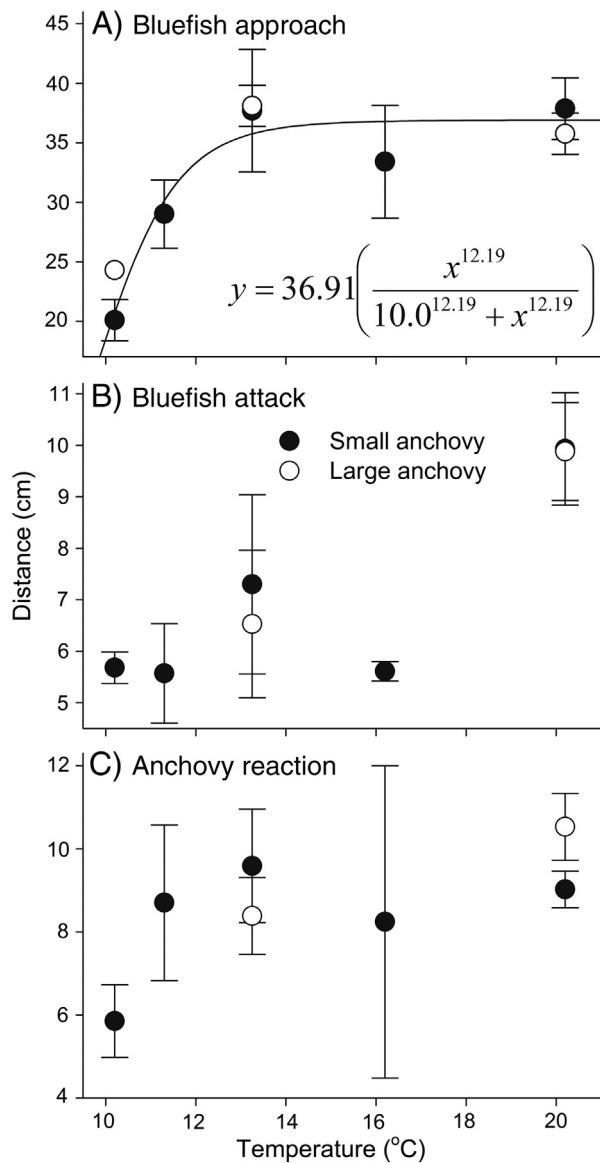
Fig. 3. Mean ($\pm$SE) distance between bluefish and bay anchovy prey of two sizes when (A) bluefish first initiated movement towards prey, (B) bluefish attacked prey, and (C) anchovy reacted to an approaching or attacking bluefish, at different temperature treatments. The sigmoid function on (A) was fitted to temperature data pooled across anchovy sizes.

The equation shown in panel A:

$$y = 36.91\left(\frac{x^{12.19}}{10.0^{12.19} + x^{12.19}}\right)$$

Another explanation for the lack of a relationship between capture success and temperature is that bluefish were more selective about the decision to attack prey at low temperatures. Three lines of evidence from our experiment support this. First, large anchovy were not attacked in the 10 °C trials, while small prey were readily consumed at this temperature. Second, if all bluefish approaches in trials below 14 °C are pooled (n = 220), only 48% resulted in attacks, compared to 59% in trials above 14 °C (n = 183). Last, at the coldest two temperatures bluefish only initiated movement towards anchovy that were relatively close to them. These three changes in predatory behavior may have mitigated against a loss of performance at low temperatures.

It is uncertain how capture success and attack rate estimates determined from laboratory experiments compare with fish in the wild. Prey may be more vulnerable to attack in a laboratory setting due to confinement, while predators may lose the advantage of surprise. Scharf et al. (2003) examined capture success of bluefish preying on Atlantic silverside *Menidia menidia* using three different tank sizes: 215, 475, and 900 L. Their study shows a significantly higher capture success
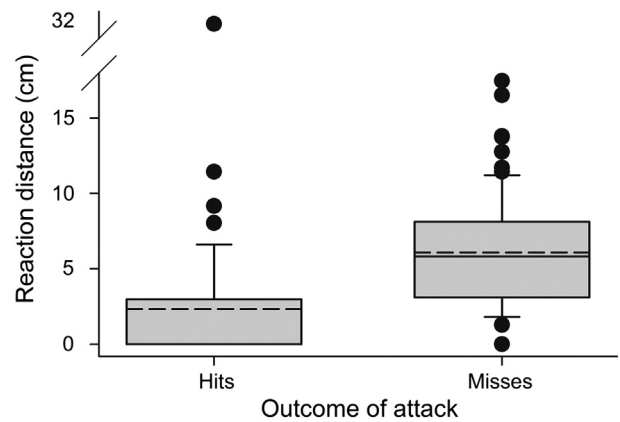

Fig. 4. Bay anchovy reaction distances from successful and missed bluefish attacks. Boxes show 25th percentile, median (solid line), 75th percentile, and the mean (dashed line); bars show the 10th and 90th percentiles, and points show outliers. Note, for hits, the median and lower percentiles are the same value.

rate with the smallest tank, and no difference between the intermediate and largest tank sizes. These results suggest that our experimental tank size of 740 L was adequate to prevent any inflation of capture success due to confinement. Further, we excluded attacks when prey were against a tank wall. In addition to confinement factors, the laboratory setting may also lead to changes in the antipredatory behavior of prey. For example, we observed that the constant presence of bluefish often inhibited anchovy schooling behavior during trials. Despite confinement, laboratory experiments are excellent tools to understand the relative influence of abiotic and biotic factors on capture success and attack rate. However, experimental estimates may only approximate what occurs in the wild.
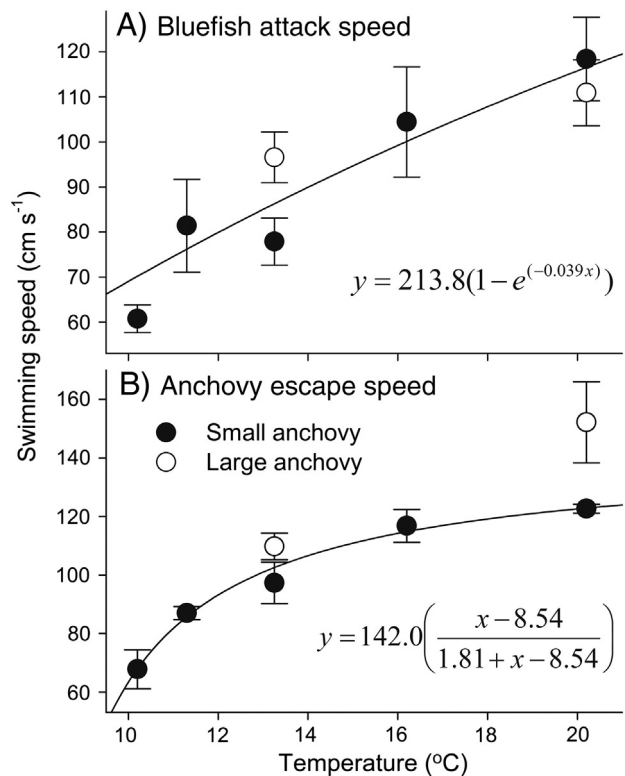

Fig. 5. Mean ($\pm$SE) swimming speed of (A) bluefish attacking two sizes of bay anchovy, and (B) two sizes of bay anchovy successfully escaping bluefish attacks, at different temperature treatments. The exponential function on (A) was fitted to temperature data pooled across anchovy sizes and the saturation function on (B) was fitted to small anchovy only.
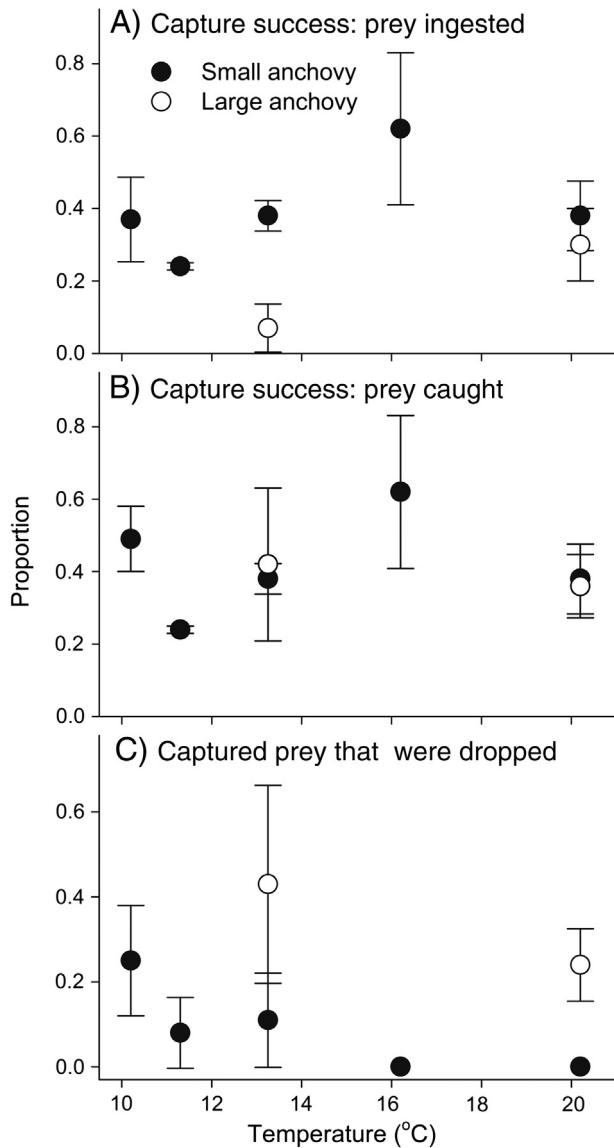
The equation shown in panel A of Fig. 5:

$$y = 213.8(1 - e^{(-0.039x)})$$

The equation shown in panel B of Fig. 5:

$$y = 142.0\left(\frac{x - 8.54}{1.81 + x - 8.54}\right)$$

Fig. 6. Bluefish preying on bay anchovy of two sizes at different temperature treatments, mean values (±SE) are shown. (A) Proportion of successful attacks where a successful capture was defined as prey ingested, (B) proportion of successful attacks where dropped prey were also considered a successful capture, and (C) proportion of successfully captured prey that were dropped.

4.2. Predator and prey behavioral interactions

Reaction distance of anchovy was an important factor determining the outcome of predator–prey interactions in this study. Anchovy that reacted at a greater distance from an attacking bluefish were more likely to escape. Further, there was no difference in reaction distance between large and small anchovy, which explains why there was no prey size effect on bluefish ability to catch prey. The importance of reaction distance is even more significant considering that when anchovy reacted during a bluefish approach, this would often prevent an attack from occurring. The important influence that reaction distance has on capture success has also been shown with rainbow trout *Oncorhynchus mykiss* preying on goldfish *Carassius auratus* (Webb and Zhang, 1994). Further, Scharf et al. (2003) compared the reaction distance of four prey species to bluefish predators and found that species with smaller reaction distances suffered higher capture success rates. They conducted their experiment at temperatures between 19 and 21 °C, which is similar to the highest temperature treatment in our study. Also, bay anchovy
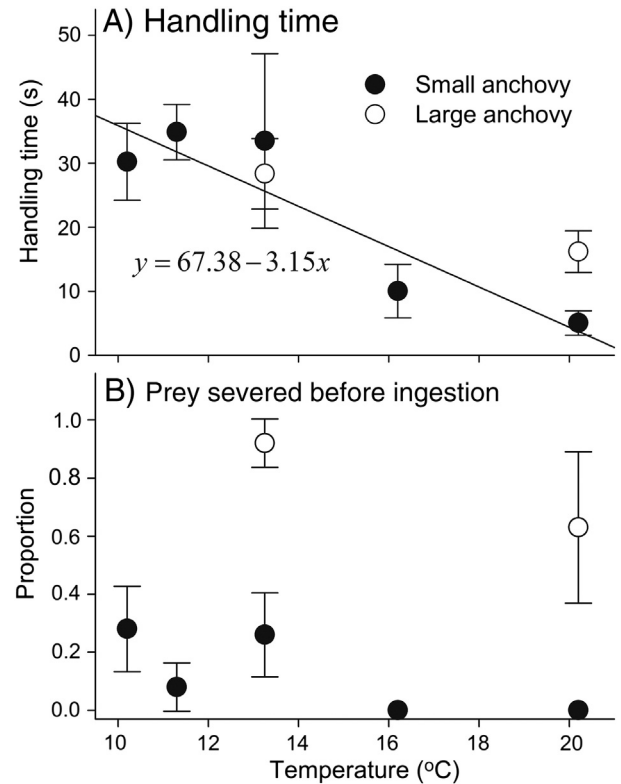

Fig. 7. Bluefish preying on bay anchovy of two sizes at different temperature treatments, mean values (±SE) are shown. (A) prey handling time, and (B) proportion of ingested prey that were first severed in half. The linear function on (B) was fitted to temperature data from small anchovy trials only.

were one of the prey species examined by Scharf et al. (2003) and this species had the lowest mean reaction distance and suffered the highest capture success rate; compared to our experiment, capture success rates were more than 20% higher for similar predator to prey length ratios. This was probably due to bay anchovy in their study having half the mean reaction distance to attacking bluefish (31 mm) than in our 20 °C trials (62 mm; n = 47). This difference in reaction distance may have resulted from different methods of prey addition to experimental tanks. Scharf et al. (2003) acclimated prey to predators within a clear holding chamber for 15 min, while our study maintained prey and predators within the same experimental tank for multiple days.

To our knowledge, no other study has examined reaction distance at different temperatures. Unfortunately, we were not able to include a functional relationship of anchovy reaction distance with temperature due to poor model fits; poor model performance resulted from the large amount of variation at the 16 °C treatment. Despite this, it is worth noting that the reaction distance of anchovy was consistently small at 10 °C. Three probable factors contributed to the small reaction distance of anchovy at the lowest temperature. First, the attack speeds of bluefish were low at this temperature, and Dill (1974) states that reaction distance will decrease if either predator speed is reduced or size of the oncoming predator is smaller. Second, bluefish approached anchovy from smaller distances at this temperature, which reduced the distance at which prey could react. Last, low temperatures probably inhibit the speed of prey response to an attacking predator.

Studies to measure the effect of temperature on burst swimming speed in fish are typically performed using an artificial stimulus to instigate an escape response (O'Steen and Bennett, 2003; Webb, 1978). In our study, the role of temperature and prey length on swimming speed was examined more realistically by examining predator–prey interactions. The results on attack and escape swimming velocity are consistent with previous research showing that maximum velocity

increases nonlinearly with temperature (O'Steen and Bennett, 2003; Wardle, 1975; Webb, 1978). The effect of temperature on swimming speed for bluefish and bay anchovy was greater at the lower temperatures (10–13 °C). This pattern was especially apparent for anchovy, which may have resulted from a behavioral response rather than a physiological limitation. For example, Webb (1976) found that escape speeds of prey were often sub-maximal when predators did not pursue, which was typical for bluefish–anchovy interactions in our experiment. By limiting escape speed and distance, anchovy reduce energetic costs and probably reduce the risk of drawing the attention of other predators.

Larger anchovy exhibited higher escape speeds, which is consistent with numerous studies showing that maximum swimming speed increases with length (Wardle, 1975; Webb, 1976). However, higher escape speeds conveyed no advantage in evading capture for larger anchovy. Fish acceleration is independent of length (Domenici and Blake, 1993; Webb, 1976, 1978), and given the small reaction distance of bay anchovy (Scharf et al., 2003), maximum speed probably does not contribute to their ability to evade capture.

The attack speed of fishes does not indicate maximum speed and is probably related to attack distance. At most temperatures, bluefish attacked from a short distance relative to their body length. As a result, attacks were often just one propulsive tail flip. Similarly, Harper and Blake (1991) compared acceleration and velocity of attacking versus escaping responses. They show that escape responses exhibit higher acceleration and velocities compared to attacks. The reason predators may attack from a short distance is to minimize the reaction distance of prey; reaction distance is dependent on the size and speed of an approaching predator (Dill, 1974). Thus, in order to minimize reaction distance, bluefish appear to get close to prey before accelerating into an attack. Similarly, Webb and Skadsen (1980) showed, with muskelunge (*Esox* sp.) feeding on fathead minnows *Pimephales promelas*, that attacks from shorter distances were more successful than attacks from longer distances. In our experiment bluefish also exhibited this trend, but the difference was not significant. We found evidence for a different foraging strategy with bluefish at higher temperatures. In trials at 20 °C, bluefish attacked from greater distances. There are two probable explanations for this change in foraging strategy. First, the temporal resolution of fish eyes are temperature sensitive (Fritsches et al., 2005). Bluefish are probably able to visually track prey more effectively as temperature increases, and thus attack from greater distances. Second, the maximum consumption rate of bluefish increases rapidly with temperature (Buckel et al., 1995; Hartman and Brandt, 1995), and given the schooling nature of bluefish, intraspecific competition may limit prey availability at higher temperatures. This may result in more aggressive feeding behavior. Consistent with this hypothesis, Buckel and Stoner (2004) found that per capita prey consumption declined with increasing bluefish numbers in a large experimental arena. Prey were never depleted during their feeding trials, and the authors hypothesized that interference competition played an important role in limiting consumption within large groups of bluefish.

Multiple fish species have been shown in the laboratory to exhibit some degree of thermal acclimation of swimming performance (Johnson and Bennett, 1995; O'Steen and Bennett, 2003). Thermal acclimation allows fish to maintain a more constant swimming ability in response to temperature variation. The capacity for bluefish or bay anchovy thermal acclimation is unknown, and we were not logistically able to use prolonged acclimation periods for this study. However, the temperature adjustment rate and acclimation period were appropriate for the behavioral responses we measured for three reasons. First, fast start swimming speeds are often found to have minor or no acclimation effects (e.g., Johnson et al., 1996; O'Steen and Bennett, 2003; but see Beddow et al., 1995), with the exception of studies that compare a large range (e.g., 25 °C) of acclimation temperatures (Johnson and Bennett, 1995). Second, MacNutt et al. (2004) show with cutthroat trout *Oncorhynchus clarki* that critical swimming speeds acclimate to

temperature changes of up to 8 °C within 48 h. Further, these authors used a rapid temperature adjustment rate of 1 °C per hour; in our study we adjusted temperature at 2 °C per day to ensure adequate acclimation time. Third, on one occasion during our experiment an extra trial was conducted with large anchovy at the lowest temperature, but using a six day acclimation period at 10 °C; bluefish still made no attacks on the larger prey.

4.3. Estimating fish location

Examining predator–prey interactions in experimental settings has been useful for interpreting large-scale patterns observed in the wild (Bystrom et al., 2006; Scharf et al., 2009). Accurate estimates of predator–prey behaviors require estimates of velocity and distance between predator and prey (Scharf et al., 2003). Studies that have measured velocity and distance typically do so in two dimensions, using only one camera angle. For benthic animals this is not a problem, but to achieve this for pelagic fish water depth is typically restricted (O'Steen and Bennett, 2003; Webb and Zhang, 1994). Limiting water depth is often not a realistic alternative for larger or more active predators and prey.

Scharf et al. (2003) estimated distance and speed without restricting depth by only examining interactions that appeared to occur within a two-dimensional plane that was perpendicular to the camera. They used a grid on the back of the tank and adjusted apparent velocity of fish across it based on location in the camera's depth of field. This method is limited because only a subset of the total interactions can be used. Further, error is introduced when interactions are not completely occurring on a two-dimensional plane, or if the location within the depth of field is not accurately estimated. Our use of two camera angles eliminated these shortcomings and the average error in determining the location of random points within the tank was small. In practice, this method is probably more accurate than the average error indicates. Typically, predator and prey are in close proximity and each have similar correction factors applied to their *apparent locations*. Further, when calculating speed, correction factors typically change slowly across sequential video-frames.

4.4. Conclusions

Juvenile bluefish feed during the winter, and feeding is particularly important for summer-spawned fish, which comprise around one third of the adult population (Morley et al., 2013). As juveniles, summer-spawned fish are relatively small and do not accumulate large energy reserves during the fall. As a result this cohort depends on feeding to prevent winter starvation mortality (Morley, 2013; Morley et al., 2007). Temperatures that bluefish encounter during the winter (Morley et al., 2007, 2013) would normally allow for a positive scope for growth (Hartman and Brandt, 1995). However, summer-spawned fish exhibit a reduction in appetite during the winter (Morley et al., 2013), which is a characteristic that has also been shown with other species (Metcalfe et al., 1988; Simpson et al., 1996). This reduction in appetite is probably an adaptation to minimize energy loss, and it may be coincident with a reduction in metabolic rate (Evans, 1984; Karas, 1990). In this experiment, we investigated one possible hypothesis for this energy conserving adaptation, that bluefish have difficulty catching and ingesting live prey during winter. Our results supported this hypothesis. At low temperatures, handling time increased and bluefish were more dependent on severing prey before ingestion. This would lead to more energetically costly meals during winter, and also increase bluefish vulnerability to predators. Also, relatively large prey become increasingly difficult to ingest as temperature declines.

Our experiment shows that bluefish are effective predators near their thermal minimum, given appropriately sized prey. This suggests that the reason bluefish exhibit an energy conserving adaptation during winter may result from a consistent limitation of prey during winter.

Field studies on overwintering fish that examine the importance of prey availability are relatively rare (Hurst, 2007). However, the abundance of prey of suitable length can have a large impact on winter mortality, especially for the smaller individuals within a cohort (Adams et al., 1982). For overwintering bluefish, the abundance of anchovy has been shown to affect short term feeding responses (Morley, 2013). This suggests that large-scale prey abundance may have important implications for winter survival and year class strength of juvenile bluefish. Further, our results show that the size distribution of prey is important; the effective available prey field may become restricted to bluefish during the winter because relatively large prey are more difficult to handle and ingest. A restriction of available prey would be of particular importance to the summer cohort, which already experiences a narrower range of potential prey due to their smaller size (Scharf et al., 2000).

Acknowledgments

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