Abstract

Morley, James Walter. Ecology of juvenile bluefish (*Pomatomus saltatrix*) overwintering off North Carolina. (Under the supervision of Jeffrey A. Buckel)

Ecology of overwintering young-of-the-year bluefish (*Pomatomus saltatrix*) off North Carolina was examined for the 2001 and 2002 year-classes. This study addressed the hypothesis that overwinter mortality affects the recruitment of summer-spawned bluefish. A trawling survey was conducted in Onslow Bay, NC from October 2001 to May 2002 and from September 2002 to June 2003. Up to four transects were sampled monthly each ranging from 0.4 to 16.1 kilometers from shore. Lipid content of white muscle and livers were determined using soxhlet extraction. Abundance of bluefish in Onslow Bay depended on winter severity, as catches during the winter were higher during the more mild winter of 2001-02. The highest catches of bluefish occurred within two miles of shore and were strongly associated with anchovy and clupeid prey. Bluefish recruitment was shown to be more complex than previously supposed; at least three young-of-the-year cohorts were observed for both year-classes. Energy reserves peaked in November with larger fish having disproportionately more energy. However, by mid-winter there was little difference in energy storage between the cohorts. These data suggest that larger fish deplete a greater portion of their energy stores as the season progresses while smaller fish defend their energy levels by feeding. Catch data show that summer-spawned bluefish survive the winter despite having lower energy reserves. However, the magnitude of overwinter mortality remains uncertain.

Ecology of Juvenile Bluefish (*Pomatomus saltatrix*)
Overwintering off North Carolina

by
James W. Morley

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Approved By:

_____   _____   _____
James A. Rice   Leonard A. Stefanski   Thomas E. Lankford Jr.
Department of Zoology   Department of Statistics   External Member

_____
Jeffrey A. Buckel
Department of Zoology
Chair of Advisory Committee

Biography

Education
August 2001 – July 2004 North Carolina State University   Raleigh, NC
Master of Science, Department of Zoology/Interdisciplinary Minor, (Expected) July 2004

August 1995 – May 2000 State University of New York College at Cortland   Cortland, NY
Bachelor of Science, Department of Biology/Cum Laude, May 2000

Acknowledgements

Table of Contents

Table of Contents (cont'd)

List of Tables

List of Figures

List of Figures (Cont'd)

Ecology of Juvenile Bluefish (*Pomatomus saltatrix*) Overwintering off North Carolina.

1.1 Introduction

Winter is a critical period for juvenile fish in temperate latitudes. Overwinter mortality can cause a significant bottleneck in recruitment at the juvenile stage (Chevalier 1973; Conover and Ross 1982; Miranda and Hubbard 1994). Mortality during the winter is often size-selective, with smaller individuals experiencing higher mortality rates (see Sogard 1997). Negative size-selective overwinter mortality has been observed in many species including Atlantic silversides (Conover and Ross 1982), yellow perch (Post and Evans 1989), largemouth bass (Adams et al. 1982; Miranda and Hubbard 1994) and striped bass (Hurst and Conover 1998; Sutton and Ney 2001).

One hypothesis for this pattern of size-selective mortality is the more rapid depletion of energy reserves in smaller individuals. Feeding ceases or is reduced during the coldest months; as a result, overwintering fish must depend on energy reserves to survive the winter (Foltz and Norden 1977; Adams et al. 1982; Cunjak et al. 1987; Foy and Paul 1999). Smaller individuals of a year-class have been shown to have disproportionately lower energy storage (Schultz and Conover 1997; Post and Parkinson 2001; Hurst and Conover 2003) and a higher mass-specific metabolic rate (Post and Lee 1996). This may result in smaller individuals exhausting their energy stores more rapidly and approaching critical starvation levels sooner than larger members of a year-class (Oliver et al. 1979; Sogard and Olla 2000). Due to this size-selective pattern in overwinter mortality, individuals spawned

1

later in the year often have a disadvantage in surviving the winter due to a shorter initial growing season.

Bluefish (*Pomatomus saltatrix*) support a valuable recreational fishery, often being the most caught marine species on the U.S. Atlantic coast (NMFS 2004a and b). However, for over a decade the annual recreational catch has persisted at much lower levels than catches in the 1980s (NMFS 2004a and b). Further evidence suggests historic, decadal-scale variation in population abundance of the northwestern Atlantic bluefish stock (Baird 1873; Wilk 1977; NMFS 2004a and b). Efforts to understand this variation have focused on recruitment dynamics and survival of juveniles.

One of the initial studies done on bluefish was conducted by Lassiter (1962) in the early 1960s. One component of his work was to collect adult bluefish and determine their length at the time of first annulus formation (age-1), using scales. Lassiter's resulting back-calculated age-1 length distribution was bi-modal (Figure 1a). He hypothesized this to be the result of two spawning peaks each year. Lassiter's hypothesis was later confirmed by larval sampling (Kendall and Walford 1979) and the consistent observation of a bimodal length distribution of young-of-the-year bluefish recruiting to the Middle Atlantic Bight (Gilmore 1985; Munch and Conover 2000). While larval bluefish are found offshore during every season of the year, a majority of recruits are thought to come from two major spawning periods (Kendall and Walford 1979). The first spawning period occurs in the spring on the western edge of the Gulf Stream in the South Atlantic Bight (Kendall and Walford 1979; Collins and Stender 1987). Progeny from this spawning period, the spring cohort, either recruit to estuaries in the South Atlantic Bight (McBride et al. 1993; Gilmore

2000) or are advected north in the Gulf Stream and recruit to estuaries and coastal waters in the Middle Atlantic Bight (Kendall and Walford 1979; Hare and Cowen 1996). The second spawning period occurs during the summer on the continental shelf of the Middle Atlantic Bight (Kendall and Walford 1979; Smith et al. 1994). Progeny from this second spawning event, the summer cohort, recruit to estuarine and continental shelf waters in the Middle Atlantic Bight (Munch and Conover 2000; Able et al. 2003). Gilmore (2000) determined the spawning dates of newly recruited juveniles from both cohorts using otoliths, and found about a 6-week difference in the mean spawning date.

In addition to the spring- and summer-spawned cohorts there is evidence of juvenile bluefish recruitment later in the year. A late-summer-spawned cohort has been observed in nearshore ocean waters off New Jersey in October (Able et al. 2003; Wilber et al. 2003). Spawning also occurs during the fall in the South Atlantic Bight (Kendall and Walford 1979; Collins and Stender 1987), however recruitment success of these progeny is unknown. During the fall, juvenile bluefish in the Middle Atlantic Bight migrate south to spend the winter in the South Atlantic Bight (Lund and Maltezos 1970; Gilmore 1985; Munch and Conover 2000).

Since Lassiter's work in the early 1960s, two projects have examined the relative contribution of spring- and summer-spawned bluefish to the adult population but have found that back-calculated age-1 size distributions were unimodal (Figure 1b and 1c) (Chiarella and Conover 1990; Conover et al. 2003). The authors concluded that the majority of these individuals were from the spring-spawned cohort and that there was little evidence of fish spawned in the summer being represented in their adult samples (Chiarella

and Conover 1990; Conover et al. 2003). Moreover, Conover et al. (2003) found this despite sampling a majority of adults belonging to year-classes when summer-spawned fish dominated as young-of-the-year. If the summer-spawned cohort is not surviving past the juvenile stage, there are major implications. Based on catch data in the Middle Atlantic Bight, the relative abundance of each cohort as YOY has shifted from spring-spawned bluefish dominating annual recruitment to summer-spawned fish dominating (Conover et al. 2003). This shift in relative abundance of YOY to a less successful cohort of bluefish may help explain the reduced state of the population.

The reason for the lack of contribution by the summer-spawned cohort in recent years is unknown. Conover (unpublished data, see Conover et al. 2003) conducted a laboratory experiment to assess the effectiveness of the back-calculation technique and to determine if differential growth between the spring- and summer-spawned cohorts during the winter existed. He found the back-calculation technique to be effective and observed no difference in overwinter growth between the two cohorts. Evidence suggests that the summer cohort experiences a higher overwinter mortality rate than bluefish spawned during the spring (see Conover et al. 2003). Despite extensive research that has been conducted on juvenile bluefish in the Middle Atlantic Bight during the summer and fall months, the ecology of juvenile bluefish has received very little attention in the South Atlantic Bight, especially during the winter.

This paper tests the hypothesis that members of the summer-spawned cohort exhaust their energy stores more rapidly than the spring-spawned cohort during the winter, consequently experiencing a higher mortality rate. Size-selective mortality is typically

examined by comparing both the mean and variability of length, from pre- and post winter length frequency distributions. This approach is amenable to closed, freshwater systems as one can more readily accept the assumption of no migration; consequently a majority of overwintering field studies have been conducted with freshwater species. To our knowledge, the only marine species that have been examined for negative size-selective overwinter mortality in the wild are Atlantic silversides (Conover and Ross 1982) and striped bass (Hurst and Conover 1998). However, both of these marine species are restricted to a certain latitudinal range during the winter (Conover and Murawski 1982; see Hurst and Conover 1998). Examining size-selective overwinter mortality in a species with the migratory capabilities of bluefish is a novel and challenging task.

The objectives of this project were to investigate juvenile bluefish overwinter ecology and to determine if the lack of contribution by the summer cohort to the adult population is due to overwinter mortality. Specifically this project aimed to: 1) determine if Onslow Bay, NC is an important overwintering area for juvenile bluefish and, if so, what factors affect distribution and abundance; 2) examine cohort structure of juvenile bluefish found in Onslow Bay throughout the winter; 3) examine energy storage dynamics throughout the winter; 4) examine the importance of feeding for winter survival; and 5) test for negative size-selective mortality using length frequency distributions.

1.2 Methods

1.2a Study Site

Onslow Bay is located in the Atlantic Ocean off the southern coast of North Carolina; it is defined by Cape Lookout to the north and Cape Fear to the south (Figure 2). Depth increases from around 7 meters at 0.4 kilometers from shore to about 18 meters at 16 kilometers from shore. Nearshore temperature in Onslow Bay typically ranges from around 26ºC during September, to 12ºC in February; salinity is consistently around 35 ppt throughout the year (Atkinson et al. 1983). There is very little fishery independent data available for this region from winter months. McBride et al. (1993) analyzed North Carolina winter oceanic trawl fishery data for the 1984-85 season and found juvenile bluefish occurring throughout the winter. Additionally, the National Marine Fisheries Service conducted the SEAMAP trawling survey from 1989 through 2000, which sampled from Cape Hatteras, NC to northern Florida. The SEAMAP survey routinely captured large numbers of juvenile bluefish off of North Carolina in November and April, however no sampling took place during the winter months (Anonymous 2000). The available literature cites no evidence of juvenile bluefish overwintering north of Cape Hatteras, therefore Onslow Bay is likely near the northern limit of the juvenile bluefish winter range. Due to the relatively cooler temperatures, this area is a logical place to look for evidence of negative size-selective overwinter mortality in juvenile bluefish.

1.2b Distribution and Abundance

Trawl Survey. Monthly sampling was conducted from October 2001 through May 2002 and from September 2002 through June 2003 aboard the 21.3-meter R/V Cape Fear in Onslow Bay. During the first season four transects were sampled monthly. These were, starting in the south and proceeding to the north, the Cape Fear, Masonboro Inlet, Topsail Beach and Cape Lookout transects (Figure 2). The Topsail Beach transect was removed after February 2002 due to unfavorable trawling bathymetry. Two transects were sampled each month during the second season (Masonboro Inlet and Cape Lookout). Each transect was comprised of six trawl-stations located 0.4, 0.8, 1.6, 3.2, 8.0 and 16.1 kilometers from shore. However, the 0.4-kilometer station was not added until December of 2001. During the first four months of the 2001-02 sampling season no bluefish were captured beyond 8 kilometers from shore so the 16.1-kilometer station was removed after January 2002. Two twenty-minute trawls were performed at each station with each trawl track running parallel with shore. A bottom trawl was used with a twelve-meter wide opening, 1.83 x 0.91 meter, 68-kilogram doors and a 1.27-centimeter mesh cod end. Depth was recorded at each trawl station as well as temperature, salinity, and dissolved oxygen, which were recorded at the sea floor and the surface with a YSI model 85. All fish caught in the trawl were counted and measured. In addition, all bluefish were kept on ice to be processed upon return to the lab.

Analysis of Catch Data. An adjusted catch per unit effort (CPUE) value (see Munch 1997) was determined at each distance from shore within each transect, month, and year for the juvenile bluefish index of abundance.

Ln (CPUE) = (S (Ln (catch + 1))) / n

where, catch = number of juvenile bluefish caught in a given trawl and n = number of tows at a given distance from shore.

A five-factor ANOVA was used to examine the spatial and temporal dynamics of bluefish abundance with the following factors: year (2001-02 or 2002-03), month, transect, distance from shore, and prey abundance. Prey abundance was entered as a value of 1-5 based on the CPUE of clupeoids (families engraulidae and clupeidae). Preliminary analyses of diet demonstrated that clupeoid prey made up 81.7% and 79.6% of juvenile bluefish diet by weight for the 2001-02 (n = 427) and 2002-03 (n = 294) sampling seasons respectively (J. Morley et al. unpublished data). Clupeoid catch per unit effort was calculated at each treatment combination (year, month, transect and distance from shore) as total catch divided by number of tows. Prey abundance values for each treatment were assigned based on the following criteria: 1 = CPUE of 0, 2 = CPUE of 1-10, 3 = CPUE of 11-100, 4 = CPUE of 101-1000, and 5 = CPUE over 1000. Temperature was not added as a covariate because it showed no discernable relationship with bluefish catch. Using the five-way ANOVA prevented the examination of interactions due to limited degrees of freedom. Therefore, a second ANOVA including second-order interactions was used after eliminating non-significant factors from the initial model.

1.2c Cohort Structure

Bluefish length data from the trawling survey and from supplemental sampling using hook and line, beach seine, gill net and stop net were used to construct length frequency distributions for each time-interval. Table 1 displays numbers of bluefish collected by each gear type for each time interval and locations of non-trawl caught fish. During certain months it was difficult to distinguish larger young-of-the-year (YOY) from smaller age-1+ bluefish based on length distributions. Larger YOY have been shown to overlap in size with smaller age-1 and age-2 bluefish (Lassiter 1962; Salerno et al. 2001). In order to ensure that only YOY bluefish were examined, whole sagittal otoliths from larger bluefish of questionable age were viewed under a dissecting microscope. Using whole otoliths for bluefish younger than age-4 has been shown to be an effective ageing technique (Carmichael et al. 2002; Sipe and Chittenden 2002). Bluefish typically lay down their first annulus in April of their second year (Barger 1990; P. Rudershausen et al. unpublished data), therefore if an annulus was present on any individual caught during the fall or winter it was a member of the previous year-class. Likewise if an individual caught during the spring had an annular mark that had not recently formed, or if two were present, it was considered a member of the previous year-class. Otoliths from bluefish that had an annulus typically appeared much different from the otoliths of similar sized YOY. Second-year growth appeared to form as a second layer over and past the edge of the proximal surface of the otolith. Age-1 otoliths were much thicker, the edges appeared clear and brittle, and layers corresponding to the first and second year of growth were evident.

In order to compare energy storage and feeding dynamics of the different juvenile

cohorts it was necessary to distinguish between them at each time interval. Length

frequency distributions of trawl-caught bluefish were independently examined by four

individuals. Each examiner used the antimodes in the length frequency distributions for

each time interval as cut-off points between cohorts. Further, during time intervals when

cohort structure was unclear, cut-off points were estimated by using antimodes from dates

immediately before and after. Final cut-off points were determined for each time interval

by choosing the one with the most agreement between examiners; if each examiner chose a

different cut-off point, an intermediate length was chosen.

1.2d Seasonal Energy Storage Dynamics

Laboratory Procedure. Juvenile bluefish collected in the trawling survey and

supplemental sampling were processed to quantify energy storage from October through

June for both the 2001 and 2002 year-classes. Table 1 illustrates numbers of bluefish used

for the analyses by cohort for each time interval. The liver and a sample of white muscle

were removed from each bluefish and individually frozen. The white muscle sample was

removed from the dorsal surface, between the lateral line and first dorsal fin. A four to five

gram muscle sample was removed when the size of the specimen permitted; with smaller

individuals the largest possible sample was obtained. After dissection, the sample was

further processed by removing any attached red muscle or skin. Bluefish tissues were

processed in the lab to quantify energy storage and described below as in Schultz and

Conover (1997). Each tissue sample was processed by first recording the wet weight

(WETWEIGHT) and then placing the tissue in a drying oven set at 60ºC until the weight

stabilized (two to four days). After desiccation, the dry weight (DRYWEIGHT) of the

tissue was taken. A pre-dried alundum extraction thimble was then weighed

(THIMBLEWEIGHT) and the sample was placed inside it. While in the thimble, the tissue

was cut into small pieces with a pair of dissecting scissors. The thimble was next placed in

a soxhlet extractor for four hours. The soxhlet extractor continually deposits petroleum

(PET) ether on the sample. Petroleum ether is a non-polar solvent that extracts non-polar

storage lipids from the sample; lipid dissolves in the solvent, which drains out through the

porous alundum thimble. After extraction, the thimble and sample were returned to the

drying oven for 48 hours. After drying, the thimble was weighed (THIMBLELEAN) and

then placed in a furnace set at 450ºC for 24 hours. At this temperature, organic material in

the tissue burns off as carbon dioxide leaving behind only inorganic matter. The thimble

was then returned to the drying oven for at least two hours before being weighed

(THIMBLEASH). The following compositional statistics were calculated:

%Dry Weight Muscle = (DRYWEIGHT / WETWEIGHT) x 100;

%Lipid Wet Muscle = (((THIMBLEWEIGHT + DRYWEIGHT) - THIMBLELEAN) / WETWEIGHT) x

100;

%Lean Wet Muscle = ((THIMBLELEAN – THIMBLEASH) / WETWEIGHT) x 100;

Lipid Weight Liver = (THIMBLEWEIGHT + DRYWEIGHT) – THIMBLELEAN;

Lean Weight Liver = THIMBLELEAN – THIMBLEASH.

Additionally, total energy in the liver and energy per gram of wet muscle were calculated

based on the energy density values of lipid (9.45 kcal / gram) and protein (4.80 kcal / gram)

reported in Brett and Groves (1979). Phospholipids and carbohydrates are minor

constituents of fish tissues (Love 1980). Thus, lean tissue weight was assumed to be

protein.

Liver Energy (kcal) = 4.80 x Lean Weight Liver + 9.45 x Lipid Weight Liver;

Muscle Energy (kcal / gram wet weight) = 4.80 x (%Lean Wet Muscle x 0.01) +

$$9.45 \text{ x } (\%\text{Lipid Wet Muscle x } 0.01).$$

Unless otherwise stated, all analyses regarding bluefish energy storage dynamics were

performed using only the two smaller body-sized cohorts. The larger bodied cohort was

excluded as it was inconsistently captured throughout the year. Additionally, only time

intervals with a range in bluefish lengths of 60mm or more and a sample size of at least 20

individuals were examined.

Analyses of Seasonal Energy Storage. Temporal changes in liver energy, muscle

energy, body weight (whole wet weight of fish), and percent dry weight muscle for each

year-class were examined using ANCOVA. By using fish length as a covariate on a ln-ln

transformed scale, the length-adjusted mean of each dependent variable can be compared

across time intervals. In addition to comparing time intervals within a year, inter-annual

comparisons were made with pre- and post-winter liver energy, muscle energy, body

weight, and percent dry weight muscle between the 2001 and 2002 year-classes. However,

adjusted means from separate ANCOVA models cannot be compared as each model is

adjusted to a different mean covariate value. Therefore separate ANCOVA models were

used for the inter-annual comparisons using the November and April time intervals for each

year-class. If slopes were not homogenous across time intervals for any of the above models, separate slopes ANCOVA was used for that particular dependent variable.

Analysis of Seasonal Allometries. The relationship between length (L) and weight (W) is described by the function

$$W = aL^b,$$

where a and b are parameters. This function is used to describe the weight of the entire organism, organs, or tissue components such as lipid and protein. The above equation can be linearized with a log transformation and analyzed with linear regression,

$$Ln (W) = a + b \times Ln (L).$$

Growth is termed isometric when $b = 3$ as body form does not change with respect to length. When the slope of the function is not equal to three, growth is termed allometric. Hyperallometric growth ($b > 3$) results in higher weight for a given length with longer individuals having disproportionately higher weight. Conversely, hypoallometric growth ($b < 3$) results in lower weight for a given length with longer individuals having relatively less weight. Bluefish body weight, liver lipid weight, and liver protein weight were related to fork-length using ln-ln transformed linear regression for each time interval. Slopes were tested against the null hypothesis of isometric growth with two-tailed t-tests. Significance levels were adjusted within each season and tissue type using the standard Bonferroni technique (a / number of tests).

Comparison with Starvation Experiment. Compositional statistics were also compared to data obtained from a starvation experiment in order to determine if bluefish approached critical weight and energy levels. From November 2001 through May 2002, 201 juvenile bluefish (175-315mm fork length) in both starved and fed treatments were held in outdoor flow-through tanks for 192 days (J. Slater et al. unpublished data). Fed treatments were given a diet of previously frozen anchovies and silversides, ad libitum each day. The lipid extraction technique and the derivation of compositional statistics performed by Slater et al. were identical to those described for this study. The purpose of the lab-field comparison was to determine if field bluefish approached critical levels of body weight, liver energy, and muscle energy when they were at their most depleted energetic state. Therefore, the time interval with the lowest length-adjusted mean value for each of these dependent variables was used for each year-class. Length-adjusted mean values were determined with the seasonal energy storage analyses described above (see section 1.2d). Body weight, liver energy, and muscle energy of bluefish in the wild during the selected time interval were compared to individuals that had starved to death in the lab using ANCOVA with fork length as covariate on a ln-ln scale.

1.2e Winter Feeding Dynamics

Laboratory Procedure. Stomachs were removed from trawl-caught bluefish and individually stored in 10% buffered formalin. Upon examination, prey were removed from stomachs and blotted dry before being weighed. Gut fullness is the weight of the stomach contents divided by the weight of the bluefish without prey.

Feeding Analyses. The principal goals of feeding analyses were to determine if bluefish length and residual body weight affects feeding. The influence of bluefish length on winter-feeding was examined using time intervals from November to April for each year-class. Bluefish were grouped into twenty-millimeter length bins and gut fullness was plotted for each bin, using box plots. The role residual body weight had in feeding activity was also examined. Body weight was plotted against fork length on a ln-ln scale for each time interval. The regression equation for each time interval was used to determine the value for residual body weight of each individual. This residual value of body weight served as an indicator of bluefish condition, specific to each time-interval. The influence of residual body weight on gut fullness was determined for each year-class by grouping bluefish into five bins based on residual body weight values; gut fullness for each bin was plotted using box plots. The cohort of largest body-size was excluded from this analysis, as it was not consistently captured across time intervals.

1.2f Negative Size-Selective Mortality

For each year the juvenile cohort of smallest body-size was analyzed for negative size-selective mortality. This cohort was chosen as it offered the likeliest chance for size-selective mortality to occur. Further, it was clearly identifiable and had length distributions that were normal or approximately normal. Length frequency distributions from months with colder temperatures were used in order to limit the possibility of growth biasing the results. For the 2001 year-class the January and February length frequency distributions were compared; the December and March 22 - April 14 intervals were compared for the

2002 year-class. These time-intervals were chosen as they had high sample sizes allowing

for accurate determination of cut-off points between cohorts. Mean and variance of length

were determined for each time-interval. Additionally, due to variance scaling positively

with mean values, the coefficient of variation, a measure of relative variability, was also

determined. If no growth or emigration is assumed, an increase in the mean length and a

decrease in the coefficient of variation between dates are due to selective mortality of

smaller individuals (Ricker 1969; Post and Evans 1989).

1.3 Results

1.3a Distribution and Abundance

During the 2001-02 sampling season, 233 trawls were completed capturing 873

bluefish from the 2001 year-class. A total of 181 trawls were performed during the 2002-

03 season capturing 848 bluefish from the 2002 year-class. Temperature differences

between the two sampling seasons were pronounced; the 2002-03 winter was more severe.

Temperature in October of 2002 was over five degrees C higher than the previous year,

however temperature rapidly declined and by December was over six degrees cooler than

the previous year (Figure 3). January and February 2003 temperatures were also colder

than in 2002.

The full ANOVA model revealed transect (p = 0.934) and distance from shore (p =

0.664) as unimportant factors affecting bluefish distribution (Table 2a) so they were not

used with the reduced model. Temporal patterns of bluefish abundance were different for

each year (year × month interaction: p = 0.013) due to a later peak in autumn abundance

and lower winter bluefish catches observed during the 2002-03 season. Bluefish abundance was highest during the fall and dropped during the winter concomitant with declining temperature and prey abundance (Figure 3). Abundance of bluefish and clupeoids increased during the spring as temperature increased (Figure 3). The association of bluefish with their prey depended on the time of year (month × prey abundance interaction: $p = 0.03$); bluefish were associated with prey during the fall and spring months but winter catches of bluefish were typically low despite the presence of prey. The majority of bluefish (95.5%) were captured within 1.6 kilometers of shore; only four individuals were captured beyond 3.2 kilometers (Figure 4). Due to strong covariation between the distance from shore and prey abundance factors, a second ANOVA model was produced excluding prey abundance (Table 2b). This model revealed distance from shore to have a significant effect on bluefish distribution (Full model $p < 0.001$; Reduced model $p = 0.003$).

1.3b Cohort Structure

Three juvenile cohorts were commonly caught during both years of the study (Figure 5a-i and 6a-g). Cohorts were labeled 1, 2, and 3 in order of decreasing fish length. Cohort-1 was present during early autumn, with cohort-2 arriving by mid to late-October. By November of each year length distributions became tri-modal, as a third cohort made up of smaller individuals was commonly caught (Figure 5c and 6b). Relatively few members of cohort-1 were caught during the winter or the following spring, the exception being late March of 2003 when they were collected by hook and line (Figure 6e). Cohort-3

17

dominated catches during the winter and early spring for the 2001 year-class (Figure 5e-h).

Very few samples were obtained during the winter of 2002-03, but the third cohort

dominated catches in late autumn and early spring (Figure 6c and 6e). During early May of

2002 a fourth cohort consisting of smaller individuals was captured (Figure 5h). These fish

do not appear to be young-of-the-year due to much thicker and more opaque otoliths when

compared to YOY bluefish of similar sizes caught during other time-intervals. This group

of bluefish was not included in energetic or feeding analyses.

1.3c Seasonal Energy Storage Dynamics

Cohort Comparison. To compare energy storage of the three juvenile cohorts, mean

values for liver energy and muscle energy were determined for each time interval. Energy

levels in both tissues reached peak values by late fall; energy stores were highest in cohort-1

and lowest in the third cohort (Figure 7a-d). Energy was depleted in both tissues during the

winter months and increased again the following spring. During both overwintering periods,

the greatest difference in energy storage between the cohorts occurred in the fall. This

difference was greater for the 2002 year-class for both tissues (Figure 7a-d). During the

winter, the energy difference between the cohorts was much lower as energy was depleted

more rapidly in cohorts with larger bluefish. For the 2001 year-class, there was no length-

based pattern in muscle energy storage during February or April and differences in liver

energy between cohorts steadily declined from December to May. The inter-cohort

difference in energy storage for the 2002 year-class declined dramatically from November to

December. However, when multiple cohorts were captured again in April, the difference was

18

more substantial than observed in April for the 2001 year-class; this was largely due to the low energy levels of cohort-3 during the early spring of 2003 (Figure 7c-d).

   Analyses of Seasonal Energy Storage.   After adjustment to a common fish length using ANCOVA, energy storage in liver and muscle tissue of juvenile bluefish from cohorts 2 and 3 combined peaked during the fall and was depleted during the winter for both the 2001 and 2002 year-classes (Figure 8a and b); month had a significant effect on adjusted mean energy values of both tissues for each year-class (Table 3). Muscle energy was at its lowest during April of each year and increased by May. The 2001 year-class had low liver energy levels during February but by April liver energy had increased (Figure 8a). For both year-classes, liver energy decreased from April to May despite increases in muscle energy.

   The two year-classes differed in both peak energy levels obtained during the fall and energy levels the following spring. After correcting for a common length between year-classes, bluefish from the 2001 year-class had significantly higher muscle energy levels in November (ANCOVA: p <0.00001) and April (p = 0.00743) than the 2002 year-class. Differences between year-classes in pre- and post-winter liver energy were not significant.

   Seasonal changes in bluefish body weight and percent dry weight muscle for cohorts 2 and 3 were significant for both year-classes (Table 3). Peak levels in body weight and percent dry weight muscle occurred in the fall of each year (Figure 9a and b). Body weight was depleted during the winter despite decreases in percent dry weight muscle. An increase in body weight occurred from April to May in each year. Percent dry weight muscle increased from April to May for the 2002 year-class. Comparing the two winter seasons revealed that the 2001 year-class had a higher pre-winter length-adjusted body weight

(ANCOVA: p < 0.0001). However, the 2002 year-class had a higher body weight in April (p < 0.0001). The 2001 year-class had significantly higher percent dry weight muscle during both pre- (p = 0.0006) and post-winter (p < 0.0001) time-intervals.

Analyses of Seasonal Allometries. Seasonal allometries for body weight, liver lipid and liver protein weight were highest during the fall of both years (Figure 10a and b). Liver lipid and protein allometries declined to their lowest levels by April 2002 and 2003 and increased again in the spring. The allometric slope for body weight reached its lowest level by June and May for the 2001 and 2002 year-classes respectively. Liver lipid and protein weight allometries exhibited much greater seasonal change than body weight. Further, variability of liver lipid and protein weight was much higher than for body weight, which resulted in few time intervals with allometries significantly different from isometric growth (Table 4). For the 2001 year-class, body weight to length relationships were found to be significantly hyperallometric for the late fall and mid-winter time-intervals (Table 4). For the 2002-03 overwintering period body weight was hyperallometric for all time-intervals but early May. Further, both liver lipid and protein weight were hyperallometric in November. During the early spring of 2003 liver lipid weight was significantly hypoallometric with a slope of 1.96. Thus, larger fish had disproportionately higher energy stores and relatively larger body weights than smaller fish in the fall. However, during the winter and spring larger fish typically had no advantage in liver lipid and protein, and the advantage in body weight by larger fish was less pronounced.

Comparison with Starvation Experiment. Critical body weight, liver energy, and muscle energy levels from lab starvation deaths (Slater et al. unpublished data) were lower

than the values observed with field-caught bluefish during their most energy depleted time intervals (Table 5; Figure 11). Liver energy appeared the most disparate when compared to bluefish starved in the lab, as there were no field-caught individuals approaching critical starvation levels. Further, bluefish captured in the wild during the spring and winter months, when they were the most depleted, more closely resembled wild bluefish during the fall than critical starvation levels determined in the lab (Figure 11). The only time interval and year-class that was not significantly greater than critical levels was body weight for the 2001 year-class (ANCOVA: p = 0.538). However, when the ANCOVA for body weight was run again, using only field caught bluefish that were within the length range of bluefish that had died in the lab, the 2001 year-class was significantly greater than critical values (p < 0.001).

1.3d Winter Feeding Dynamics

Seasonal trends in gut fullness generally followed the pattern of temperature changes throughout the overwintering season (Figure 12a and b). In both years gut fullness was highest in November and decreased by December concomitant with declining temperature. Gut fullness and temperature were both at their lowest levels in January for the 2001 year-class, however by February both temperature and mean gut fullness had increased. During April of each year temperature had markedly increased however gut fullness remained low until May. Seasonal gut fullness data need to be interpreted with caution.

Comparing gut fullness levels of the cohorts separately for both seasons reveals similarities between year-classes. During October 2002 and November of each year, mean gut fullness increased with cohort length. However, during the winter and spring of 2001-02,

21

cohort-3 had the highest gut fullness levels. Gut fullness data were not available during the winter of 2002-03, but the pattern observed during April 2003 was slightly different than the previous year as cohort-2 had higher gut fullness values than the third cohort.

Comparing gut fullness across bluefish length bins revealed similar length-based feeding patterns in both year-classes. The median and 75th percentile values for gut fullness dropped substantially in bluefish less than 181mm for the 2001 year-class (Figure 13a). The decline in median and 75th percentile values with decreasing length was more gradual for the 2002 year-class; however, gut fullness values were low below 161mm (Figure 13b). Examining the role of residual body weight revealed a pattern of individuals with a higher residual weight having higher gut fullness values for both year-classes. Median and 75th percentile gut fullness values generally increased with residual weight (Figure 14a and b).

1.3e Negative Size-Selective Mortality

For the 2001 year-class, there was no evidence of negative size-selective mortality; there was a non-significant increase ($t = 0.4778$, $p = 0.633$) in the mean length and a non-significant decrease in variance ($p = 0.647$) for cohort-3 from January to February (Figure 5e-i) along with a decrease in the coefficient of variation (Table 6). However, negative size-selective overwinter mortality was evident during the winter of 2002-03. A significant increase in mean length ($t = 7.699$, $p < 0.0005$) and a significant decrease in variance ($p < 0.0005$), along with a decrease in the coefficient of variation for cohort-3 occurred from December 2002 to April 2003 (Figure 6c and 6e).

1.4 Discussion

1.4a Distribution and Abundance

This study has shown coastal Onslow Bay, NC to be an important overwintering area for juvenile bluefish. However, a number of factors affect the extent of their abundance. Month was a significant factor affecting trawl CPUE of bluefish, however ultimately temperature is likely the stimulus bluefish are responding to. Juvenile bluefish have a preferred temperature range of 18-25°C (Olla and Studholme 1975; Munch 1997). The significant interaction between year and month with bluefish catch may be explained by differences in water temperature between the two years. Peak catch in bluefish occurred in October of 2001, however in 2002 the highest catches occurred in November. Near-shore temperature in Onslow Bay during October of 2002 was over 26°C, which was much higher than the preceding year. If temperatures were also relatively high in the Middle Atlantic Bight, the southern migration of YOY bluefish may have been delayed. Munch (1997) presents data that supports a temperature-mediated southern migration; bluefish reside in their preferred temperature range during their southward migration during the fall.

Winter severity may also contribute to the interaction between year and month. Bluefish may change the extent of their southern migration in response to winter water temperature. During the milder winter of 2001-02, bluefish were caught in every month with the exception of March. However, during the more severe winter of 2002-03 only one individual was caught by trawl in Onslow Bay during the months of January through March.

Based on gut-fullness patterns, bluefish captured in Onslow Bay were feeding during the winter. Therefore, the interaction between month and prey abundance with bluefish catch

23

is also likely due to low temperatures in Onslow Bay forcing bluefish out of the area despite the availability of prey.

Bluefish remain near shore while present in Onslow Bay and appear to travel south when temperatures become too low, despite a steeper positive temperature gradient when moving offshore (Atkinson et al. 1983). During this study only 4 bluefish were caught beyond 3.2 kilometers from shore. Munch (1997) observed the majority of summer-spawned bluefish staying within 10 kilometers from shore in the Middle Atlantic Bight during their fall migration south despite members of the spring cohort commonly being caught up to 40 kilometers from shore.

Temporal trends are evident in bluefish CPUE at each transect that would suggest a near shore southern migration during the winter. For the 2001 year-class, the two northern transects yielded a higher CPUE than those in the south during December and January. In February, the two southern transects produced the highest CPUE of bluefish for the 2001-02 sampling season, however, the two northern transects were not sampled due to equipment problems. No bluefish were captured during March, and by April catches were relatively high at both northern and southern transects. Temporal trends in abundance for the 2002 year-class were more apparent. Catches in November were much higher at the northern transect while December CPUEs were very high at the southern transect. Only one bluefish was caught during the following three months; however, in April the majority of bluefish were caught at the southern transect suggesting a northward return from southern latitudes as temperature increased. Greater sampling effort, including areas outside of Onslow Bay,

would be useful to determine if bluefish stay near shore and migrate further south as temperature becomes intolerable.

Bluefish size may also play a role in overwintering range. During the fall of each year cohort-1 was relatively common, however once temperature dropped below 15$^{\mathrm{o}}$C they were rarely captured, suggesting they are overwintering in warmer areas. The second cohort dominated catches during mid-fall of each year. However, by December of each year, cohort-3 had arrived and dominated catches. The third cohort may be the most tolerant of low temperatures as they were the only cohort caught in large numbers when temperature dropped below 12$^{\mathrm{o}}$C. The difference in overwintering temperature range among the three juvenile cohorts may contribute to the lack of a relationship between temperature and CPUE when all cohorts are combined. During the overwinter laboratory experiment conducted by Slater et al. (unpublished data), smaller bluefish exhibited a higher tolerance of low temperature extremes. Increasing cold tolerance with decreasing length has also been shown with Atlantic croaker (Lankford and Targett 2001). The overwintering range of each cohort may extend farther to the south with increasing body size. A cohort-specific examination of juvenile bluefish overwintering range has yet to be conducted. If the severity of winter temperatures experienced by juvenile bluefish increases with decreasing body size, cohorts spawned later in the year may have a disadvantage in surviving the winter.

While temperature and body size appear to determine overwintering range, both prey abundance and temperature likely affect fine-scale distribution. When bluefish were present in Onslow Bay they were strongly associated with clupeoid prey. These results are in contrast to Wilber et al. (2003) who did not observe a significant correlation between

25

juvenile bluefish and their prey on ocean beaches in the Middle Atlantic Bight. However,

even during months when bluefish are showing limited feeding they are still found near shore

despite the high positive thermal gradient with offshore movement (Atkinson et al. 1983).

This may be due to a number of reasons. It may be advantageous for bluefish to remain in

relatively cooler waters to reduce the energetic demands associated with higher temperatures

(Schultz and Conover 1999). Bluefish have experimentally been shown to prefer

increasingly lower temperatures as the fall season progresses (Olla et al. 1985). The

selection of cooler temperatures during the winter has also been shown in the lab with

Atlantic salmon (Morgan and Metcalfe 2001). Further, the active selection of cooler

temperatures by starving fish in order to limit energy expenditure has been shown in the

laboratory for a number of species (Javaid and Anderson 1967; Sogard and Olla 1996; van

Dijk et al. 2002). In addition to the role behavioral thermoregulation may play in bluefish

distribution, the location of prey may also be an important influence. Prey abundance was

very low in deeper waters, thus the ability to feed in order to offset the increased energy

demands of inhabiting warmer water would be limited. Therefore, provided temperature is

within physiological limits, staying in cooler, near shore waters may be beneficial. Further,

feeding below $11^{o}C$ occurred, thus the potential for an occasional meal may be important

even at very low temperatures. Both striped bass and Pacific herring have also been shown

to feed during the coldest winter months (Hurst and Conover 2001; Foy and Paul 1999).

Both prey abundance and predation risk are known to shape fish distribution (Gilliam

and Fraser 1987; McIvor and Odum 1988). While we have shown prey to be abundant near

shore, the influence of predation risk in deeper waters on bluefish distribution is unknown.

Spring-spawned and age-1+ bluefish are found in deeper waters (Lund and Maltezos 1970; Gilmore 1985; Munch 1997), which may be a result of decreased predation risk with increasing body size. To our knowledge no study has examined the diets of large predators in the South Atlantic Bight during the winter. Bluefin tuna are captured on the North Carolina continental shelf during the winter; they have been shown to feed on bluefish in the Middle Atlantic Bight (Chase 2002). Adult bluefish may also be an important predator on juveniles during the winter. Lassiter (1962) found smaller bluefish to be an important prey item of larger bluefish, particularly during December and March, but bluefish were not collected during January or February.

1.4b Cohort Structure

The three cohorts observed in this study were numerically labeled instead of being labeled spring, summer, and late-summer cohorts as has traditionally been done. The reason for this terminology is due to uncertainty in assigning cohort labels. Bluefish greater than 150mm are unable to be aged accurately using daily otolith rings (Gilmore 2000), therefore determining the spawning dates of each cohort was precluded. Two possible scenarios of cohort structure for these data are apparent and each one is defendable. The first scenario is that the smallest cohort is composed of summer-spawned individuals and the two larger cohorts are subcohorts of spring-spawned bluefish. The second scenario is that cohort-3 is a late-summer cohort and the other two cohorts represent summer- and spring-spawned bluefish. These two scenarios will be addressed separately below.

27

Scenario 1. Two cohorts of spring-spawned bluefish have yet to be documented, but may be explained by a difference in growth rates, growing season length, and/or spawning date between spring-spawned fish recruiting in the South Atlantic Bight and the Middle Atlantic Bight. Bluefish recruiting to the South Atlantic Bight experience much warmer temperatures and likely have a higher growth rate. Temperature has been shown to have a strong influence on bluefish consumption and growth rates in the laboratory (Buckel et al. 1995); however, reviewing other field studies leads to inconclusive results. Growth rates of spring-spawned YOY bluefish collected in the South Atlantic Bight during 1987-88 ranged from 1.2 - 1.9mm / day (McBride et al. 1993), however, growth rates ranging from 1.17 – 2.06mm / day were reported for the spring cohort from southern New England during the same years (McBride et al. 1995). Despite the lack of a clear pattern in growth rates across latitudes, Munch (1997) found the size of spring-spawned bluefish to increase with decreasing latitude in the Middle Atlantic Bight. Two spring cohorts may be a result of bluefish recruiting to the South Atlantic Bight earlier and having a longer growing season. Bluefish collected in the South Atlantic Bight during 1987-88 had spawning dates as early as January and February (McBride et al. 1993) whereas initial recruits to the New York Bight during the same years were spawned in mid- to late-March (McBride and Conover 1991). However, YOY bluefish caught off Maine have been shown to be spawned as early as February (Creaser and Perkins 1994). Despite these inconclusive findings, the spring cohort does recruit over a much greater range of the coast and have a greater range of spawning dates when compared to summer-spawned fish. The available literature documents spring-spawned bluefish recruitment from Maine to South Carolina (Creaser and Perkins 1994;

McBride et al. 1993; Gilmore 2000), whereas the summer cohort has only been reported to recruit in the Middle Atlantic Bight north of Virginia (McBride et al. 1993; Munch and Conover 2000). The spring cohort has also been shown to be produced over a range of over eleven weeks (Gilmore 2000) whereas the summer cohort has had a range in spawning dates of around eight weeks (McBride and Conover 1991). This difference in spawning duration likely results in the spring cohort having a greater size range by the fall.

Additional evidence supporting scenario 1 comes from the length of individuals in the third cohort. In this study, cohort 3 has a modal length of 140-150mm during each year in December. Based on length data in the Middle Atlantic Bight, the summer-cohort had a modal length of around 130mm in October of 1995 through 1998 (Able et al. 2003). If growth during the fall is reduced (i.e. only 10 to 20 mm growth from October to December), cohort 3 is likely the summer-spawned cohort. Evidence for limited growth can be observed using length distributions for this study. The increase of the estimated cut-off point between cohorts 2 and 3 from the 10/18-11/13/01 and 11/18-12/6/01 time intervals and from the November to December 2002 time intervals suggests about a 5 – 10mm increase in length per month during the fall. However, confidence in estimating the cut-off points was not high for either year.

Scenario-2. The second possible scenario is that cohort 3 is the late-summer-spawned cohort that has been identified during the fall off New Jersey (Able et al. 2003; Wilber et al. 2003) and the other two cohorts represent spring- and summer-spawned bluefish. For this scenario to be valid, considerable growth would have to occur from October through December. Based on modal lengths of all three cohorts during October off

29

New Jersey (Able et al. 2003) and modal lengths of bluefish in December for this study, this hypothesis would require growth rates of around 1.42, 1.25, and 0.92mm per day for the late-summer, summer, and spring cohort, respectively. These are realistic growth rates based on the available literature (McBride and Conover 1991; Juanes and Conover 1994). However, information on the growth rates of bluefish during the fall is limited. Based on five individual tag-recaptures of juvenile bluefish off New Jersey during late-September and early-October (Able et al. 2003) growth decreased to below 1mm per day during the late summer and early fall. However, the lengths of these individuals were not provided. Furthermore, bluefish off New Jersey during late-September and early-October may be in cooler water than what bluefish would experience later in the fall south of Cape Hatteras, NC. Further evidence supporting scenario 2 is provided by preliminary work calculating daily ages of cohort 3, using otoliths, that suggests a late-summer spawning date (P. Rudershausen et al. unpublished data). However, daily otolith rings might not be forming if growth is limited in the autumn; this would result in underestimating age and biasing spawning date estimates to a later date.

Further evidence supporting scenario 2 can be found when comparing the length range of Lassiter's back-calculated age-1 size distribution (Figure 1a) with length ranges from YOY bluefish. Able et al. (2003) captured three juvenile cohorts in late October off of New Jersey that likely corresponded to the spring, summer, and late-summer cohorts of bluefish, and the total range of lengths was around 195mm. The length range of Lassiter's back-calculated age-1 size distribution was around 270mm. It is likely that Lassiter's back-

30

calculated distribution encompassed all three cohorts recently identified in the Middle Atlantic Bight.

There are problems with using published length data from previous year classes to identify the cohorts observed in this study. Interannual variation in spawning date and growth may affect the lengths of juvenile bluefish during the fall. Mean length of each juvenile cohort during the fall is variable from year to year (McBride et al. 1995). Munch (1997) found length for a given date to be variable between years, particularly with the summer cohort. He also found temperature during July-September to be positively correlated with mean length of the spring cohort. For the present study, the estimated cut-off point between cohorts 2 and 3 during November was 25mm higher in 2002 than 2001.

1.4c Seasonal Energy Storage Dynamics, Winter Feeding Dynamics, and Negative Size-Selective Overwinter Mortality

Larger juvenile bluefish possess an advantage in energy storage going into the winter. This is evident based on the large discrepancy between the three cohorts in muscle energy density during the fall of each year and the high allometric slope of body weight, liver lipid, and liver protein. This increase in relative energy stores with length is a common trend observed in fishes during the fall (Schultz and Conover 1997; Post and Parkinson 2001; Hurst and Conover 2003). The observed size-based pattern in energy storage is likely due to different allocation strategies for energy consumed, with smaller individuals putting more energy into growth and larger individuals storing energy during the fall. The reason for different allocation strategies is likely due to the relative risks of predation mortality and

31

starvation mortality during the winter (Post and Parkinson 2001). Piscivory is known to be

negatively size-selective (see Sogard 1997); if predation risk declines with increasing length

for overwintering juvenile bluefish, smaller individuals may gain a greater survival

advantage in gaining size and becoming less vulnerable to predation. Larger individuals

invoke an energy storage strategy for winter survival and apportion a greater amount of

ingested energy to storage rather than growth.

While larger individuals have relatively greater energy stores in the autumn, this

energetic advantage declines during the winter; the rate of energy depletion increases with

bluefish length. This is supported by the convergence of the mean muscle energy density of

the three cohorts during the winter. Cohort 1 experienced the greatest reduction in muscle

energy density, while the third cohort changed the least. Additionally, the allometries of

body weight, and liver lipid and protein weight declined over the winter. Following peak

levels in the fall, liver lipid and protein allometries were typically below three during the

following months, meaning the relative amount of liver energy actually decreased with

increasing length. Evidence for overwinter energy expenditure increasing with fish length

has also been shown for Pacific herring in Prince William Sound, Alaska (Paul et al. 1998).

If smaller individuals are depleting energy stores more slowly during the winter

despite having a higher mass-specific metabolic rate (Post and Lee 1996; Schultz and

Conover 1999), they are likely reducing energy depletion by feeding during the winter.

Cohort-3 had the highest gut fullness levels during the winter and spring of 2001-02 and

during December of 2002 (Figure 12a-b), however differences were not that great. The

reason for the lack of a clear difference may be due to the smaller members of cohort 3

having low gut fullness levels, causing the mean to decrease (Figure 13). During February of 2002 gut fullness was highest in fish that were around 155mm, which corresponds to the right-hand tail of cohort 3's length distribution. A similar peak in gut fullness for the 2002 year-class corresponds to the right-hand tail of the third cohort's distribution during November, December, and April. One would expect gut fullness to increase with decreasing length due to the increased metabolic needs of smaller individuals and their relatively low energy stores during the fall. Under controlled conditions, gut fullness is inversely related to fish size (Elliott 1975). Since smaller bluefish are relatively tolerant of cold temperatures (J. Slater et al. unpublished data), the reason for the lack of feeding in these smaller bluefish may be attributed to the lack of appropriately sized prey. An examination of predator-prey dynamics of overwintering bluefish has yet to be conducted. If smaller bluefish are unable to feed adequately they may experience a higher mortality rate during the winter.

The low gut fullness levels observed in smaller individuals of cohort 3 during the winter of 2002-03 likely contributed to the negative size-selective mortality observed in that year. A lack of feeding by these small individuals may have precluded their ability to maintain energy storage levels throughout the winter. A similar situation has been observed with YOY largemouth bass in a Tennessee reservoir; individuals that were unable to attain a certain size by the end of their first growing season experienced a higher overwinter mortality rate due to a lack of appropriately sized prey during the spring (Adams et al. 1982). Further evidence for prey size-structure affecting overwinter mortality has been observed with age-0 pikeperch in the Netherlands; smaller individuals that were unable to prey on

smelt during the late summer and fall lost condition, whereas larger individuals that were able to prey on smelt had an increase in condition (Buijse and Houthuijzen 1992).

It is unlikely that the increase in mean length and decrease in variation of cohort 3 from late-fall 2001 to early spring 2002 was due to growth. This is supported by the lack of an increase in the right end of the length distribution. Further, the lower end of the distribution increased by around 25mm; it is unlikely these smaller individuals grew during such a severe winter. Other studies that have examined negative size-selective mortality were conducted in more closed systems that limited the possibility of migration biasing results. It is possible that the negative size-selective mortality observed with the 2002 year-class was due to size based migration northward from overwintering areas to the south of Onslow Bay. Assuming smaller YOY bluefish stay nearshore, sampling would need to extend to the southern limit of cohort 3's overwintering range in order to more confidently examine size-selective mortality.

No evidence of size-selective mortality was found with the 2001 year-class. This may be due to the time intervals used in the analyses. Only one month separated the length distributions used, whereas four months separated time-intervals used for the negative size-selective analyses for the 2002 year-class. Additionally, sample size of the 2001 year-class was relatively low during January, which may have precluded the accurate determination of mean and variance of length for cohort 3. Last, energy depletion mortality may not exert an effect until later in the season; this would limit the likelihood of detecting size-selective mortality using January and February samples. Evidence of negative-size selective mortality in the 2001 year-class may be present when comparing February and April time-intervals.

The lower length limit of cohort 3's distribution in early April was 131-135mm, which was 10mm higher than in February. April was not used in the analyses due to an abnormally shaped distribution and uncertainty in placing the upper length limit of cohort 3.

In addition to bluefish length, residual body weight was also shown to affect gut fullness. Laboratory studies have shown that individuals with relatively low energy stores due to starvation exhibit a compensatory feeding response when food becomes available and regain lost energy stores to reach levels of control fish that were never starved (Metcalfe and Thorpe 1992; Bull et al. 1996). Additionally, Hurst and Conover (2001) found higher gut fullness levels in fish with lower lipid densities. One may expect bluefish that are below expected values of body weight for a given length to feed at a higher rate to either reach a target weight level or lose weight at a slower rate than fish in relatively good condition. However, data from this study do not suggest this is occurring. Bluefish with relatively higher body weight had higher gut fullness values for both year-classes. This would suggest bluefish in better condition were feeding more and thus depleting weight more slowly. Bluefish with relatively low body weight may be less successful at feeding during the winter and subject to higher mortality rates.

The differences in temperature between the two winter seasons provided an opportunity to examine how winter severity may affect juvenile bluefish overwinter survival. The effects that the harsher winter of 2002-03 had on juvenile bluefish can be seen in a number of ways. There was strong evidence for negative size selective mortality of cohort 3 during the more severe winter of 2002-03. Additionally, given their extended absence in Onslow Bay during the more severe winter, juvenile bluefish may migrate greater distances

to avoid physiological limitations of cold tolerance during harsh winters. Further, there was a sharp decline in temperature from November to December 2002, which may have prevented the additional accumulation of energy reserves during the late-fall; when adjusted to a common length, the 2001 year-class had significantly higher levels of muscle energy and body weight during the fall compared to the 2002 year-class. Following the winter, the 2001 year-class had significantly higher energy levels in muscle tissue when adjusted to a common length between years. Despite lower muscle energy levels, the 2002 year-class did have a higher length-adjusted body weight during April, although the water content in their muscle tissue was higher.

The focus of this study was to determine if the lack of contribution by the summer cohort to the adult population was due to overwinter mortality. Although negative size-selective mortality in the second year was observed, the presence of both cohorts 2 and 3 in relatively large numbers during the spring of both years provides evidence that they do survive the winter. However, no single cohort was captured consistently enough through time to estimate winter mortality rates using catch curve analyses. Sampling in areas extending over a greater portion of the coastal South Atlantic Bight may be necessary to track each juvenile cohort throughout the winter and allow estimation of cohort-specific survival rates.

Juvenile bluefish caught in the field did not appear to be approaching critical starvation levels of body weight or liver and muscle energy. Length-adjusted means of body weight and energy storage for field-caught bluefish during the most energy-deficient time intervals were significantly greater than critical starvation values determined in lab

experiments. Low values for the allometric slopes in early spring for liver lipid and protein weight indicate increasing liver energy with decreasing length. Additionally, each year-class experienced a drop in liver energy from April to May despite increases in muscle energy. This would suggest excess energy was available in the liver following the winter and was allocated to other structures or purposes.

Caution should be used when comparing fish from the wild with individuals starved in the lab. In the laboratory, starvation mortalities may solely be due to the depletion of energy reserves, whereas bluefish in the wild are also vulnerable to predation. Bluefish approaching critical energy levels in the field probably have an increased susceptibility to predation and therefore they may rarely be collected.

1.4d Alternative Hypotheses and Management Implications

The examination of these data suggests that while negative size-selective overwinter mortality may occur during more extreme winters, it is not a suitable explanation for the unimodal back-calculated age-1 length distributions observed in previous studies (Chiarella and Conover 1990; Conover et al. 2003). A possible explanation for what is thought to be a lack of contribution by the summer cohort to the adult population depends on what scenario is used to describe cohort structure of overwintering bluefish; these scenarios will be addressed below.

Scenario 1. If cohort 3 is the summer cohort, the reason for the lack of summer-spawned bluefish in the adult population may be that the overwinter survival of the summer cohort is affected by certain abiotic or biotic factors that during this study and Lassiter's

work during the early 1960s, did not exert a strong influence. If scenario 1 is accurate, using the fall abundance of the spring cohort alone may not be an accurate index of year-class strength as has been suggested (Conover et al. 2003) due to evidence of winter survival by the summer cohort.

Scenario 2. If cohort 3 is a late-summer-spawned cohort, the apparent lack of summer-spawned bluefish in the adult population would be explained by a misinterpretation of back-calculated age-1 distributions. Back-calculated age-1 length distributions have been interpreted based on lengths of bluefish during the fall and have assumed no growth to occur from late fall up to the time of first annulus formation the following spring. Bluefish with back-calculated age-1 sizes greater than 200mm have been classified as spring-spawned and individuals determined to be less than 200mm are assumed members of the summer cohort (Chiarella and Conover 1990; Conover et al. 2003). Based on scenario 2, back-calculated age-1 distributions should be interpreted differently as juvenile bluefish continue to grow relatively fast as they migrate south. Further evidence suggests that the cut-off point between the summer and spring cohort is much higher than previously thought at the time of first annulus formation. The 2001 year-class had a cut off point of 240-250mm during April when their first annulus was likely formed. The cut-off point for the 2002 year-class is less clear as the latest date where the two cohorts were clearly identifiable was in November when the cut-off point was around 255mm.

The late-summer cohort may be an important contributor to bluefish recruitment. The cut-off point between the late-summer and summer cohorts appears to be around 180-200mm during the early spring. Therefore, the late-summer cohort is likely corresponding to the

smaller mode found in Lassiter's (1962) back-calculated age-1 distribution. If scenario 2 is accurate, the summer cohort has consistently been contributing to the adult population, as they reach lengths greater than 200mm at age-1. However, a bimodal length distribution of summer- and spring-spawned bluefish is not clear in any of the back-calculated age-1 distributions (Figure 1b and c). The bimodality may be obscured as the fall and winter season progresses and bluefish from nursery areas across the entire east coast mix during the winter. A clear bimodal pattern for cohorts 1 and 2 was not evident in collections beyond November, but too few members of cohort 1 were captured during the winter and spring to confidently determine if bimodality was present.

If one accepts scenario 2, the cohort that shows inconsistent contribution to the adult population is the late-summer cohort. This may be explained by inter-annual variation in the production of this cohort or differential age-1 migration between the cohorts. Members of the late-summer cohort may not migrate north during their second year, instead remaining in the South Atlantic Bight as age-1+ fish. If this were the case, they may be locally abundant off North Carolina where Lassiter collected his bluefish to determine length at age-1. The late-summer cohort dominated spring catches in the trawl and was present in the area until at least June. A majority of bluefish with back-calculated age-1 sizes less than 200mm in Lassiter's study were age-1 (n = 92), however 62 individuals were age-2 and older. The other two projects that examined the relative contribution of each cohort to the adult population used bluefish collected in the Middle Atlantic Bight. If spring- and summer-spawned bluefish numerically dominate, the likelihood of capturing a late-summer-spawned adult in the Middle Atlantic Bight may be low. If scenario 2 is accurate both summer- and

late-summer-spawned bluefish should be considered in assessing year-class strength as they both showed evidence of winter survival.

1.4e Summary and Future Direction

Near-shore waters in Onslow Bay, NC are important for juvenile bluefish during the winter. However, when bluefish southern migration has reached its full extent, the northern limit of their winter range may be south of Cape Fear, NC. Bluefish are strongly associated with prey during the winter and were observed to feed even during the coldest months. Indeed, winter feeding may be essential for smaller individuals to survive as they enter the winter with relatively less energy stores than larger individuals. During the winter, the rate of energy storage depletion increases with increasing bluefish length.

Three cohorts of juvenile bluefish were observed in Onslow Bay, NC; however, it was uncertain which cohorts corresponded to the spring- and summer-spawned bluefish that are observed in the Middle Atlantic Bight. Evidence of negative size-selective mortality was found in the cohort of the smallest length during the more severe winter. However, all three cohorts survived the winter. The hypothesis that summer-spawned bluefish have not contributed to the adult population in recent years due to high overwinter mortality was not supported.

Cohort structure on the U.S. east coast is more complex than previously supposed. In order to assess the relative contribution of the different cohorts to the adult population, cohort structure of YOY bluefish needs to be understood so back-calculated age-1 length distributions can be confidently interpreted. A coordinated research project examining

juvenile bluefish recruitment, distribution and abundance synoptically over the entire U.S. east coast would be an effective way to understand bluefish population dynamics. If all three cohorts can be successfully captured throughout the winter, the understanding of how important the winter period is for bluefish survival will be greatly enhanced. Additionally, the timing of annulus formation in scales and otoliths needs to be more thoroughly examined. Barger (1990) showed annuli to form annually around April, however it appears he only used spring-spawned bluefish. If there is a relationship between length and timing of annulus formation, back-calculated length distributions may be misinterpreted. Further, adult bluefish need to be sampled in years following successful overwinter survival of the summer cohort in both the Middle and South Atlantic Bights to help elucidate potential cohort-based differences in age-1+ distribution and migration. Last, the predator prey dynamics of overwintering bluefish needs to be examined to help determine how the availability of appropriately sized prey mediates size-selective mortality.

Table 1. Number of young-of-the-year bluefish caught from North Carolina waters during each time-interval by gear type and location along with number of bluefish processed for energy storage analyses for each time-interval by tissue type and cohort.

Year-class	Time-Interval	Gear	Location	n	Cohort-1 Liver	Cohort-1 Muscle	Cohort-2 Liver	Cohort-2 Muscle	Cohort-3 Liver	Cohort-3 Muscle
2001	9/27-10/6/01	Hook &Line	Bogue Sound	35						
			Masonboro Sound	21						
		Beach Seine	Atlantic Beach	2						
		Gill Net	Beaufort Inlet	1						
			Total	59	16	24	0	0	0	0
	10/18-11/13/01	Trawl		64						
		Hook & Line	Masonboro Sound	34						
			Masonboro Inlet	3						
			Bogue Sound	19						
			Beaufort Inlet	37						
		Beach Seine	Atlantic Beach	1						
		Gill Net	Neuse River	9						
			Total	167	29	34	40	41	1	1
	11/18-12/6/01	Trawl		132						
		Hook & Line	Bogue Sound	41						
			Back Sound	10						
			Masonboro Inlet	7						
			Total	190	19	21	26	24	27	31
	12/13-12/21/01	Hook & Line	Beaufort Inlet	20						
			Bogue Sound	14						
			Total	34	23	24	10	10	0	0
	1/5-1/15/02	Trawl		40	2	2	1	1	25	20
	2/3-2/13/02	Trawl		529	5	4	26	20	25	19
	4/2-4/8/02	Trawl		63	0	1	14	14	27	26
	4/30-5/17/02	Trawl		46						
		Hook & Line	Onslow Bay	18						
			Total	64	0	0	9	9	38	36
	6/9-6/20/02	Hook & Line	Bogue Sound	15						
			Albemarle Sound	1						
		Beach Seine	Atlantic Beach	1						
		Gill Net	Newport River	5						
			Total	22	1	1	4	4	17	17

Table 1 (continued). Number of young-of-the-year bluefish caught from North Carolina waters during each time-interval by gear type and location along with number of bluefish processed for energy storage analyses for each time-interval by tissue type and cohort.

Year-class	Time Interval	Gear	Location	n	Energy Storage					
					Cohort-1		Cohort-2		Cohort-3	
					Liver	Muscle	Liver	Muscle	Liver	Muscle
2002	9/29-10/22/02	Trawl		4						
		Hook & Line	Beaufort Inlet	29						
		Gill Net	Neuse River	11						
		Total		44	21	21	4	4	0	0
	11/3-11/25/02	Trawl		329						
		Hook & Line	Beaufort Inlet	25						
			Bogue Sound	9						
			Cape Lookout	2						
		Beach Seine	White Oak River	1						
		Gill Net	Newport River	5						
		Stop Net	Beaufort Inlet	10						
		Total		381	17	17	15	15	22	22
	12/12-12/17/02	Trawl		394	0	0	19	19	29	29
	1/5-1/22/03	Trawl		9	1	1	7	7	1	1
	3/22-4/14/03	Trawl		100						
		Hook & Line	Beaufort Inlet	7						
			Bogue Sound	57						
			Onslow Bay	5						
		Total		169	12	12	24	24	35	35
	4/24-5/21/03	Trawl		5						
		Hook & Line	Bogue Sound	16						
			Onslow Bay	1						
		Total		22	0	0	17	17	5	5
	5/29-6/22/03	Trawl		15						
		Hook & Line	Beaufort Inlet	26						
		Total		41	7	7	6	7	27	27

Table 2. Full and reduced analyses of variance models for distribution and abundance analyses with ln(CPUE) of juvenile bluefish as the dependent variable and (a) year, month, transect, distance from shore, and prey abundance as independent variables, and (b) year, month, transect, and distance from shore as independent variables.

(a) Effect	df	Sum of Squares	F	P
Full Model				
Year	1	0.07	0.107	0.744
Month	9	11.29	1.915	0.053
Transect	3	0.28	0.142	0.934
Distance from shore	5	2.12	0.647	0.664
Prey abundance	4	13.72	5.237	0.001
Reduced Model				
Year	0	----	----	----
Month	4	6.48	3.297	0.013
Prey abundance	1	2.82	5.73	0.018
Year × month	7	9.13	2.654	0.013
Year × prey abundance	4	4.51	2.295	0.062
Month × prey abundance	30	24.13	1.637	0.030

(b) Effect	df	Sum of Squares	F	P
Full Model				
Year	1	0.68	0.947	0.332
Month	9	14.91	2.306	0.018
Transect	3	0.18	0.082	0.97
Distance from shore	5	23.44	6.525	<0.001
Reduced Model				
Year	0	----	----	----
Month	3	8.48	4.472	0.005
Distance from shore	4	10.66	4.217	0.003
Year × month	7	10.46	2.364	0.026
Year × distance from shore	4	0.65	0.255	0.906
Month × distance from shore	39	28.29	1.148	0.279

Table 3. Analyses of covariance models for the seasonal energy storage of the 2001 and 2002 year-classes of bluefish with ln(fork length) as covariate.

Dependent variable	Effect	df	Sum of Squares	F	P
2001 year-class					
ln(liver energy)	Month	5	9.47	6.40	< 0.001
ln(muscle energy)	Month	5	0.093	3.758	0.003
ln(body weight)	Month	5	0.15	5.0	<0.001
ln(percent dry weight muscle)	Month	5	0.038	2.868	0.015
2002 year-class					
ln(liver energy)	Month	4	1.72	2.90	0.023
ln(muscle energy)	Month	4	0.046	3.80	0.005
ln(body weight)	Month	4	0.10	3.0	0.011
ln(percent dry weight muscle)	Month	4	0.131	11.95	<0.001

Table 4. Allometries of juvenile bluefish body weight, liver lipid weight, and liver protein weight during each time-interval for the 2001 and 2002 year-classes. Two-tailed t-tests are tested against H_o: for isometric growth (slope = 3), with Bonferroni adjusted significance values of 0.0083 and 0.01 for the 2001 and 2002 year-class respectively.

| Time-interval | Body weight | | | | | Liver lipid weight | | | | | Liver protein weight | | | | |
	Slope	SE	*df*	T	*P*	Slope	SE	df	T	*P*	Slope	SE	df	T	*P*
2001 year-class															
10/18-11/13/01	3.18	0.107	107	1.682	0.095	3.111	1.863	38	0.06	0.953	1.987	1.308	39	-0.77	0.443
11/18-12/6/01	3.398	0.06	114	6.633	<0.001*	4.415	0.91	51	1.555	0.126	4.159	0.608	52	1.906	0.062
2/3-2/13/02	3.201	0.043	98	4.674	<0.001*	2.72	0.36	50	-0.78	0.44	2.763	0.198	50	-1.33	0.19
4/2-4/8/02	3.056	0.057	56	0.983	0.33	1.821	0.52	39	-2.27	0.029	2.003	0.429	39	-2.32	0.025
4/30-5/7/02	3.065	0.078	48	0.833	0.409	2.398	0.87	45	-0.69	0.493	2.599	0.325	45	-1.23	0.224
6/9-6/20/02	2.874	0.106	19	-1.19	0.249	2.155	1.253	19	-0.67	0.508	2.215	0.473	19	-1.66	0.113
2002 year-class															
11/3-11/25/02	3.309	0.035	151	8.829	<0.001*	4.697	0.515	35	3.295	0.0023*	3.999	0.269	35	3.714	0.0007*
12/12-12/17/02	3.246	0.032	390	7.688	<0.001*	2.8	0.472	46	-0.42	0.674	3.308	0.246	46	1.252	0.22
3/22-4/14/03	3.133	0.026	126	5.115	<0.001*	1.96	0.35	57	-2.97	0.0043*	3.075	0.173	57	0.434	0.666
4/24-5/21/03	3.091	0.179	20	0.508	0.617	3.89	0.709	20	1.255	0.224	3.606	0.32	20	1.894	0.073
5/29-6/22/03	3.269	0.067	26	4.015	<0.001*	2.562	0.366	31	-1.2	0.241	3.239	0.259	31	0.923	0.363

Table 5. Analyses of covariance models for the comparison of field caught juvenile bluefish from the 2001 and 2002 year-classes with bluefish starved in the laboratory (Slater et al. unpublished), with ln(fork length) as covariate.

Dependent variable	df	Sum of Squares	F	P
ln(body weight)	2	5.09	541.0	< 0.01
ln(liver energy)	2	1.80	8.43	< 0.001
ln(muscle energy)	2	10.47	102.3	<0.001

Table 6. Descriptive statistics of cohort-3 length during time-intervals used for negative size-selective overwinter mortality analyses.

Year-class	Time Interval	n	Mean Length	Minimum Length	Maximum Length	Coefficient of Variation
2001	1/5 – 1/15/02	37	145.57	125	175	6.86
	2/3 – 2/13/02	396	146.35	122	175	6.51
2002	12/12 – 12/17/02	367	146.56	106	180	8.71
	3/22 – 4/14/03	90	157.46	131	180	5.33
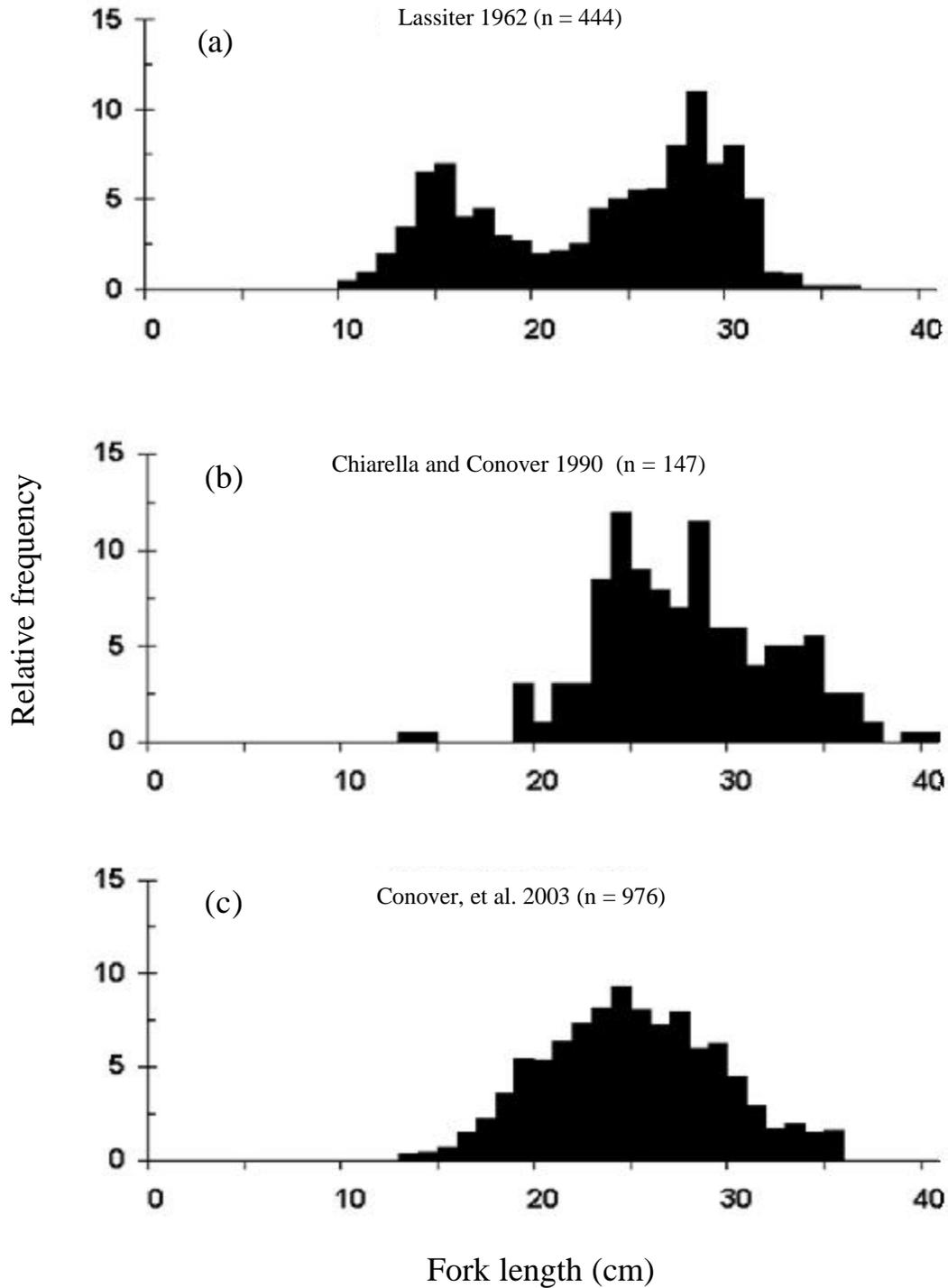
Figure 1. Length frequency distributions of back-calculated size at age-1 for adult bluefish from three different studies. a) Lassiter (1962), representing 1956-1960 year-classes, b) Chiarella and Conover (1990), representing 1975-86 year classes, c) Conover et al. (2003), representing 1991-98 year classes.
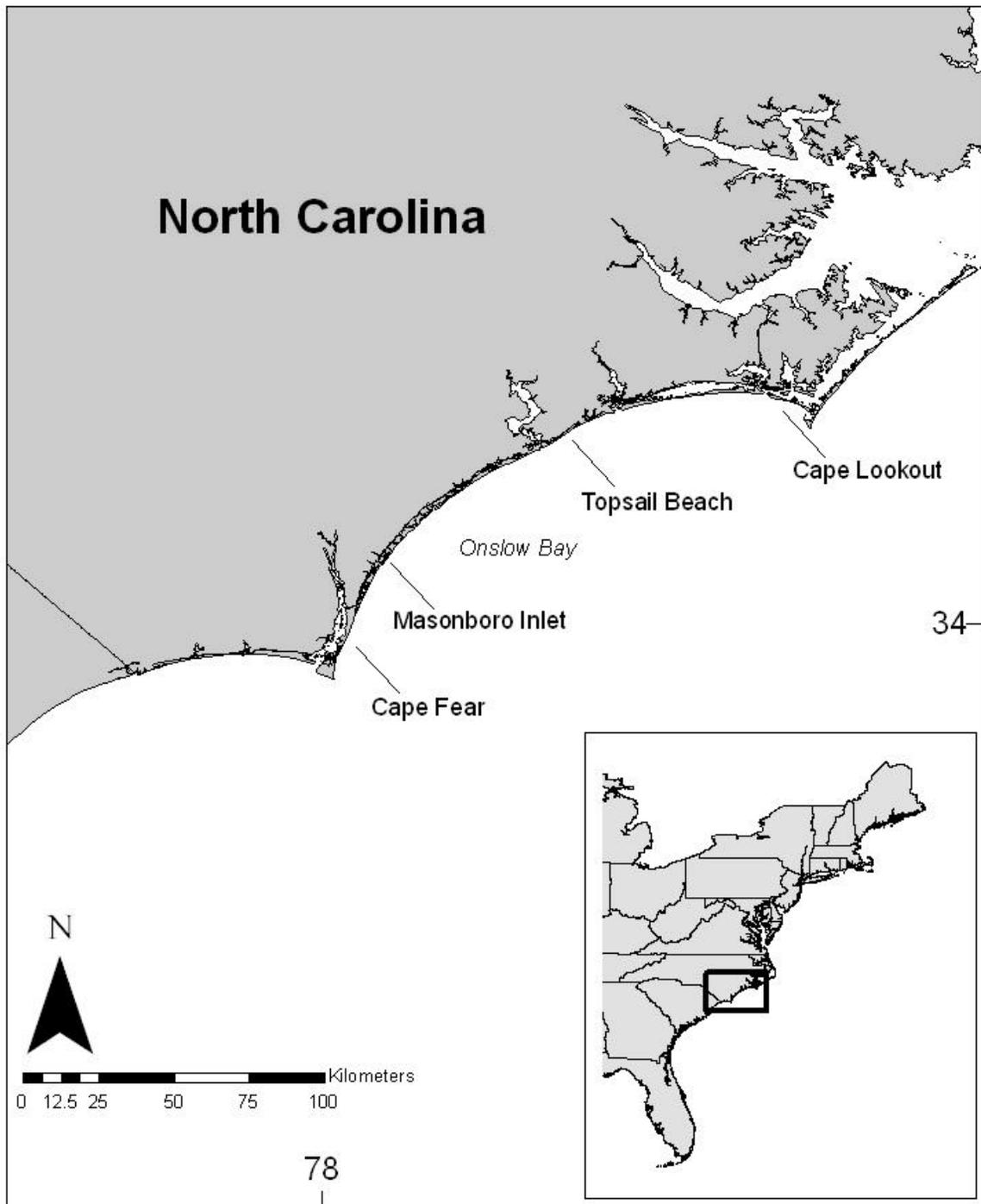
Figure 2. Sampling area in Onslow Bay, North Carolina showing the location of the Cape Fear, Masonboro Inlet, Topsail Beach, and Cape Lookout transects. Transect lines are not to scale, sampling took place up to 16.1 kilometers from shore.
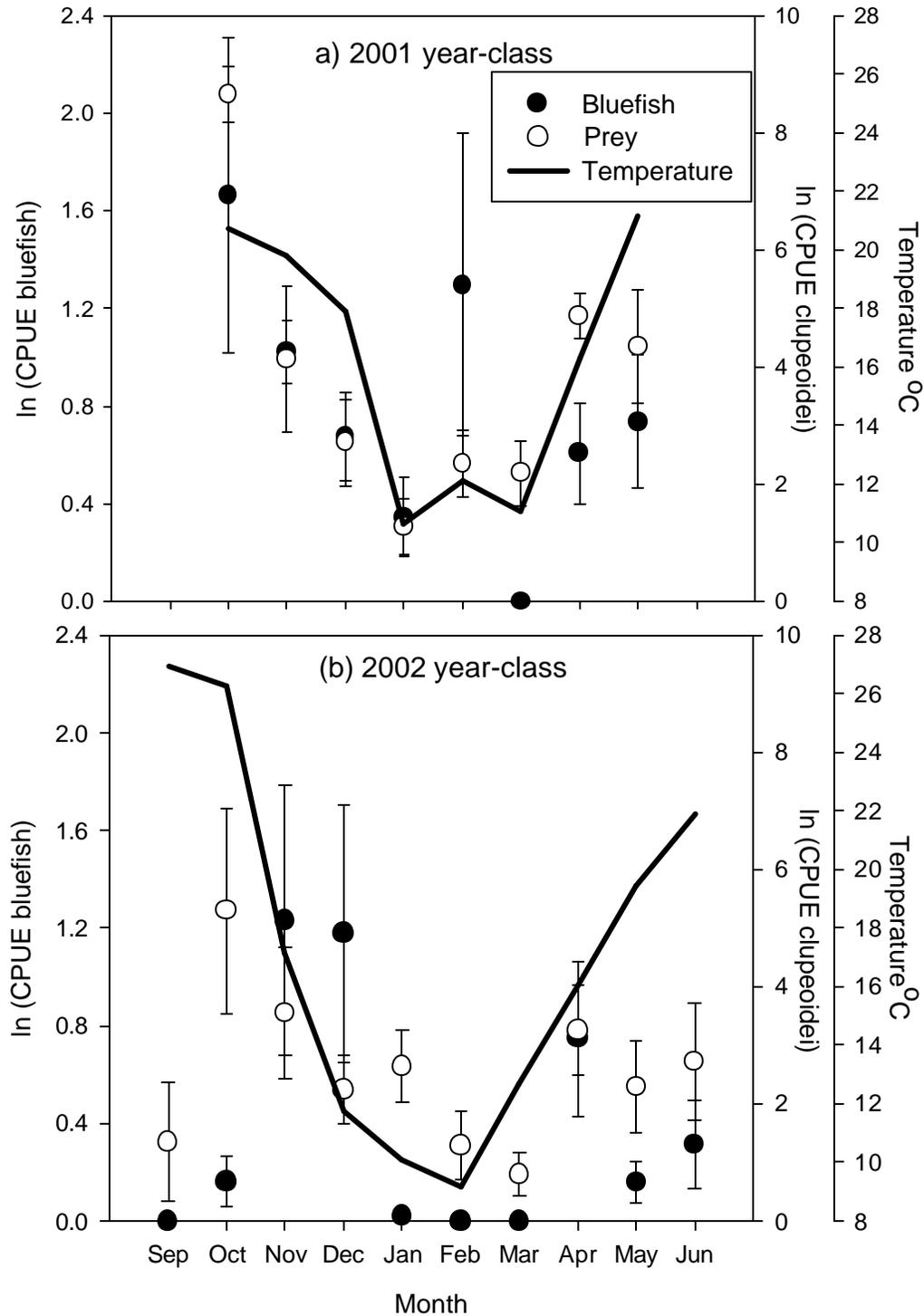
Figure 3. Monthly mean ln(CPUE) ($\pm$ SE) for young-of-the-year bluefish and prey captured by bottom trawl and mean temperature in Onslow Bay, NC for a) the 2001 year-class, and b) the 2002 year-class. Note the separate y-axes for each variable.
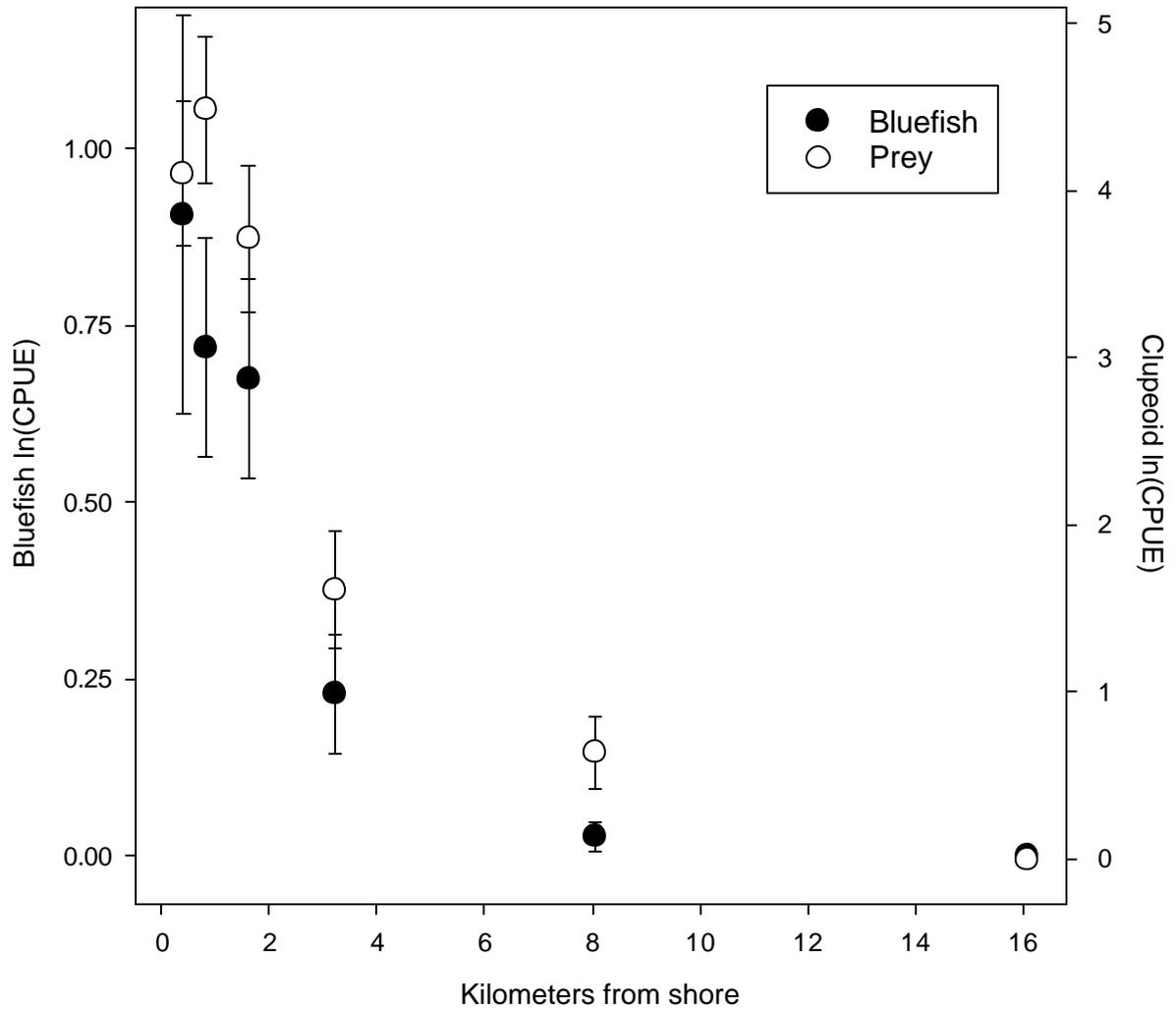
Figure 4. Mean ln(CPUE) ($\pm$ SE) vs. distance from shore for young-of-the-year bluefish and prey captured monthly by bottom trawl in Onslow Bay, NC from October 2001 – May 2002 and from September 2002 – June 2003. Note separate y-axes for each variable.
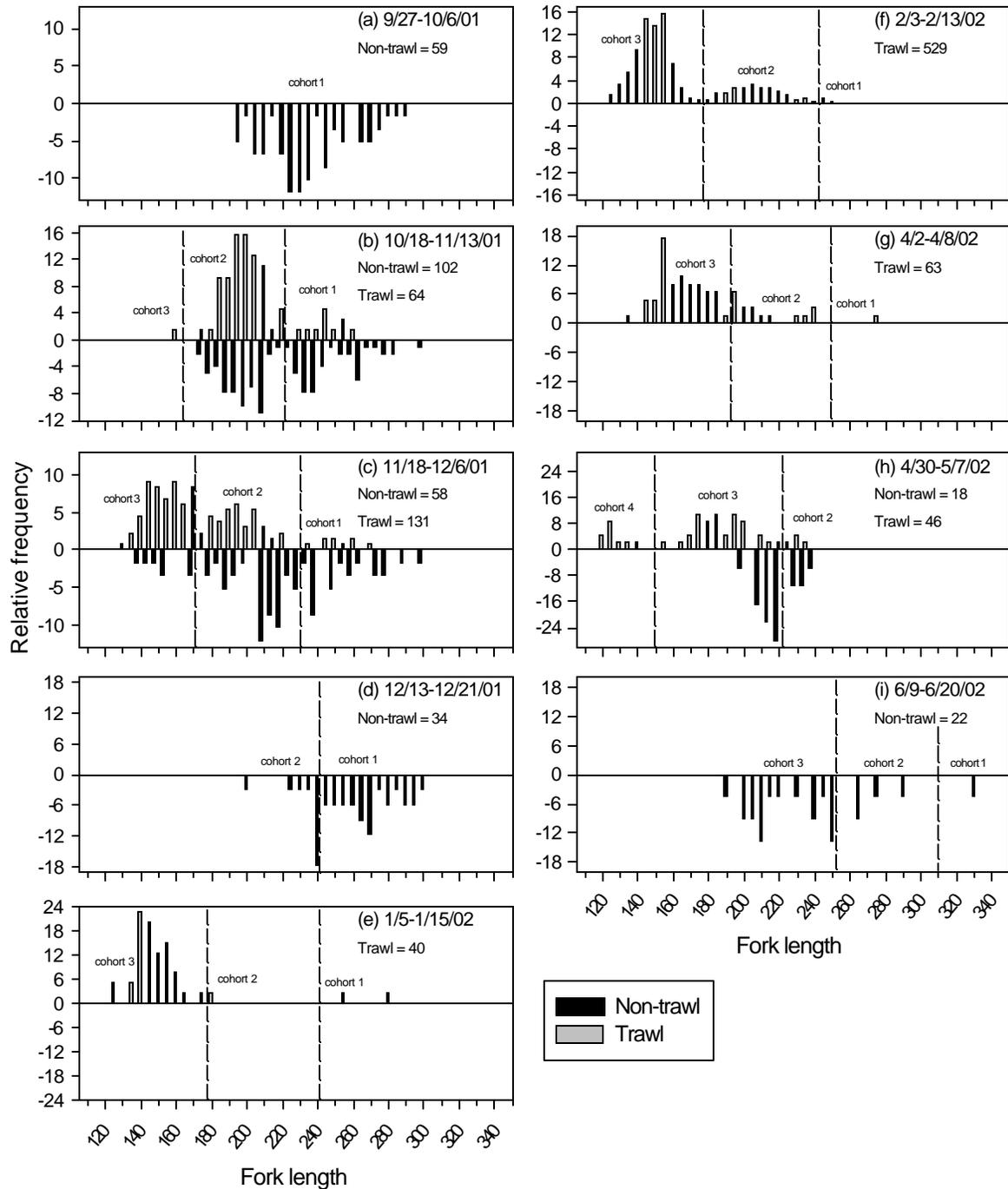
Figure 5. Length frequency distributions of young-of-the-year bluefish from the 2001 year-class captured in Onslow Bay, North Carolina and adjacent estuaries during each sampling period using both trawl and non-trawl gear. Dashed lines indicate cut-off points between cohorts 1,2, and 3.

53
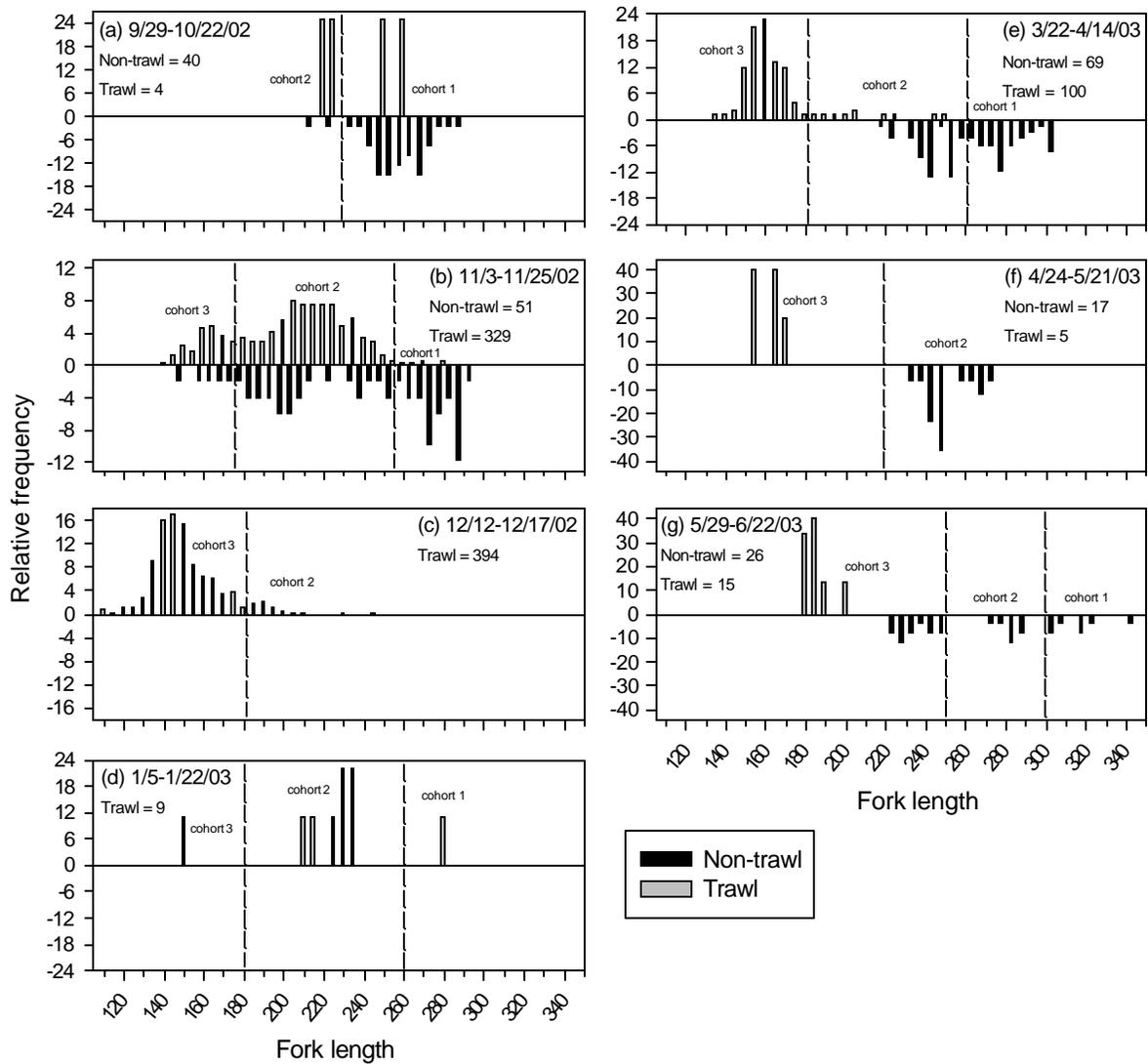
Figure 6. Length frequency distributions of young-of-the-year bluefish from the 2002 year-class captured in Onslow Bay, North Carolina and adjacent estuaries during each sampling period using both trawl and non-trawl gear. Dashed lines indicate cut-off points between cohorts 1,2, and 3.
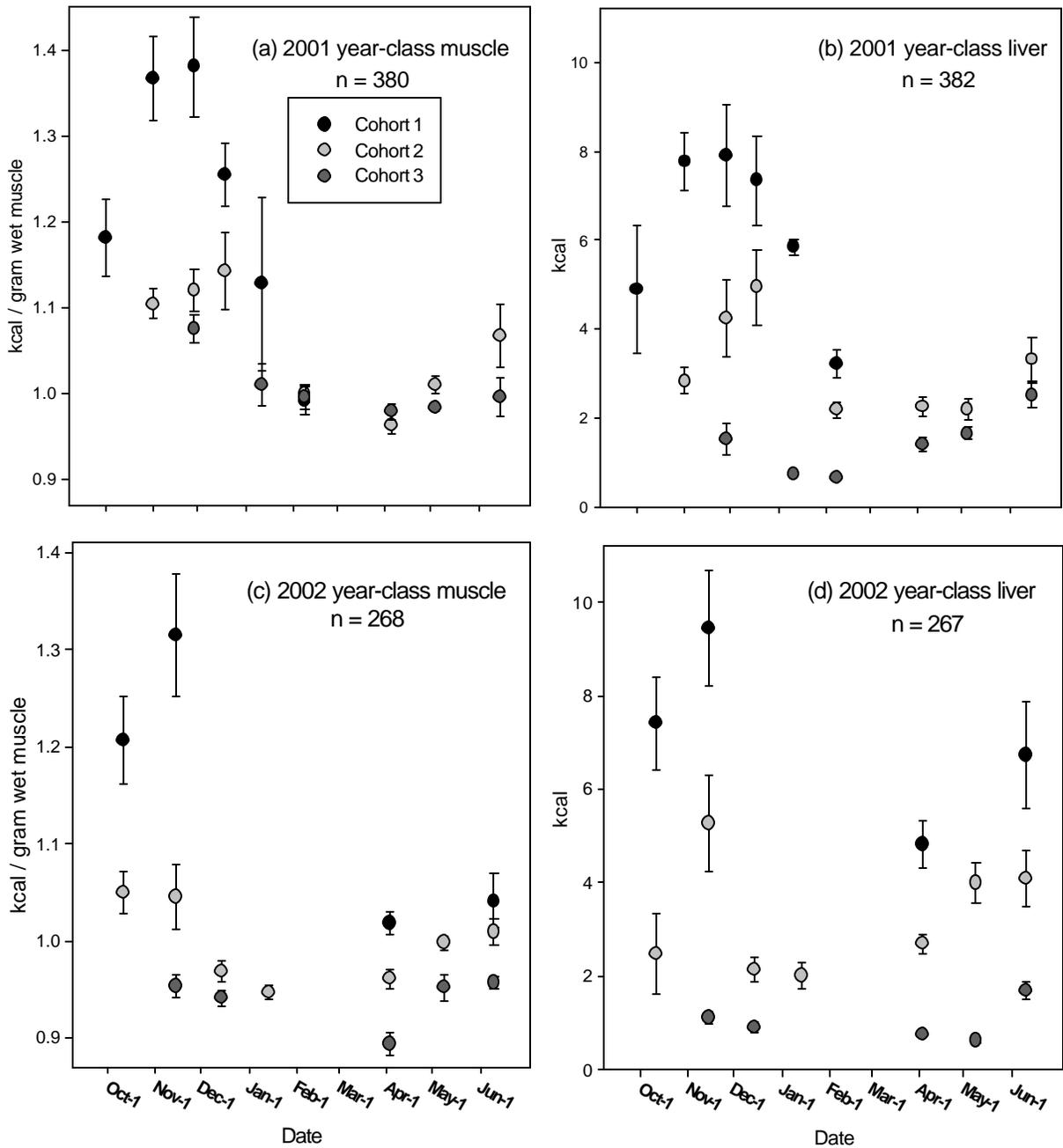
Figure 7. Mean (±SE) muscle and liver energy for young-of-the-year bluefish captured in Onslow Bay, North Carolina. Values for bluefish cohorts 1,2, and 3 are shown for each time interval. a) muscle energy per gram wet weight for the 2001 year-class, b) total liver energy for the 2001 year-class, c) muscle energy per gram wet weight for the 2002 year-class, d) total liver energy for the 2002 year-class.
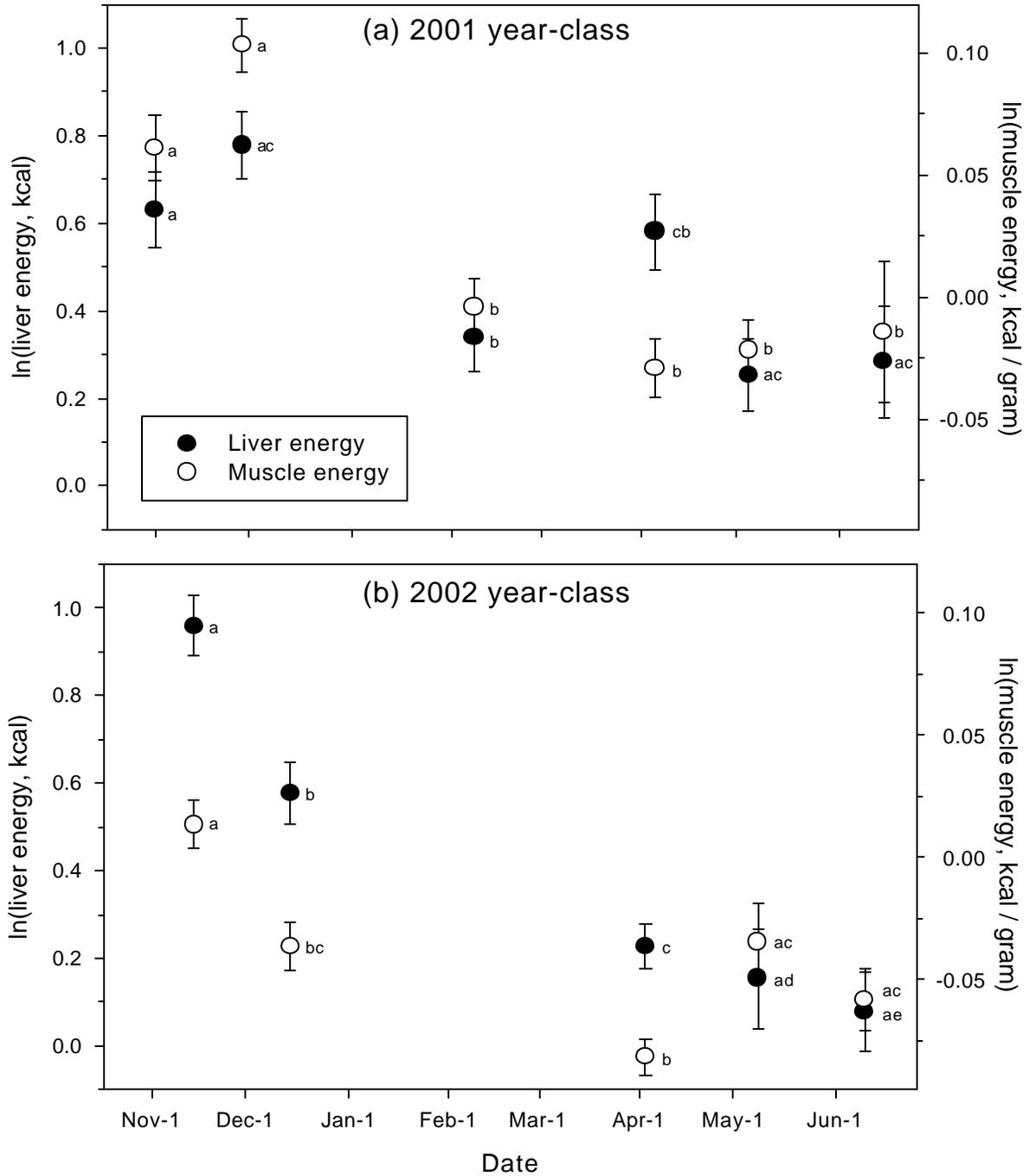
Figure 8. Mean (±SE) liver and muscle energy, adjusted to a common length within each season, for young-of-the-year bluefish from cohorts 1 and 2 captured in Onslow Bay, North Carolina for a) the 2001 year-class, and b) the 2002 year-class. ln(liver energy (kcal)) is in black and corresponds to the left y-axis, ln(muscle energy (kcal / gram wet weight)) is in white and corresponds to the right y-axis. Like letters within each year-class and tissue indicate no significant difference between time-intervals as determined with ANCOVA.
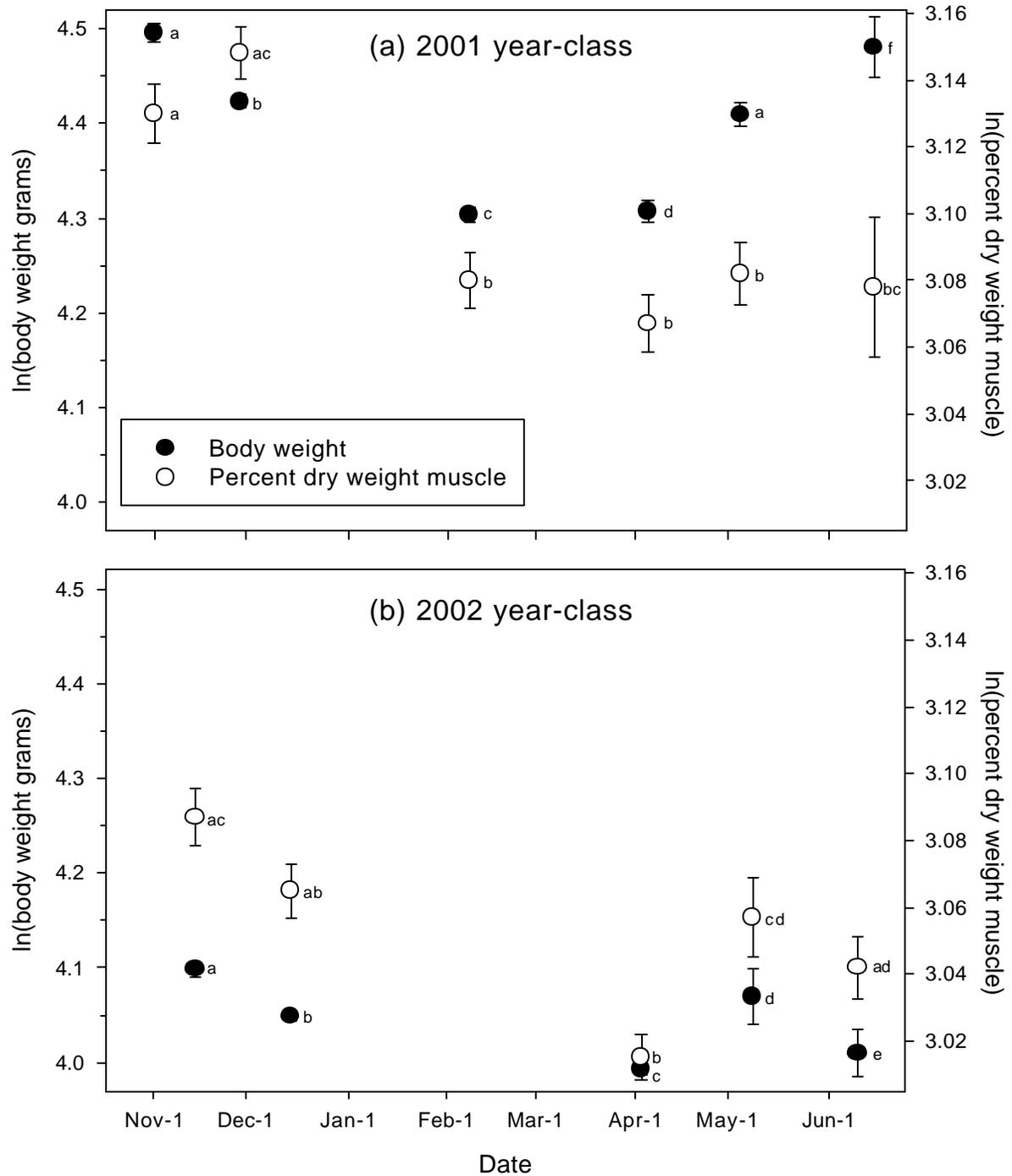
Figure 9. Mean (±SE) body weight and percent dry weight muscle, adjusted to a common length within each season, for young-of-the-year bluefish from cohorts 1 and 2 captured in Onslow Bay, North Carolina for a) the 2001 year-class, and b) the 2002 year-class. ln(body weight (grams)) is in black and corresponds to the left y-axis, ln(percent dry weight muscle) is in white and corresponds to the right y-axis. Like letters within each year-class and tissue indicate no significant difference between time-intervals as determined with ANCOVA.
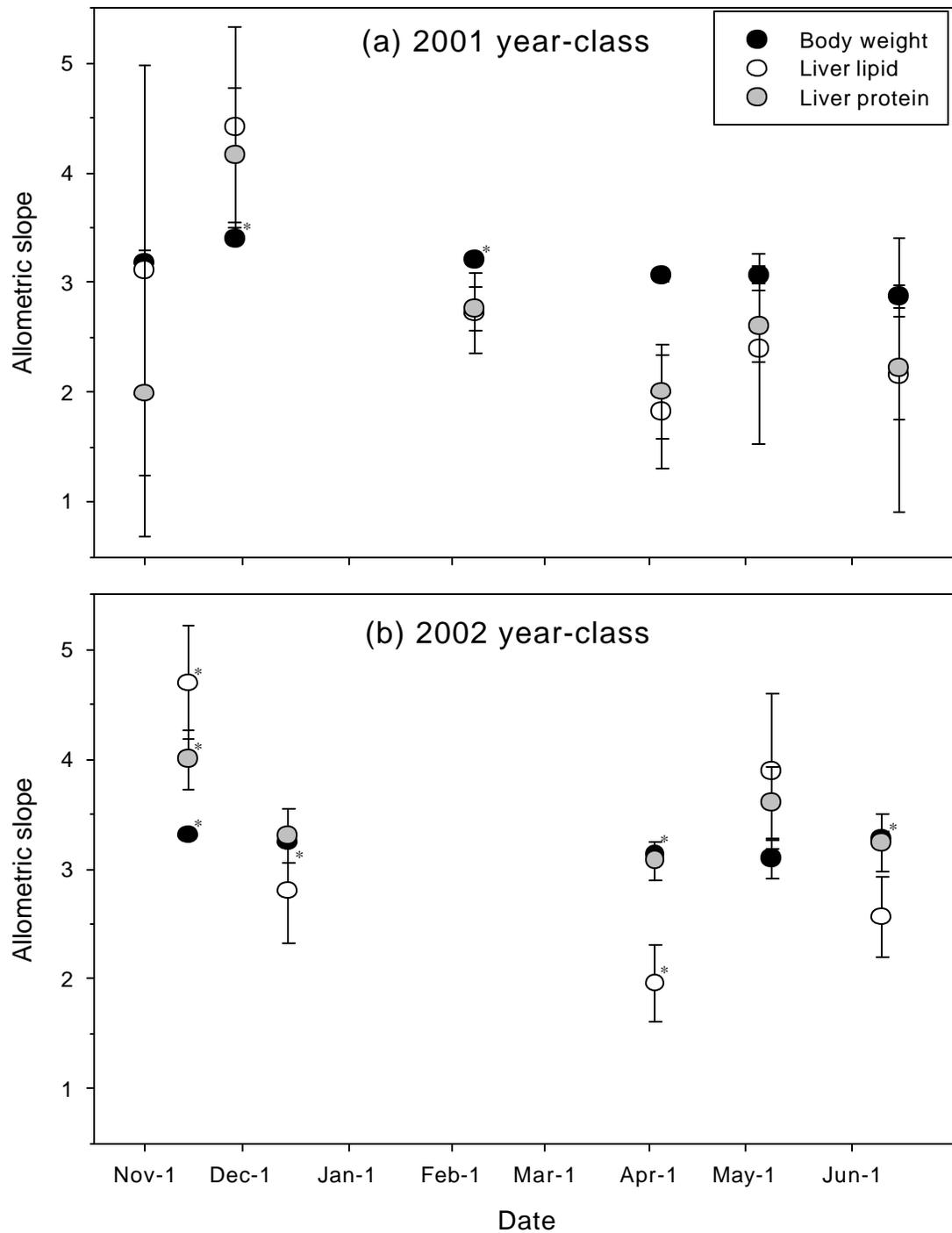
Figure 10. Allometric slopes (±SE) for young-of-the-year bluefish from cohorts 1 and 2 captured in Onslow Bay, North Carolina for body weight (black), liver lipid weight (white), and liver lean weight (gray) during each time-interval for a) the 2001 year-class, and b) the 2002 year-class. Time intervals with a slope significantly different from 3 are marked with an asterisk (*).
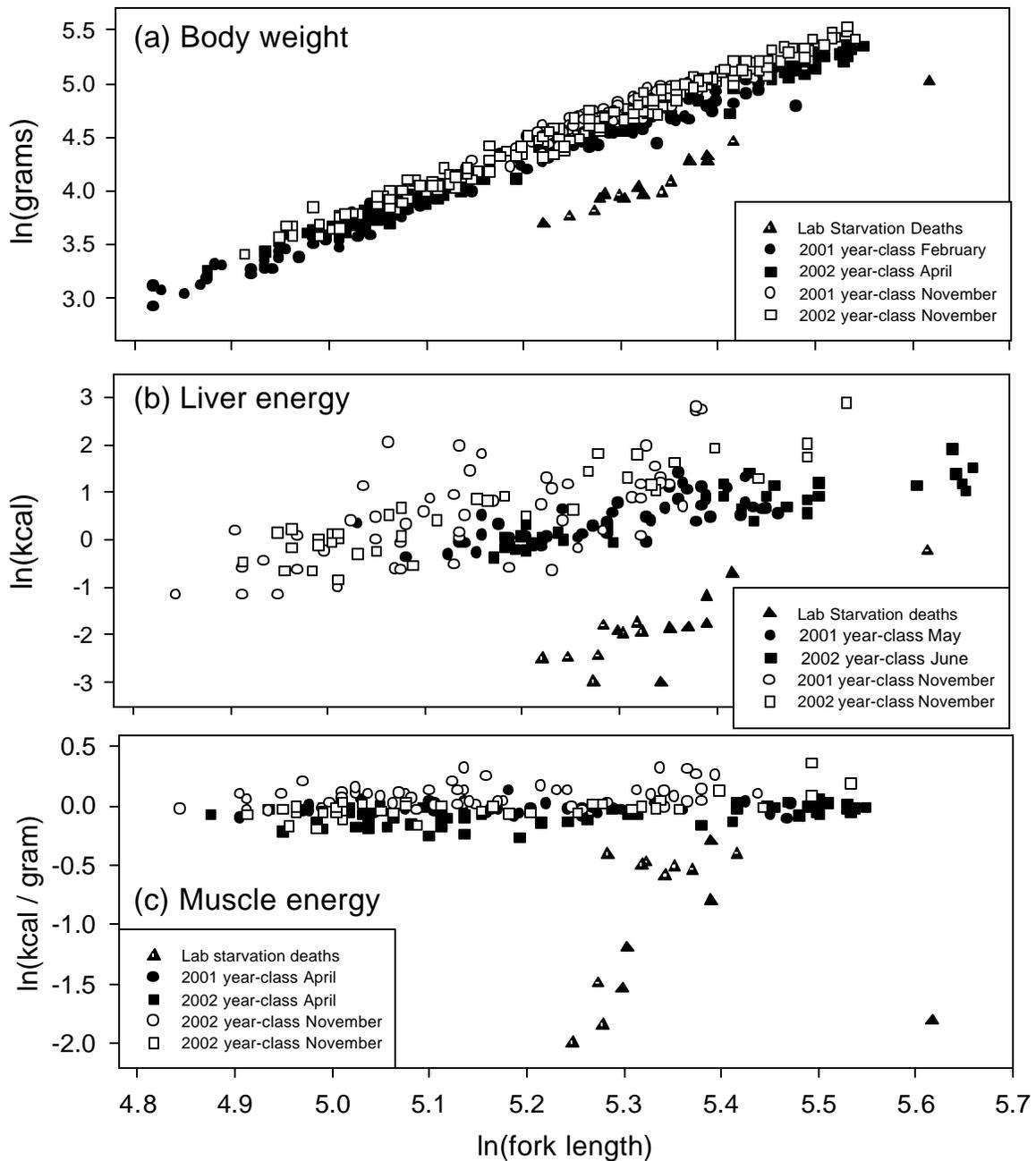
Figure 11. Comparison of wild young-of-the-year bluefish from the 2001 and 2002 year-class captured in Onslow Bay, North Carolina with bluefish that had starved to death in a laboratory starvation experiment (Slater et al. unpublished data). Time-intervals used for the wild bluefish were those with the lowest and highest length-adjusted mean values as determined from ANCOVA. Comparisons were made with a) ln(body weight (grams)) vs. ln(fork length), b) ln(liver energy (kcal)) vs. ln(fork length), and c) ln(muscle energy (kcal / gram)) vs. ln(fork length).

59
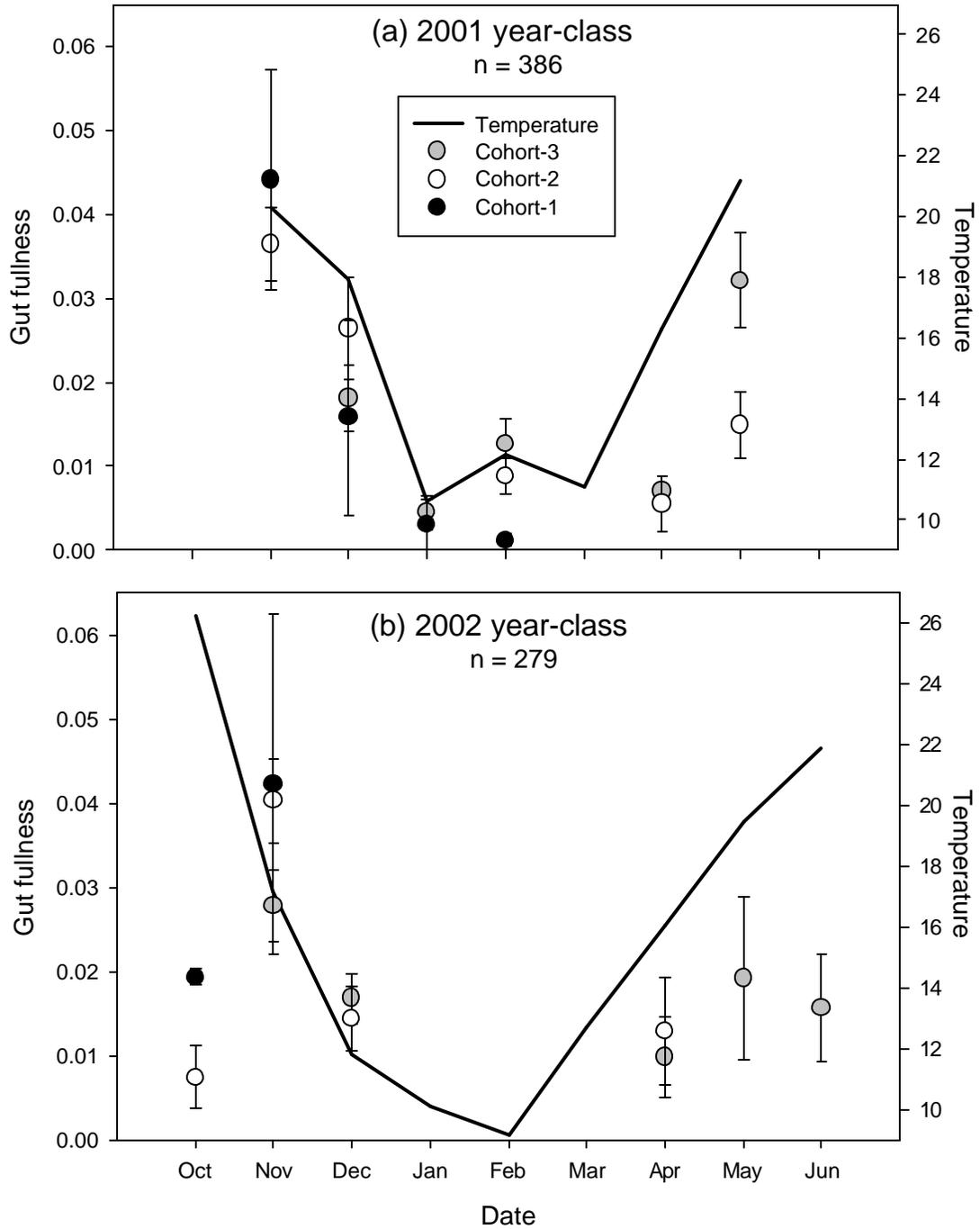
Figure 12. Mean (±SE) monthly gut fullness for young-of-the-year bluefish from each cohort captured by bottom trawl in Onslow Bay, North Carolina, corresponding to the left y-axis for a) the 2001 year-class, and b) the 2002 year-class. Mean monthly temperature (^{o}C) in Onslow Bay corresponds to the right y-axis.
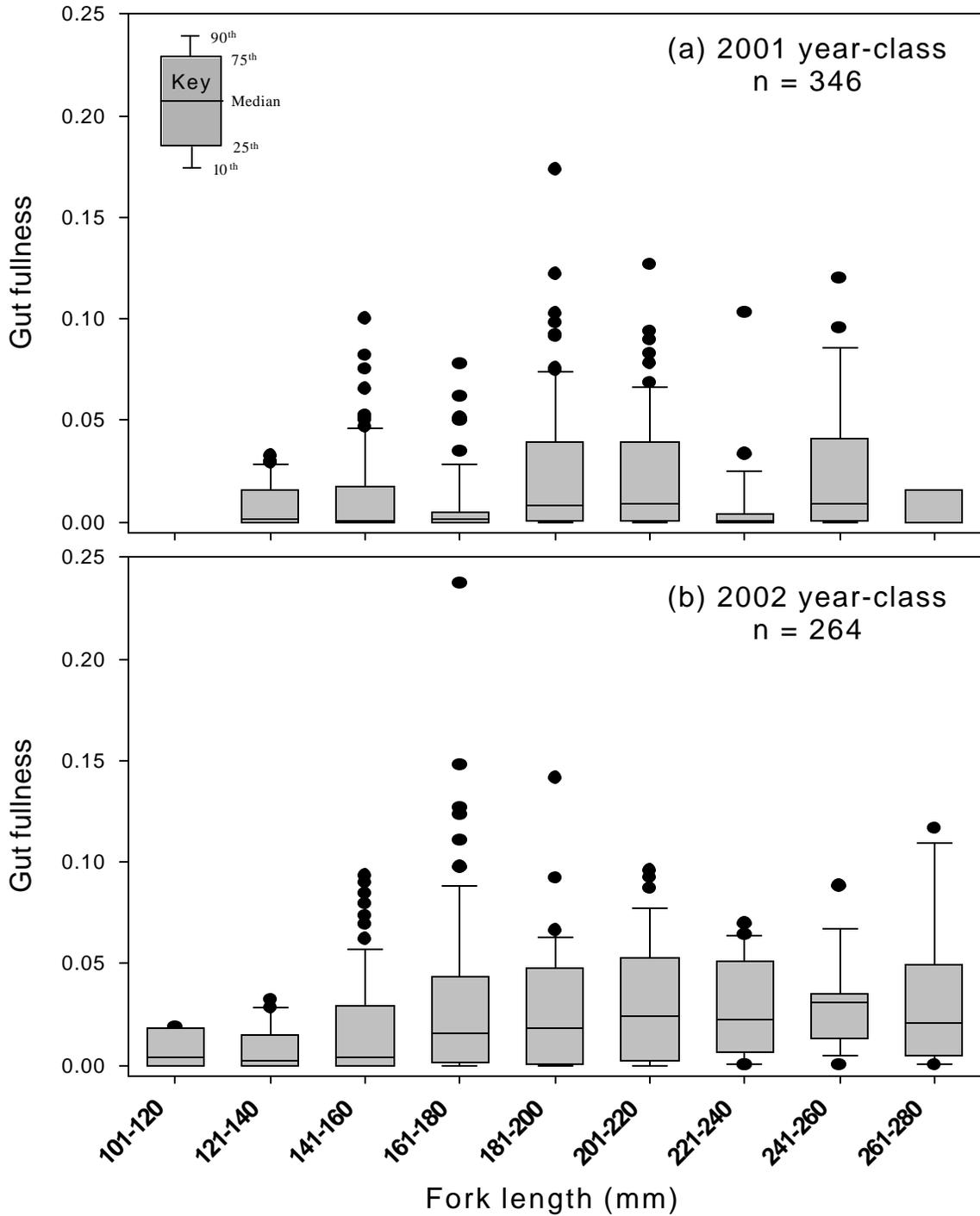
Figure 13. Box plots of young-of-the-year bluefish gut fullness for each 20mm length bin from November through April for a) the 2001 year-class, and b) the 2002 year-class. Boxplots indicate the median, and the 90th, 75th, 25th, and 10th percentiles. Bluefish were captured by bottom trawl in Onslow Bay, North Carolina between October and June.
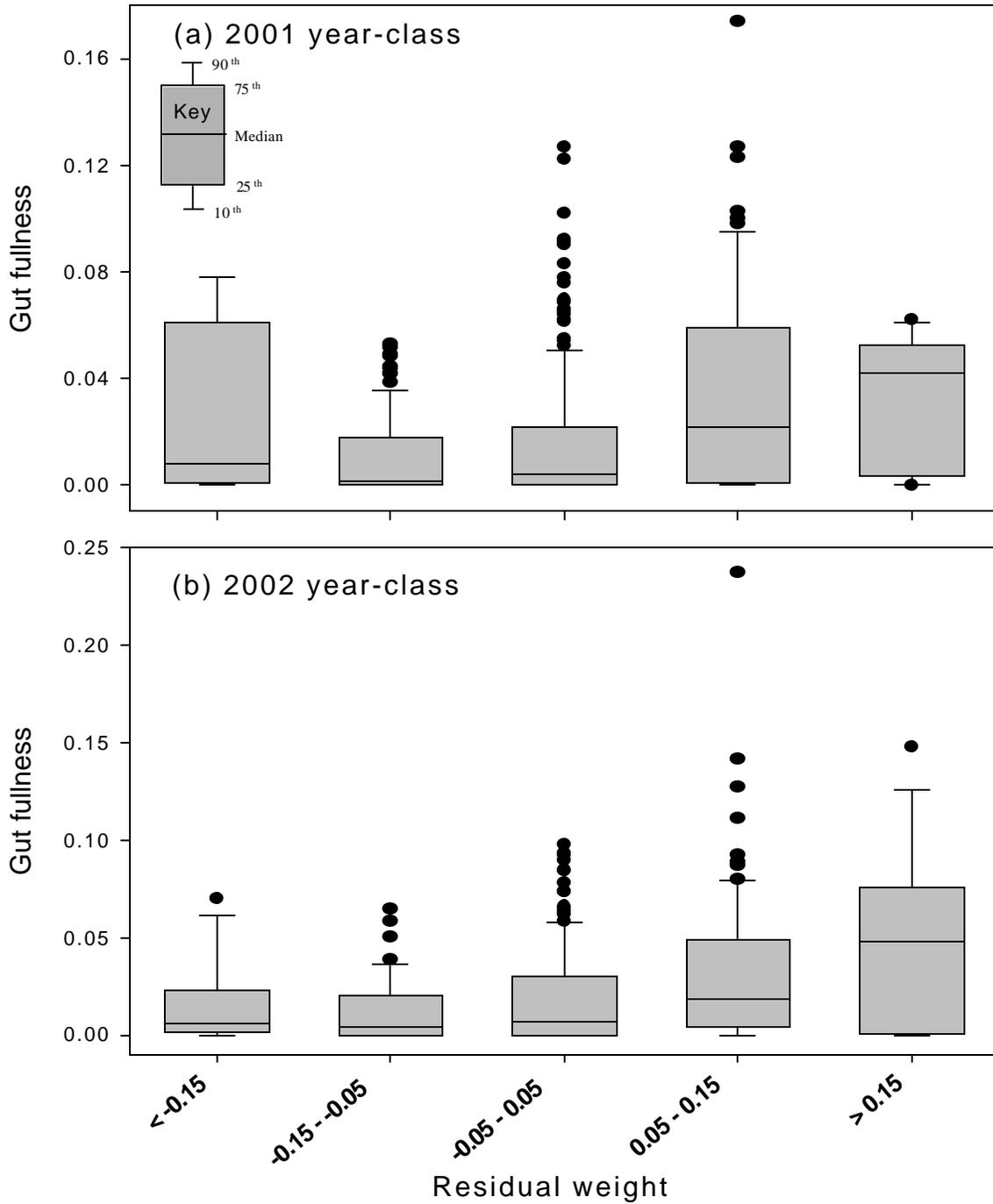
Figure 14. Box plots of young-of-the-year bluefish gut fullness vs. residual body weight for a) the 2001 year-class, and b) the 2002 year-class. Boxplots indicate the median, and the 90th, 75th, 25th, and 10th percentiles. Bluefish were captured by bottom trawl in Onslow Bay, North Carolina between October and June.

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