Abstract

BUTLER, CHRISTOPHER MATTHEW. Atlantic Bluefin Tuna (*Thunnus thynnus*) Feeding Ecology and Potential Ecosystem Effects During Winter in North Carolina. (Under the direction of Dr. Jeffrey A. Buckel)

Atlantic bluefin tuna (*Thunnus thynnus*) occupy North Carolina waters during winter months. Their potential impact on prey populations during this time has largely been unexplored. Diet, prey-size selectivity, predator-prey size relationships, gastric evacuation rates, daily ration, and population-level predatory demand were estimated for Atlantic bluefin tuna in North Carolina during winter. Quantitative analyses of bluefin tuna stomachs collected from commercial fishers during two winters (2004-2005) were examined. Bluefin tuna diet was dominated by Atlantic menhaden with other teleosts, portunid crabs, and squid being of mostly minor importance. By weight, I found no major inter-annual differences in diet; however, intra-seasonal diet variability was evident with more diverse diets in late-fall and less diverse diets (predominantly Atlantic menhaden) during winter for one out of two years examined. Lengths of Atlantic menhaden collected from bluefin tuna stomachs were compared with lengths of Atlantic menhaden captured from the Atlantic menhaden purse seine fishery; no significant differences were observed suggesting no prey size selection. Minimum and median-sized Atlantic menhaden prey increased with increased bluefin tuna size, while maximum-sized Atlantic menhaden did not change. Diel patterns in mean gut fullness values were used to estimate the first known field derived gastric evacuation rate for this species. Daily ration from mean gut fullness values and gastric evacuation rates were used along with a range of bluefin tuna population sizes and residency to estimate population-level consumption by bluefin tuna on Atlantic menhaden. I found that, at current population levels, bluefin tuna predation on Atlantic menhaden is minimal relative to

consumption of Atlantic menhaden by other known predators and commercial harvest. This was corroborated with an independent estimate of Atlantic menhaden consumption using an Ecopath model. Bluefin tuna appear to occupy coastal waters in North Carolina to prey upon Atlantic menhaden; thus, changes in the Atlantic menhaden stock status or distribution could alter winter foraging locations of bluefin tuna. This study has helped fill a gap in the knowledge of bluefin tuna natural history and provided data necessary for implementing multispecies fisheries management.

Atlantic Bluefin Tuna (*Thunnus thynnus*) Feeding Ecology and Potential Ecosystem Effects During Winter in North Carolina.

by

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A thesis submitted to the graduate faculty of
North Carolina State University
in partial fulfillment of the requirements for the
Degree of Master of Science

Zoology

Raleigh, NC

2007

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Butler, C.M., Rudershausen, P.J., and Buckel, J.A. Winter Feeding Ecology of North Carolina Bluefin Tuna. Talk at NC Sea Grant Bluefin Tuna Handling Workshop: How Handling Effects Price. Morehead City, NC. December 6, 2006.

Butler, C.M., Rudershausen, P.J., Smith, J.W., McNeill, N.A., and Buckel, J.A. Atlantic Bluefin Tuna (*Thunnus thynnus*) Feeding Ecology and Potential Effects on Menhaden During Winter in North Carolina. Poster presentation at NC Sea Grant/Division of Marine Fisheries Public Forum. New Bern, NC. March, 2006.

Butler, C.M., Rudershausen, P.J., Smith, J.W., McNeill, N.A., and Buckel, J.A. Atlantic Bluefin Tuna (*Thunnus thynnus*) Feeding Ecology and Potential Ecosystem Effects During Winter in North Carolina. Poster presentation at AFS Tidewater Chapter Meeting. Atlantic Beach, NC. January, 2006.

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Acknowledgements

First, and foremost, I would like to express my profound gratitude to my advisor Dr. Jeff Buckel for allowing me the opportunity to do this project and for providing invaluable guidance and support throughout this journey. I would also like to thank my other committee members, Dr. John Miller and Dr. Jason Osborne, for their involvement and input during the development and completion my thesis.

I would like to give special thanks to any past and present members of the Buckel laboratory, including but not limited to, Dana Bethea, Jim Morley, Nate Bachelor, Warren Mitchell, Jeff Merrell, Jason Edwards, Tyler Everett, Amos Williams, and Melissa May. I am extremely appreciative to Paul Rudershausen for his assistance and advice during numerous aspects of my project.

I am deeply indebted to various people who have provided either data or knowledge on Atlantic bluefin tuna or Atlantic menhaden ecology, namely Joe Smith, Neil McNeill, Joe Bizzarro, Dr. Barbara Block, Dr. Andre Boustany, Andreas Walli, Dr. Fred Scharf, Brad Chase, John Logan, Alan Bianchi, Dr. Ellis Loew, and Felix Del Toro Silva.

Special thanks go to all the commercial fishermen and tuna buyers who participated in the study, especially George Leone, Alex Ng, and Jack Cox. Additionally, I would like to thank North Carolina Sea Grant for providing funding for the project.

Finally, I am eternally grateful to my family. Words fail to describe the continual support you have given me. My accomplishments only exist because of your perpetual encouragement, and I would not be who I am today without you.

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1.1 Introduction

Ecosystem-based management in marine fisheries as a complementary approach to single-species stock assessments is now recommended (Christensen et al. 1996; NMFS 1999; NRC 1999; Jackson et al. 2001; Latour et al. 2003; Hinke et al. 2004; Neira and Arancibia 2004). Ecosystem-based models incorporate ecological interactions to evaluate the potential flows of biomass among interacting populations within an exploited ecosystem (Pauly et al. 2000; Hinke et al. 2004). Some of these models allow the user to compare removals by natural predators and fisheries to help answer questions concerning tradeoffs (e.g., harvest more predators to allow for more prey) when both predator and prey are commercially harvested species.

Atlantic menhaden (*Brevoortia tyrannus*) play a vital role in the ecological processes of estuarine and coastal waters throughout the eastern coast of the United States (U.S.) (Quinlan et al. 1999). In 2005, Atlantic menhaden comprised 28.3% of the total U.S. commercial landings in the Atlantic and represented one of the largest commercial fisheries in America (National Marine Fisheries Service (NMFS), website). They also serve as a primary forage species to several commercially and recreationally important predators, such as striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) (NEFSC 2006).

The Northeast Fisheries Science Center (NEFSC) has recently constructed a multispecies model which examined the predatory impact of these three predators on the Atlantic menhaden population. However, Kade (2000) found that Atlantic menhaden were a major component of Atlantic bluefin tuna (*Thunnus thynnus*) (hereafter referred to as bluefin tuna) diet during one winter (1999) in North Carolina waters. As an apex predator, bluefin tuna may significantly impact this prey when the Atlantic menhaden population aggregates in winter to spawn. An understanding of the feeding ecology of bluefin tuna is needed to determine their importance as an Atlantic menhaden predator and their potential impact on Atlantic menhaden populations.

Bluefin tuna is a highly migratory pelagic species that is distributed throughout the Atlantic Ocean and Mediterranean Sea; in western-Atlantic (west of 45^{o} meridian) waters, the species is found from Nova Scotia to Brazil (Scott et al. 1993; Block et al. 2001; Block et al. 2005). They are capable of retaining body heat generated during swimming which allows them to exploit cold waters in search of prey that are often inaccessible to other predators due to thermal stress. Bluefin tuna also have complex and extensive migration patterns related to spawning and feeding events. Beginning in late November, bluefin tuna migrate into North Carolina's coastal waters for a period of several months to feed upon local prey resources (Boustany 2006). Variations in prey availability directly influence the aggregations of bluefin tuna and locations of harvest by the commercial bluefin tuna fishery (Chase 2002).

Detailed studies of life history traits of bluefin tuna are often problematic due to its extensive range, and to date, work on the feeding ecology of large-medium and giant size-classes (see Table 1 for sizes) during the winter has been limited (Kade 2000). Previous diet studies have concluded that all size-classes of bluefin tuna are generally opportunistic predators, eating primarily teleosts, cephalopods, and crustaceans throughout the western North Atlantic (Crane 1936; De Sylva 1956; Krumholz 1959; Dragovich 1970; Mason 1976; Matthews et al. 1977; Holliday 1978; Eggleston and Bochenek 1990; Kade 2000; Chase 2002); similar results have been documented for the Pacific bluefin tuna, *Thunnus orientalis*, (Pinkas 1971) and southern bluefin tuna, *Thunnus maccoyii*, (Young et al. 1997).

Specialized morphological features, such as countercurrent heat exchangers, give bluefin tuna standard metabolic rates that are among the highest of any teleost species (Dickson and Graham 2004). High metabolic demands require predators to consume large amounts of prey and potentially influence the abundances of other species within an ecosystem (Libralato et al. 2006). To my knowledge, no attempt has been made to estimate daily ration from a wild bluefin tuna population in the North Atlantic. Gut fullness data collected over a diel period can be coupled with gastric evacuation rates to estimate daily ration (Elliott and Persson 1978). The exponential model is regarded as the most suitable pattern of food evacuation in teleosts and has been supported by numerous studies (Doble and Eggers 1978; Ruggerone 1989; Buckel and Conover 1996; Holker and Temming 1996; Shoji and Tanaka 2005); exponential models may better describe the evacuation rates of fish which require rapid digestion rates due to high metabolic demands (Bromley 1994). When examined, the predatory demand of large tunas is relatively high (Maldeniya 1996; Essington et al. 2002; Kitchell et al. 2002). Overholtz (2006) estimated predation demand of bluefin tuna on Atlantic herring (*Clupea harengus*) in the Northwest Atlantic; however, no estimates of exist for wild bluefin tuna feeding on Atlantic menhaden.

In the current study I provide a quantitative description of the diet of large-medium and giant bluefin tuna off North Carolina during two winters. I also determine prey size-selectivity, calculate a field-derived estimate for gastric evacuation rate and daily ration, estimate the population-level consumption of bluefin tuna on their primary prey, Atlantic menhaden, and compare population-level consumption with the predatory demand from other known Atlantic menhaden predators. Lastly, I construct an Ecopath model (www.ecopath.org; Christensen and Pauly 1992) to independently determine the relative importance of bluefin tuna as a predator of Atlantic menhaden in the South Atlantic Bight ecosystem.

1.2 Materials and Methods

1.2a *Study area*

Currently, the North Carolina commercial bluefin tuna fishery is based primarily from ports in Beaufort and Morehead City, NC, and operates from November through January (length of season determined by government regulations) in areas near Cape Lookout (Figure 1). Trolling, where a dead-baited hook (with or without lure) is pulled behind a moving vessel to imitate a live prey, is the predominant fishing method utilized to capture bluefin tuna in North Carolina; the bait of choice is ballyhoo (*Hemiramphus brasiliensis*). Most fishers begin fishing prior to dawn and continue to fish until late afternoon or until they meet the daily catch limit (three fish per vessel per day in 2006-07). Commercially caught bluefin tuna are generally harvested on either side of Cape Lookout shoals within a 28-km radius from the Knuckle Buoy (see inserts in Figure 1).

1.2b *Collection of samples*

Bluefin tuna stomachs were collected from commercial fishers during the winters of 2002-03, 2003-04, 2004-05, and 2005-06 off the coast of North Carolina; the first two winters were pilot years with small sample sizes. Stomachs were extracted through the gill plate by cutting the esophagus above the pylorus. In most instances, stomachs and other viscera were removed at sea by the fishers in order to rapidly cool the meat to maintain its quality for the Japanese market (Chase 2002). Because of stomach removal and disposal at sea, I had to advertise with fishers that I would accept donated stomachs or would provide a monetary reward for stomachs samples (Figure 2). Upon excision, all stomachs were stored on ice.

Coolers and data sheets (Figure 2) were distributed to local fish buyers and collected on a daily basis. The fisher was responsible for providing information such as time and location of capture, curved fork length (CFL), and dressed weight (DW). CFL was measured from the tip of the snout to the fork of the tail over the contour of the body. DW was obtained after the head, tail, and viscera had been removed. In instances where a DW was not recorded, one was estimated using the allometric relationship for CFL to DW defined from the current study as:

$$DW = 8 \times 10^{-6} \cdot CFL^{3.088}, \quad r^2 = 0.871$$

Where DW = the dressed weight (kg) of a bluefin tuna; and

CFL = the curved fork length (cm) of a bluefin tuna.

Dressed weights were converted to round (i.e. the total weight of a live fish) weights using the functional regression equation developed by Baglin (1980) as:

$$RW = -7.922 + 1.296 \cdot DW$$

where RW = the total weight (kg) of a bluefin tuna; and

DW = the dressed weight (kg) of a bluefin tuna.

The Atlantic menhaden purse seine fishery often targets large schools of adult Atlantic menhaden which gather in North Carolina's coastal waters during the winter to spawn. Atlantic menhaden were obtained from commercial purse seine sets in 2004-05; measurements were collected by the National Oceanic and Atmospheric Administration (NOAA) lab in Beaufort, NC (Joseph Smith, unpublished data). All measurements were obtained following NOAA sampling protocol, where a random sample of ten Atlantic menhaden from an 18.9 L subsample was measured for fork length (cm). All subsamples were collected from the top of the fish hold and assumed to be from the last purse seine set location (see purse seine set locations on Figure 1). Only purse seine data (i.e., the last set on a trip) that could be spatially (i.e. offshore) and temporally (i.e. +/- 1 month) matched with catches of bluefin tuna were used in further analysis (Figure 1).

1.2c *Analysis of the diet*

Laboratory processing of bluefin tuna stomachs was performed at North Carolina State University's Center for Marine Sciences and Technology in Morehead City, North Carolina. Stomachs were opened and the contents placed in labeled plastic bags; contents that could not be analyzed immediately were frozen for later analysis. All stomach contents were identified to the lowest taxon possible. Total and/or fork lengths (cm) and weight (g) were recorded for individual prey items when possible. Prey items that were identifiable, but could not be measured for length due to advanced stages of digestion, were grouped together by stage of digestion and weighed. Contents that could not be identified but obviously teleosts or invertebrates were measured and recorded as unidentified (e.g., “unidentified fish remains”).

Bluefin tuna diets were grouped by size-class [e.g., large-medium (185.4 - 205.7 cm CFL) or giant (> 205.7 cm CFL)] and intra-seasonal and inter-annual time effects were examined. Diets were expressed using indices of percent frequency of occurrence (%O) and percent by weight (%W) (Hyslop 1980). Percent frequency of occurrence was calculated as the number of bluefin that had ingested a specific prey item divided by the total number of bluefin tuna which contained prey. Percent composition by weight was estimated as the total wet weight of a specific prey type divided by the total wet weight of all prey ingested.

1.2d *Correspondence Analysis*

Dietary data often violate the assumptions required for parametric testing. Therefore, intra-seasonal, inter-annual, and size-class effects were examined using a non-parametric simple correspondence analysis for both %O and %W (Graham and Vrijenhoeck 1988). Correspondence analysis is a multivariate technique which allows the user to visualize associations between row (e.g., intra-seasonal, inter-annual, and size-class effects) and column (e.g., prey category) variables from a two-way contingency table (Davis 1986). Eigenvalues (i.e., variation) and eigenvectors containing the Chi-squared distances between all data points are generated from the contingency matrix; the eigenvectors become the principle axes of the graph. When row and column values are simultaneously plotted, the resulting biplot explains the correspondence of the effect of interest with prey category (Davis 1986).

1.2e *Cumulative prey curves*

Cumulative prey curves were constructed *a posteriori* by year and size-class for intra-seasonal, inter-annual, and size-class comparisons (Ferry and Cailliet 1996). Prey species were grouped by family and cumulative numbers of novel prey were plotted against number of stomachs to determine sample size sufficiency. In order to minimize bias and provide a more precise estimate of sample size requirements, the mean and standard deviation of the cumulative number of unique prey (Adams 2004) was calculated after 500 randomizations of the number of stomachs which contained prey (Bizzarro et al. in press) and plotted against the cumulative number of stomachs analyzed (Ferry and Cailliet 1996). Sample size sufficiency for each prey curve was tested using the linear regression method (Bizzarro et al. in press), where the slope from a regression of the mean number of unique prey items from the last four stomach samples versus total number of stomachs was compared to a slope of zero (Student's t-test of equality of two population regression coefficients; Zar 1999).

1.2f *Prey size-selectivity*

Size-selective feeding was tested for winter 2004-05 by comparing lengths of ingested Atlantic menhaden against lengths sampled from the Atlantic menhaden purse seine fishery by the National Marine Fisheries Service, Beaufort, NC (Joseph Smith and Neil McNeill, NOAA, unpublished data). Size-selective feeding patterns of bluefin tuna (e.g., large-medium, giant, and pooled size-classes) were examined by comparing length-frequency histograms of ingested Atlantic menhaden versus a length-frequency histogram of Atlantic menhaden from the environment; statistical comparisons were made with a Chi-square median test (Zar 1999).

1.2g ***Quantile regressions***

Bluefin tuna - Atlantic menhaden length relationships were examined using quantile regression analysis to determine the median (50th quantile) as well as the edges [minimum (5th quantile) and maximum (95th quantile) boundaries] of the prey size-predator size scatter (Scharf et al. 1998, 2000). The 5th, 50th, and 95th quantiles were selected based on sample size (Scharf et al. 1998). Quantile regression analyses were performed using BLOSSOM software (Cade and Richards 2001). Additionally, the relationship between prey to predator size ratio and predator size was determined.

1.2h ***Gastric evacuation rate and daily ration***

Stomach fullness (kg prey · kg predator^{-1}) were binned by one hour time periods. Gastric evacuation rates (G_e) of bluefin tuna were estimated using an exponential decay model:

$$S_t = S_0 \cdot e^{-G_e t}$$

where S_t = the stomach fullness (kg prey · kg predator^{-1}) at time t;

S_0 = the stomach fullness (kg prey · kg predator^{-1}) at time t=0;

G_e = the instantaneous rate of gastric evacuation (h^{-1}); and

t = time in hours.

G_e for large-medium and giant size-classes were compared by determining if the difference between their G_e values were different from zero using the NLIN procedure of SAS (SAS 1996).

Daily ration estimates of large-medium, giant, and pooled bluefin tuna size-classes were calculated using the Eggers (1977) approach:

$$D_R = 24 \cdot \overline{S} \cdot G_e$$

where D_R = the daily ration estimate (kg prey · kg predator^{-1} · day^{-1}) ;

$\overline{S}$ = the mean stomach fullness (kg prey · kg predator^{-1}) of 24 time point means; and

G_e = the instantaneous rate of gastric evacuation (h^{-1}).

Estimates of mean gut fullness values for missing time-points were calculated using the corresponding gastric evacuation equation; these were: 19:30, 20:30, 21:30, 22:30, 23:30, 00:30, 01:30, 02:30, and 03:30.

1.2i *Population-level consumption*

Population-level consumption was estimated as follows:

$$C_{pop} = P_{NC} \cdot \overline{W}_{BFT} \cdot D_R \cdot \%W_{Mh} \cdot t_{NC}$$

where C_{pop} = bluefin tuna consumption of Atlantic menhaden in North Carolina during winter;

P_{NC} = the number of bluefin tuna estimated to be in North Carolina waters;

W_{BFT} = the mean weight of Atlantic bluefin tuna captured in North Carolina;

D_R = this study's estimate of bluefin tuna daily ration (kg prey · kg predator^{-1} · day^{-1});

$\%W_{Mh}$ = the percentage of bluefin tuna diet (by weight) that is composed of Atlantic menhaden;

t_{NC} = the amount of time (days) that bluefin tuna and Atlantic menhaden co-occur in the coastal waters of North Carolina.

Total consumption estimates were then compared to consumption estimates of other known Atlantic menhaden predators (e.g., bluefish, striped bass, and weakfish) including the commercial harvest.

In order to determine P_{NC} , I had to convert the sizes of bluefin tuna found in North Carolina to ages; bluefin tuna were aged using size-at-age regressions (Mather and Schuck 1960; Ólafsdóttir and Ingimundarsdóttir 2003) and determined to be predominantly age 6+ fish. The most recent (2002) bluefin tuna abundance-at-age data (Restropo et al. 2003) for age 6+ fish were coupled with the mean weight of bluefin tuna sampled during the current study. However, it is unknown what percentage of the age 6+ bluefin tuna population occurs off North Carolina during this time period. Therefore, both the mean annual catch from NC (i.e. winters of 2003-04, 2004-05, and 2005-06) and percentages (e.g., 5%, 10%, 25%, 50%, 100%) of the total population biomass of the age 6+ western Atlantic bluefin tuna were coupled with my field-derived daily ration estimate and dietary composition data to calculate a range of population-level demand on Atlantic menhaden prey. These calculations were made over a range of potential days of residency that both species co-occur in local waters as determined from pop-up satellite-tagged bluefin tuna and Atlantic menhaden purse seine catches (Boustany 2006; Joseph Smith, NOAA, unpublished data). Additionally, to fully restore the western Atlantic bluefin tuna population, the International Commission for the Conservation of Atlantic Tunas (ICCAT) has recommended a targeted biomass level equivalent to that from 1975 (Restropo et al. 2003). Thus, a second analysis was performed using bluefin tuna abundance-at-age data (age 6+) from 1975.

1.2j *Ecosystem modeling*

The South Atlantic Fisheries Management Council (SAFMC) is building an Ecopath model (Okey and Pugliese 2001) for the South Atlantic Bight (SAB) region. The ultimate goal of the model is to aid in the long-term sustainability of the entire ecosystem including economically important fisheries. However, many parameters are unknown or require validation before the model can be applied to multispecies based fisheries management. To help the SAFMC accomplish these goals, I conducted a literature review to help to parameterize an ecosystem model of the SAB with particular focus on the pelagic community. Many of these species are predators of Atlantic menhaden, including bluefin tuna. Thus, the Ecopath model I constructed can be used to examine the relative importance of multiple predators of Atlantic menhaden in the SAB (e.g., king mackerel, red drum, striped bass, bluefish, and weakfish).

Ecopath uses specific parameters to balance the mass and energy within a system and is expressed as follows:

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + \sum B_j \cdot (Q/B)_j \cdot DC_{ji} + NM_i + BA_i$$

where B = the biomass of prey species i and predator j;

$(P/B)_i$ = the ratio of production to biomass of prey species i (equal to the total mortality (Z)) at equilibrium;

EE_i = the ecotrophic efficiency (equal to the fraction of production of prey type i that is consumed or removed from the system;

Y_i = total fishery landings of prey species i;

$(Q/B)_j$ = the ratio of consumption to biomass for predator group j that forage on prey item i;

DC_{ji} = the proportion of the diet of predator j that consists of prey item i;

NM_i = the net migration of prey group i (emigration minus immigration); and

BA_i = the biomass accumulation rate of i.

For each trophic group, Ecopath requires information for at least three of the four following input parameters: *B*, *P/B*, *Q/B*, and *EE*; the fourth parameter is estimated by Ecopath software during the mass balancing process. When all four parameters are known and entered, the model assumes *EE* to have the greatest uncertainty. A diet composition matrix and fisheries landings are also required.

The continental shelf of the SAB encompasses an area of 90,600 km^2, which extends from the Straits of Florida to Cape Hatteras, North Carolina (Yoder 1991). Individual species were placed into trophic groups that were based upon diet composition and characteristics of each organism's natural history (Okey and Pugliese 2001). Ecopath parameters for each functional group were assembled from previous literature and used as a base for the current Ecopath model (Mackinson et al. 2000; Okey and Pugliese 2001). The parameters used are averages and account for annual and ontogenetic changes (Okey and Pugliese 2001). The literature sources of input paramaters for all functional groups and details on mass balancing this Ecopath model can be found in the Appendix.

1.3 Results

1.3a *Quantitative analysis of the diet*

The stomach contents of 448 Atlantic bluefin tuna were examined from fish collected during the winters of 2002-03, 2003-04, 2004-05, and 2005-06 (Table 2). Of these, 124 (100 non-empty) were large-mediums and 324 (252 non-empty) were giants. Samples were further categorized by year and intra-seasonal time period (i.e. December 1-14, December 15-31, and January 1-31). Stomachs that were either empty or from which no length and weight data were recorded were eliminated from further statistical analysis. Additionally, sample sizes were low in 2002-03 and 2003-04 so these years were not included in statistical tests.

Overall, stomach contents of Atlantic bluefin tuna contained fourteen families of teleosts, five species of portunid crabs, cephalopods (mainly *Loligo pealeii*), one species of elasmobranch (*Mustelus canis*), and unidentified algae (Table 3). Atlantic menhaden (*Brevoortia tyrannus*) were the most common prey item by frequency of occurrence (84.94% O) and accounted for 95.53% of the diet by weight (%W) over all years combined (Table 3). Atlantic needlefish (*Strongylura marina*) were the second most important identifiable prey item by weight (2.47% W, 5.40% O). Although individual species of portunid crabs and cephalopods appeared with some regularity in stomachs (range, 0.28-6.82 %O), they contributed little in terms of biomass. Other prey including teleosts, elasmobranchs, bivalves, and algae were rare items that contributed little to diet.

There was little intra-seasonal variation of the diet of large-medium bluefin tuna collected during 2004-05 (Table 4; Figure 3A & 4A). Atlantic menhaden dominated the diet during 2004-05 for both %O and %W; they occurred in nearly every stomach (96.88% O) and contributed approximately 98.97% to the overall weight of prey consumed for all intra-seasonal time-periods combined. The diets of large-medium bluefin tuna collected throughout the 2005-06 season were similarly dominated by Atlantic menhaden (Table 5; Figure 3B & 4B). Although prey items such as portunid crabs and squid appeared more frequently than in the 2004-05 season, they remained of minor importance in terms of biomass contribution. Pooled diet data for the entire season mirrored the results described above (Figure 3C & 4C).

During 2004-05, giant bluefin tuna consumed a variety of prey items including crabs and miscellaneous fish when examined by occurrence (Table 6; Figure 5A); however, Atlantic menhaden remained the most abundant prey and accounted for approximately 99% of the total stomach-contents biomass during each intra-seasonal time period (Figure 6A). The diet of giant bluefin tuna collected from the 2005-06 season had the greatest diversity for any year or size-class examined (Table 7; Figure 5B). Atlantic needlefish were found in 58.33% of stomachs and accounted for 56.77% of the total prey biomass from the early December time-period (Figure 6B). Atlantic menhaden, although found at the same %O as

Atlantic needlefish, only contributed 37.97% of the stomach-contents biomass during the early December time-period. Stomachs collected from giants during the late-December and January time-periods resembled the diet composition of giants collected throughout the 2004-05 season; Atlantic menhaden became the dominant prey during these time-periods, and pooled diet data for all time-periods showed that Atlantic menhaden were the primary prey source for the majority of bluefin tuna that season (83.21% O, 92.97% W). Pooled diet data for the entire season showed that portunid crabs were the second-most important prey item with a high (combined over species) occurrence (Figure 5C) but low prey biomass (Figure 6C).

The pooled diets of large-medium and giant bluefin tuna were compared (Table 8). Atlantic menhaden occurred in 91.00% of stomachs examined and composed 98.42% of the total prey biomass for all large-medium bluefin tuna. As with large-medium bluefin tuna, Atlantic menhaden were the dominant prey item (82.54% O, 94.71% W) of the giant size-class; however, the diet composition of giant bluefin tuna was more diverse than large-mediums. Atlantic needlefish were the second most important identifiable prey item for all giant data combined (7.14% O, 3.16% W). Portunid crabs and squid were regularly observed in giants, but comprised little of the total prey weight.

1.3b *Cumulative prey curves*

Randomized cumulative prey curves did not reach an asymptote for any of the intra-seasonal time periods for large-medium bluefin tuna ($p<0.05$; Figure 7 & 8), while all giant bluefin tuna periods, with the exception January 2006, reached an asymptote (Figure 9 & 10).

Both large-medium (Figure 11) and giant (Figure 12) size-classes reached asymptotes when data were pooled over each season. This indicates that sample sizes were adequate to describe the diet for intra-seasonal analyses on giants as well as all inter-annual and ontogenetic comparisons. The intra-seasonal analyses of large-medium bluefin tuna are likely biased due to low sample sizes.

1.3c *Correspondence analysis*

Correspondence analysis using %O showed that diets of both large-medium and giant size-classes were dependent upon intra-seasonal time period in both years (Table 9); intra-seasonal correspondence analyses for large-medium bluefin tuna are presented despite insufficient sample sizes. Correspondence analysis of the first two axes accounted for 100% of the total variation for all intra-seasonal comparisons of both large-medium and giant size-classes using %O (Figure 13). Large-medium bluefin tuna collected throughout December of the 2004-05 season grouped closely with Atlantic menhaden, while large-mediums collected during January 1-31, 2005 corresponded with portunid crabs and other teleosts (Figure 13A). Large-mediums grouped with: Atlantic menhaden, portunid crabs, and Atlantic needlefish during December 1-14, 2005; Atlantic menhaden, portunid crabs, and cephalopods during December 15-31, 2005; and Atlantic menhaden and other teleosts during January 1-31, 2006 (Figure 13B). During all intra-seasonal periods in 2004-05, giants grouped near Atlantic menhaden; however, they also grouped with portunid crabs during December 15-31, 2004; and with portunid crabs, cephalopods, and other teleosts during January 2005 (Figure 13C). Giants collected during the early December time-period of 2005 corresponded with Atlantic needlefish, cephalopods, and other teleosts; giants collected during the late December and January time-periods grouped closely with Atlantic menhaden (Figure 13D). Chi-square test results of giants from both years indicated that prey types were dependent upon intra-seasonal time period (Table 9).

The first two axes of correspondence analysis of %W accounted for 100% of the total variation for all intra-seasonal comparisons of large-medium and giant size-classes (Figure 14). Correspondence analysis plots of %W indicated that prey type was independent of intra-seasonal time period for both size-classes of bluefin tuna collected during the 2004-05 season but not independent for the two size groups in 2005-06 (Table 9). Although the 2005-06 analysis was statistically significant, large-mediums from both years grouped closely with Atlantic menhaden (Figure 14A & 14B). Giant bluefin tuna diets during all three time periods of 2004-05 grouped closely with Atlantic menhaden (Figure 14C). There was a significant difference in diets of giants collected during the 2005-06 season (Table 9; Figure 14D); this was likely due to the abundance of Atlantic needlefish consumed during the early December time-period of that year.

Correspondence analysis indicated significant inter-annual and size-class differences using %O; however, %W showed prey items were independent of year and size-class (Table 9). Comparisons using %O and %W for both size-classes from both years are represented in Figures 15A and 15B; these figures are for visual representation purposes only and the p-values for each test are presented on Table 9. Correspondence analysis of both size-classes using %O showed large-medium bluefin from 2004-05 and 2005-06 as well as giant bluefin from 2004-05 grouped closest with Atlantic menhaden (Figure 15A). Giant bluefin tuna from 2005-06 were separated from the other size-class and years by grouping with cephalopods and other teleosts. For %W, correspondence analysis showed no significant inter-annual or size-class effects with respect to prey type (Table 9). Large-mediums and giants in 2004-05 and 2005-06 grouped with Atlantic menhaden and portunid crabs (Figure 15B).

1.3d ***Predator-prey size relationships***

Length frequency distributions of Atlantic menhaden fork lengths from the purse seine fishery (n=50) were compared to lengths of Atlantic menhaden retrieved from bluefin tuna stomachs (n=281) during the 2004-05 season (Figure 16). Prey sizes found in the stomachs of large-medium (Fig. 16A), giant (Fig. 16B), and pooled size-classes (Figure 16C) were not significantly different from the sizes of Atlantic menhaden found in North Carolina waters during winter (Large-medium, $\chi^2 = 0.014$, $p = 0.904$; Giant, $\chi^2 = 0.007$, $p = 0.935$; Pooled, $\chi^2 = 0.022$, $p = 0.882$).

A total of 928 Atlantic menhaden prey lengths was recorded from 200 large-medium and giant bluefin tuna stomach samples; Atlantic menhaden fork lengths ranged from 19.7 to 34.1 cm. Minimum and median-sized prey increased significantly with increased bluefin tuna size (5^{th} quantile, $p = <0.01$; 50^{th} quantile, $p = <0.01$; Figure 17A). Predation on maximum-sized prey did not significantly vary with increased predator length (95^{th} quantile, $p = 0.83$). There was a significant ($p<0.001$) negative relationship between prey length - predator length ratios and predator fork length (Figure 17B). Both size-classes of bluefin tuna preyed on Atlantic menhaden that were small relative to predator body length (Figure

18). Over 56% of large-medium bluefin tuna diets consisted of Atlantic menhaden that were between 13-17% of their body length (Figure 18A); 92.56% of Atlantic menhaden prey were less than 15% relative body length. This contrasted with giants, in which 84% of consumed Atlantic menhaden were less than 13% of predator length (Figure 18B); however, giants were similar to large-mediums in that 99.44% of Atlantic menhaden prey lengths were less than 15% of predator length.

1.3e *Gastric evacuation rates and daily ration*

The diel feeding patterns of large-medium (Figure 19A) and giant (Figure 19B) bluefin tuna collected during winters off coastal North Carolina suggest both size-classes of bluefin tuna display diurnal feeding (2004-05 and 2005-06 combined). Mean gut fullness values for both size-classes were approximately zero during pre- and post-dawn hours. Gut fullness levels increased throughout the morning (09:00 to 12:00) and reached maximum levels during the early afternoon. Large-medium bluefin reached a mean (±SE) maximum gut fullness of 1.59% ± 0.32 (kg prey / kg predator) at 12:00 to 13:00 hours (Figure 19A). The estimate of G_e (±SE) for the large-medium size-class was $0.13 \pm 0.06\ hr^{-1}$. Giant bluefin attained a mean (±SE) maximum gut fullness of 1.66% ± 0.37 (kg prey / kg predator) between 13:00 and 14:00 hours (Figure 19B), and had a G_e (±SE) of $0.12 \pm 0.04\ hr^{-1}$. No significant differences were found between estimates of G_e from the two size-classes; thus, a combined (large-medium and giant) G_e was determined and used for the remainder of this study (Figure 20). The combined diel feeding pattern of both size-classes had a maximum gut fullness (±SE) of 1.52% ± 0.29 (kg prey / kg predator) at the 13:00 to 14:00 hour period.

The mean (±SE) gastric evacuation rate was $0.11 \pm 0.03\ hr^{-1}$.

The mean daily ration estimate of bluefin tuna in North Carolina was 1.74% (kg prey·kg predator^{-1}·day^{-1}). When multiplied by the mean weight of bluefin tuna in the North Carolina fishery, the absolute daily ration was 2.73 kg·day^{-1}.

1.3f *Population-level consumption*

The most recent (2002) population estimate of western Atlantic bluefin tuna predicted there were 104,535 individuals age 6 or older (Restropo et al. 2003). As expected, estimates of Atlantic bluefin tuna consumption on Atlantic menhaden varied greatly with the duration (days) and abundance (numbers) of the bluefin tuna population estimated to be in North Carolina waters during the winter; annual consumption of Atlantic menhaden by bluefin tuna ranged between 38 and 32,658 mt · year^{-1} (Table 10).

At current population levels of bluefin tuna, the average consumption of Atlantic menhaden was found to be lower than most consumption estimates for other known predators, including the commercial menhaden fishery (Figure 21A). Maximum predatory demands by the current population size of bluefin tuna were near the lower estimates of coastwide predation for weakfish, striped bass, or bluefish. The potential maximum consumption of Atlantic menhaden by a completely restored bluefin tuna population (Figure 21B) does approach levels that are comparable to the other recognized Atlantic menhaden predators. However, none of the predatory impacts expressed by natural Atlantic menhaden predators compares to the Atlantic menhaden commercial fishery; the fishery has historically harvested nearly 14 times the maximum estimate of Atlantic menhaden biomass consumed by the current bluefin tuna population.

1.3g *Ecopath model*

The balanced Ecopath model for the SAB is presented in Table 11. Trophic levels were estimated by Ecopath software and ranged from 1.00 for primary producers, such as "Phytoplankton" and "Macroalgae + Sea grass", to 4.35 for "Bottlenose dolphin". "Zooplankton," "Invertebrates," and "Atlantic menhaden" were at trophic level two. Most fish species, as well as "Marine birds", occupied trophic level three. "Bluefin tuna" were estimated to have a trophic level of 3.29, while the "Bluefish, Striped Bass, Weakfish" group were assigned a trophic level of 3.64. "Small tuna species" and "Large coastal sharks", along with "Bottlenose dolphin," were the only trophic groups listed above trophic level four. The *EE* for many trophic groups approached one (Table 11), suggesting loss to mortality (both natural and fishing) was near the upper limits of production for each of these groups. This pattern was not only observed at lower trophic levels such as phytoplankton and invertebrates, but also at upper trophic groups such as the "Bluefish, Striped Bass, Weakfish" group.

Annual consumption for functional groups is summarized in Table 12. "Invertebrates" and "Zooplankton" comprised 60.07 and 34.70% of the total food intake in the SAB ecosystem, respectively. The total amount of Atlantic menhaden consumed by natural predators in the SAB was 973,044 mt·year^{-1} (Table 13). "Pelagic piscivores" (e.g., king mackerel, cobia, and tarpon) accounted for 65.47% of the total consumption of Atlantic menhaden by all predators presented in my Ecopath model. The second largest fraction

(33.64%) of the total consumption was by the "Bluefish, Striped Bass, and Weakfish" group. All other trophic groups combined consumed 8,697.60 mt of Atlantic menhaden$\cdot$yr^{-1}; this represents 0.89% of the total amount of Atlantic menhaden consumed in the SAB. Bluefin tuna were estimated to consume 1,630.80 mt (0.17%) of Atlantic menhaden annually (Table 13).

1.4 Discussion

1.4a *Importance of Atlantic menhaden to bluefin tuna*

Quantitative diet studies of bluefin tuna have been reported for various size-classes, seasons, and locations (Crane 1936; Krumholz 1959; Dragovich 1970; Mason 1976; Matthews et al. 1977; Holliday 1978; Eggleston and Bochenek 1990; Kade 2000; Chase 2002). However, with the exception of Kade (2000), there has been little research done on the diets of large-medium and giant bluefin tuna during winter. When examined by weight, Atlantic menhaden were consistently important throughout a winter fishing season, for all years, and for both large-medium and giant bluefin tuna. Although other prey often occurred in relatively high amounts (e.g., portunid crabs) they contributed little in terms of biomass. Atlantic menhaden is generally not considered a dominant prey of bluefin tuna (Holliday 1978; Chase 2002); however, the predominance of Atlantic menhaden has previously been observed by Kade (2000) who studied bluefin tuna diets during the 1999 North Carolina winter fishery. Kade's (2000) result for 1999 and now my results for multiple years have confirmed that bluefin tuna are a potentially important predator of Atlantic menhaden; although these are the first modern studies to identify this predator-prey linkage, historic anecdotal information described bluefin tuna voraciously feeding on schools of Atlantic menhaden off New England in the 1800's (Goode 1879).

The dietary composition of bluefin tuna has been shown to be dependent on prey availability and tuna body size (Chase 2002). In this study, the diets of large-medium and giant bluefin tuna were dominated by Atlantic menhaden in terms of %O and %W; thus, there was no shift in diet with increase in bluefin tuna length. Chase (2002) stated the diet of bluefin tuna from any particular study location has historically been dominated by "a single, pelagic, schooling prey species," such as silver hake (*Merluccius bilinearis*), mackerel (*Scomber ssp.*), sand lance (*Ammodytes ssp.*), and Atlantic herring (Krumholz 1959; Mason 1976; Holliday 1978; Eggleston and Bochenek 1990; and Chase 2002). During winter in North Carolina coastal waters, Atlantic menhaden appear to match Chase's (2002) prey description. However, no quantitative information exists on the distribution and abundance of other potential prey; thus, conclusions regarding prey-type selectivity cannot be made.

Squid (*Loligo spp*.) and portunid crabs were regularly observed during stomach content analysis from the current study. Squid have been suggested as the second-most important prey item, behind teleosts, in several bluefin tuna diet studies (Dragovich 1970; Mason 1976; Matthews et al. 1977; Eggleston and Bochenek 1990; and Kade 2000). Portunid crabs have previously been documented by Kade (2000), and authors such as Krumholz (1959), Dragovich (1970), Holliday (1978), and Chase (2002) have found minor amounts of crustaceans in bluefin tuna diets. Inclusion of such prey species in bluefin tuna diet locally may result from an over-abundance of cephalopods and crustaceans relative to Atlantic menhaden; Juanes et al. (2001) found this to be the explanation for another primary piscivore that often included invertebrate prey in their diet.

To my knowledge, no other stomach content analysis studies have investigated the intra-seasonal or inter-annual diet variations for bluefin tuna. Variability within and between years differed for each of the two quantitative indices used. Using prey occurrence data, intra-seasonal and inter-annual differences for both size-classes were found. Although variable within size classes and years, there was an overall pattern of a moderate occurrence of non-Atlantic menhaden prey in early December changing to diets being dominated by Atlantic menhaden by late December and January. There was a higher occurrence of non-Atlantic menhaden prey in 2005-06 compared to 2004-05, which appears to be driven by Atlantic needlefish in early December. When examined by percent weight, two out of four intra-seasonal changes were significant; sample sizes were likely inadequate for the first of these (large-medium 2005-06) but the availability of Atlantic needlefish with respect to Atlantic menhaden may have driven this difference for giant bluefin tuna in 2005-06. I speculate that, in some years, bluefin tuna might arrive to their winter feeding areas before Atlantic menhaden arrive (or before they gather in larger spawning concentrations).

Compared to the number of giants, fewer large-mediums were collected during each year. Randomized cumulative prey curves suggested samples sizes were not sufficient to describe intra-seasonal comparisons of large-medium bluefin tuna; sample sizes were adequate to describe the intra-seasonal comparisons of giants as well as effects of year on both size-classes. The lack of defined asymptotes from specific size-classes is not uncommon in other apex species such as elasmobranchs, given the difficulty in collecting large numbers of individual stomachs (Simpfendorfer 1998; Gelsleichter et al. 1999; Bethea et al. 2004; Bethea et al. 2006; Maia et al. 2006; McElroy et al. 2006).

1.4b *Size-selectivity and prey size patterns*

I found no evidence of size-selection for bluefin tuna feeding on Atlantic menhaden. To my knowledge, this is the first test of size-selective feeding in a wild bluefin tuna population. However, tests of prey size-selectivity have been made under controlled conditions in a net pen. Hanrahan (1999) fed mummichog (*F. heteroclitis*) to captive school-sized bluefin tuna (~1 m FL); mummichogs were 6, 8, and 9% of mean bluefin tuna length. He found positive size-selective feeding in the net pens where larger prey were selected first in 86% of his observations. In another set of experiments, he used Atlantic menhaden that were either 12 or 14% of mean bluefin tuna length; similar to my study, he found no evidence of size-selective feeding on Atlantic menhaden for these predator-prey size ratios. In my study, Atlantic menhaden lengths measured from the Atlantic menhaden purse seine fishery were assumed to represent the prey sizes available from the offshore environment (Joseph Smith, NOAA, NMFS, personal communication). Since the Atlantic menhaden purse seine fishery uses the same gear inshore to harvest smaller (100-200 mm) fish as they do offshore to capture larger (> 200 mm) fish, it is unlikely the gear missed smaller Atlantic menhaden in the offshore environment. However, the low sample sizes of Atlantic menhaden lengths from the purse seine fishery may not completely represent the size distributions found in the environment.

For a number of piscivorous species, prey size increases with increasing predator size (Scharf et al. 2000). Median, as well as minimum, prey sizes of Atlantic menhaden lengths increased significantly with increasing bluefin tuna size; however, maximum prey sizes were unaffected by increasing predator size. Previous studies of piscivores have found that minimum-sized prey remain relatively constant with increased predator size, whereas the maximum and median prey sizes increase significantly (Scharf et al. 2000; Bethea et al. 2004; Rudershausen et al. 2005). Although the slopes are relatively shallow, my results for minimum and maximum prey relationships do not match these previous findings. Prey-predator length ratios generally average 20-30% for piscivores (Juanes 1994); large-medium and giant bluefin tuna from my study consumed prey that averaged 12.98% ± 0.06. Here, the largest prey only represented about 17% of the length of the smallest tuna. Therefore, the most likely explanation for my result is that all the sizes of Atlantic menhaden that were available to the predator were highly vulnerable; that is, bluefin tuna of all sizes examined here displayed no morphological or behavioral constraints on prey capture or handling. Several studies have also reported that no relationship exists between bluefin tuna sizes and the sizes of their prey. Young et al. (1997) found no relationship between southern bluefin tuna lengths and the length of their prey. Similarly, Chase (2002) found little evidence of a predator size-prey size relationship in western Atlantic bluefin tuna. That author found the average prey size of all bluefin tuna sampled off New England (104-297 cm) was only 8.05% of mean bluefin tuna length; however, he stated the largest prey were only consumed by the largest predators. In my study, the significant positive slopes of lower and median bounds may be driven by low sample sizes for the largest tuna or could be a real pattern where giant bluefin tuna begin to drop the smallest prey from their diet as predicted by optimal foraging theory (Juanes 1994).

1.4c *Gastric evacuation and daily ration*

Based on capture times and gut fullness values, a small number of bluefin tuna began feeding several hours before sunrise (i.e., caught on trolled baits). However, sample sizes were largest after dawn (~07:00) and remained high throughout the morning with concomitant increases in gut fullness values; a peak in gut fullness values occurred at 13:00 to 14:00 hours. The bulk of fish caught in late afternoon and early evening exhibited lower gut fullness values than that observed at peak. Only a few stomachs were collected during pre-dawn hours and were typically empty or contained food in the final stages of digestion, suggesting that the digestion occurred throughout the night with feeding not resuming until pre-dawn. The bluefin tuna fishery in North Carolina operates approximately 2 hours prior to sunrise through the remainder of daylight hours. Catch could match bluefin tuna feeding periods or could be an artifact of fishing times. I suggest the former given that there have been numerous attempts to catch bluefin tuna at night in North Carolina with little to no success (personal observation); this is further corroborated by observed diurnal feeding patterns in other tuna species such as southern bluefin (Talbot and Penrith 1963; Young et al. 1997), yellowfin, *Thunnus albacares*, (Reintjes and King 1953; Yamaguchi 1969; Grudinin 1989; Ortega-Garcia et al. 1992; Buckley and Miller 1994; Josse et al. 1998), blackfin, *Thunnus atlanticus*, (Josse et al. 1998), and skipjack, *Euthynnus pelamis* (Magnuson 1969). Additionally, increased foraging activity has been observed during transitional light periods in New England for Atlantic bluefin tuna and in Alaska for Pacific bluefin tuna (Hobson 1986; Lutcavage et al. 2000). Given the feeding behavior of other tuna species, the absence of tuna catch during nocturnal periods, and the state of digested prey observed in pre-dawn stomach samples, I conclude that the majority of bluefin tuna feeding in North Carolina occurs during daylight hours.

Scombrids are sight oriented predators (Magnuson 1963) and have one of the most well developed visual systems of any teleost species (Margulies 1997). However, as described above, a few bluefin tuna were caught during pre-dawn periods. This implies bluefin tuna have the capabilities to capture prey during times of low luminescence. However, their visual acuity and resolution are diminished during scotopic (i.e. nighttime) levels (Ellis Loew, Cornell University, personal communication), suggesting that nocturnal feeding may be a result of high prey concentrations.

To my knowledge, this is the first estimate of G_e for wild Atlantic bluefin tuna. Young et al. (1997) estimated an exponential G_e for southern bluefin tuna as the greatest decline in gut fullness from one time point to the next (i.e., over a one hour period). Given the way G_e was calculated in their study, their rate is not comparable to my estimate. The only other G_e for a tuna species that I am aware of is that of Olson and Boggs (1986); under laboratory conditions, the G_e of yellowfin tuna depended on the type, surface area, and digestibility of the prey. Their results showed that mackerel, which contained the highest lipid level of any examined prey, were the most digestion resistant and consequently took longer to evacuate. Since the diets of bluefin tuna in my study were dominated by Atlantic menhaden, my G_e estimates are representative of Atlantic menhaden prey only and should be used with caution if applied to bluefin tuna feeding on other prey, particularly those that might differ in digestibility (e.g., lipid levels).

In the present study, several key assumptions were made to estimate G_e. First, I assumed that feeding is negligible during night since no fish were landed between 19:00 and 04:00. If bluefin tuna do feed throughout the night, then my G_e and 24-h mean gut fullness values could potentially be biased low. I also had to assume that stomachs were not completely emptied several hours before my first pre-dawn samples were collected; if this were true then my estimates of G_e would be biased low (assuming a longer time to digest than actually true). As mentioned above, many of the samples collected during pre-dawn hours contained prey in the final stages of digestion (e.g., bones, scales, eye lenses, and the pyloric stomachs of Atlantic menhaden). This observation supports the fit of the gastric evacuation rate model.

Estimates of digestion times in pen-held and wild Atlantic bluefin tuna further corroborate our results. Butler and Mason (1978) used stomach content analysis on pen-held tuna and determined that it took 18-20 hours for giant (>200 kg) bluefin tuna to completely empty a full stomach (other than viscous liquid). Using acoustic telemetry, Stevens et al. (1978) identified gradual increases of stomach temperatures which lasted 14 to 20 hours following a feeding event in giant (> 200 kg) bluefin tuna held in captivity. Although unexplained at the time of Stevens et al.'s (1978) study, these temperature increases were later described by Carey et al. (1984). Carey et al. (1984) used acoustic transmitters in pen-held fish to measure stomach contractions and temperature increases after bluefin tuna feeding events and concluded it took 18 to 21 hours before liquefied food was moved out of the stomach and into the intestine and pyloric caeca. Andreas Walli and Barbara Block (Stanford University, personal communication) found that free-ranging, archival-tagged giant bluefin tuna reached a peak visceral temperature (mean ±SD) within 8.7 ± 3.65 hours after feeding with complete evacuation at approximately 32 hours after the initial feeding event. These studies suggest complete evacuation time is not reached in less than 18 to 20 hours supporting my result of a digestion time of ~19 hours (i.e., from peak gut fullness to gut fullness near zero).

Several studies have estimated the daily ration of giant bluefin tuna using various methodologies. Andreas Walli and Barbara Block (Stanford University, personal communication) estimated a daily ration of 1.1% ± 0.3 body mass per day based on heat incremented feeding of archival-tagged bluefin tuna tracked throughout the western Atlantic. Palomares and Pauly (1989) estimated a daily ration of 1.08% body mass per day for maximum-sized (e.g., L_{∞} = 332.0 cm) bluefin tuna using a multiple regression model based on growth, mortality, and maximum length. Aguado-Giménez and García-García (2005) found that large (mean weight = 237 kg) bluefin tuna held under fattening conditions consumed 1.56% body weight per day. Although my mean daily ration estimate (1.74%) is somewhat greater than previous studies, if anything, my estimate is potentially negatively biased for two reasons. First, I used the longest time between periods of peak and empty stomach fullness; increasing the time required for gastric emptying ultimately decreases the amount of food consumed on a daily basis. Second, stomach fullness values had the potential to be lowered due to regurgitation during hook and line capture and continued digestion after death. Although not measured, the uncertainty surrounding our value of daily ration likely encompasses the other estimates.

I assumed that minimal prey was lost due to regurgitation during capture or continued digestion after the fish had been killed. Regurgitation, which is often denoted by distended stomach rugae, has been found to be dependent on gear type and has been indicated as a significant source of variation of stomach fullness levels in several previous bluefin tuna studies (Dragovich 1970; Mason 1976; Holliday 1978; Chase 2002). Those authors found fewer instances of regurgitation for fish that were captured via rod and reel as opposed to other methods of capture such as purse seining. As previously mentioned, trolling with a rod and reel is the exclusive method of capture of bluefin tuna in North Carolina and only a few stomachs from the present study showed signs of regurgitation. Digestion is partly a chemical process and any food items that remain in the stomach after death could potentially be further dissolved by gastric enzymes, potentially lowering stomach fullness levels and yielding a decreased mean prey weight and daily ration estimate (Bromley 1994). Since stomach contents were removed from the stomach on the day of capture, I assumed continued digestion did not greatly affect the weight or identification of potential prey.

1.4d *Predation on Atlantic menhaden*

Currently, the Atlantic States Marine Fisheries Commission and the Northeast Fisheries Science Center consider bluefish, striped bass, weakfish, and human fishers as the dominant predators of Atlantic menhaden in their multispecies management models (ASMFC 2005a; NEFSC 2006); bluefin tuna are not considered an important predator of Atlantic menhaden because several studies along the U.S. east coast which were conducted during spring-fall have indicated only minor amounts of Atlantic menhaden in bluefin tuna diet (Holliday 1978; Chase 2002). Thus, the population-level consumption of Atlantic menhaden by bluefin tuna during winter appeared unimportant and remained unknown.

At their current (2002) population size, bluefin tuna consume a small amount of Atlantic menhaden relative to other Atlantic menhaden predators. However, ICCAT plans to rebuild the biomass of western Atlantic bluefin tuna to their 1975 levels by 2018; if successful, annual consumption of Atlantic menhaden by bluefin tuna will increase. The maximum estimated potential consumption of Atlantic menhaden imposed by a fully-rebuilt western bluefin tuna population may warrant the consideration of bluefin tuna as an important predator of Atlantic menhaden.

Similar to my result for bluefin tuna, individual estimates of coastwide consumption of Atlantic menhaden by bluefish (Buckel et al. 1999; NEFSC 2006), striped bass (Hartman 2003; Uphoff 2003; NEFSC 2006), and weakfish (NEFSC 2006) were lower than any of the annual coastwide estimates of Atlantic menhaden harvest during the last 24 years. However, with continued attempts at rebuilding populations of bluefish, striped bass, and weakfish stocks, predation mortality may become a more important component of the overall mortality rate of Atlantic menhaden. One important difference that should be taken into account if age-structured multispecies models are used is the differences in size/age of bluefin tuna prey; striped bass, bluefish, and weakfish prey on age 0-2 Atlantic menhaden (Uphoff 2003; Scharf et al. 2004; NEFSC 2006) while bluefin tuna were found to prey on age 2+ Atlantic menhaden.

There were several sources of uncertainty in my analysis of predatory demand. First, my study was dependent on the commercial fishery which is limited to only those fish greater than 185 cm (CFL). Although their capture is infrequent, smaller bluefin have been captured locally (Brian Efland, NC Sea Grant, personal communication). If smaller size-classes are consuming Atlantic menhaden, they should be considered in future impact estimates. Second, the stock assessment of western Atlantic bluefin tuna is uncertain given the debate regarding the influence of trans-Atlantic mixing; the most recent assessment assumed a mixing rate of 1-2% between the east and west bluefin tuna stocks. Estimates of mixing for large-mediums and giants might be as high as 83% (Rooker et al. 2006). Additional biomass from the eastern stock may have to be considered to establish the potential maximum impact by bluefin tuna on Atlantic menhaden once mixing rates have been refined. Last, the maximum days of residency that both Atlantic menhaden and bluefin tuna occupy North Carolina are unknown. In recent years, both species have been commercially captured in late November through the end of January which is the latest that the fishery has been opened. Bluefin tuna fitted with pop-up satellite tags have been documented in local waters through the end of May (Boustany 2006). However, adult Atlantic menhaden tend to disperse from North Carolina by the end of March after spawning (Quinlan et al. 1999). For this reason, the potential residency of cohabitation for both species was limited to a maximum of 120 days.

The Ecopath model allowed me to make comparisons between several predators of Atlantic menhaden in the SAB. The estimate of the biomass of Atlantic menhaden consumed by bluefin tuna from the Ecopath model supports the moderate levels of consumption estimated using the daily ration approach; the lower end of population percentage (5-20%) and moderate to longer residency (30-120 d) are required to provide similar consumption estimates to Ecopath (Table 10). This is an encouraging result given that these population percentages and residency times appear reasonable even though the Ecopath model presented here is preliminary.

The Ecopath model determined that the "Bluefish, Striped Bass, Weakfish" group are important Atlantic menhaden predators in the SAB. However, the large amount of Atlantic menhaden consumed by "Pelagic piscivores," such as king mackerel, cobia, tarpon, and red drum, indicate their potential importance as predators of Atlantic menhaden. As described above, it is only the former group that is currently considered as dominant predators of Atlantic menhaden on a coastwide basis. Several "Pelagic piscivores" consumed other members within their functional group (e.g., Atlantic needlefish consumption by king mackerel, Spanish mackerel, and barracuda). Ecopath considers these interactions to be "cannibalistic" and allows a maximum cannibalism value of 20%; therefore, the diet parameters of this group were reduced to meet this criterion. If diet inputs exactly matched those given by the literature, the overall biomass of "Pelagic piscivores" would be reduced, yielding a smaller impact on Atlantic menhaden. Despite having obvious assumptions, the findings presented from my Ecopath model warrant expanded research on the consumption of Atlantic menhaden by "Pelagic piscivores" in any future multispecies models. It is also hoped that results from my model can be linked with a Mid-Atlantic Bight model to assist agencies charged with taking an ecosystem-based approach to management; for example, such a coastwide model could be used to address questions about tradeoffs (e.g., reduce prey harvest to allow for more predators) when both predator and prey are harvested.

In summary, this study has filled a gap in the knowledge of the natural history of bluefin tuna and determined their potential impact on Atlantic menhaden. During the winter, North Carolina serves as a spawning ground for several abundant forage species, including Atlantic menhaden. The diets of large-medium and giant bluefin tuna from the present study were dominated by Atlantic menhaden over multiple seasons (Kade 2000; this study); thus, the migrations to-and residence times in North Carolina will likely depend on the abundance of Atlantic menhaden. Intra-seasonal shifts in bluefin tuna diets do occur; however, it is uncertain whether dietary changes are a result of the relative abundances of Atlantic menhaden compared to other prey. Quantitative data of prey type availability are lacking and should be considered in future studies.

An understanding of predator-prey interactions is vital for ecosystem-based assessment models. At current population levels, predation on Atlantic menhaden by bluefin tuna appeared to be minimal when compared with other known predators including the commercial harvest. If, however, management plans for bluefin tuna in the western Atlantic succeed and the population recovers, the predatory demand expressed by bluefin tuna should potentially be considered in future multispecies models where Atlantic menhaden are a focal prey as well as the management plan for the Atlantic menhaden fishery.

Table 1. Atlantic bluefin tuna size-class information from NMFS (2005).
http://www.nmfspermits.com/other/BFTsizeclass.doc.

Size Class	**Curved Fork Length**		**Pectoral Fin Curved Fork Length**		**Approx. Round Weight**	
	inches	cm	inches	cm	lbs.	kg.
Young-school	<27"	<68.6	<20"	<50.8	<14	<6.35
School	27 - <47"	68.6 - <119.4	20 - <35"	50.8 - 88.9	14 - <66	6.35 - <29.94
Large-school	47 - <59"	119.4 - <149.9	35 - <44"	88.9 - 111.8	66 - <135	29.94 - <61.24
Small-medium	59 - <73"	149.9 - <185.4	44 - <54"	111.8 - 137.2	135 - <235	61.24 - <106.60
Large-medium	73 - <81"	185.4 - <205.7	54 - <60"	137.2 - 152.4	235 - < 310	106.60 - <140.62
Giant	81" or >	205.7 or >	60" or >	152.4 or >	310 or >	140.62 or >

Table 2. Summary of number of commercially-caught bluefin tuna stomachs collected during each year off Cape Lookout, NC, December-January 2002-03, 2003-04, 2004-05, and 2005-06.

	2002-03	2003-04	2004-05	2005-06	All years combined
Large-medium (185-206 cm)					
with prey		13	64	23	100
Empty		1	16	7	24
Giant (>206 cm)					
with prey	1	14	100	137	252
Empty		13	39	20	72
Total stomachs analyzed	1	41	219	187	448
Number (%) with prey	1 (100)	27(65.9)	164 (74.9)	160 (85.6)	352 (78.6)
Number (%) empty	0 (0)	14(34.1)	55 (25.1)	27 (14.4)	96 (21.4)
Mean length of tuna (cm)	251.46	210.25	212.70	221.34	216.10
SE		1.70	1.11	1.23	0.80
Mean weight of tuna (kg)	264.27	140.13	148.84	168.62	156.50
SE		3.46	2.71	3.36	2.00

Table 3. Stomach contents of Atlantic bluefin tuna collected off Cape Lookout, North Carolina during 2002-03, 2003-04, 2004-05, and 2005-06. Prey species are combined for all years and both size classes (large-medium and giant). Diet by frequency of occurrence, total weight (g), percent frequency of occurrence (%O), and percent prey weight (%W).

Prey Item	Common name	Frequency of occurrence	Total weight (g)	%O	%W
Brevoortia tyrannus	Atlantic menhaden	299	439364.90	84.94	95.53
Strongylura marina	Atlantic needlefish	19	11356.75	5.40	2.47
Loligo pealeii	Longfin squid	6	1284.31	1.70	0.28
Teleostei	Unidentified fish	50	1164.91	14.2	0.25
Cynoscion regalis	Weakfish	2	1123.18	0.57	0.24
Cephalopoda	Squid	14	913.07	3.98	0.20
Portunus gibbesii	Iridescent shore crab	24	858.64	6.82	0.19
Mugil cephalus	Striped mullet	1	573.39	0.28	0.12
Mustelus canis	Smooth dogfish	1	383.11	0.28	0.08
Archosargus sp.	Sparid	4	377.43	1.14	0.08
Portunus spinimanus	Blotched swimming crab	11	328.27	3.13	0.07
Ovalipes sp.	Lady crab	11	317.03	3.13	0.07
Menticirrhus littoralis	Gulf kingfish	1	238.04	0.28	0.05
Portunus sp.	Swimming crab	12	198.90	3.41	0.04
Portunidae	Unid. swimming crab	8	187.87	2.27	0.04
Crustacea	Crab	16	183.70	4.55	0.04
Pomatomus saltatrix	Bluefish	2	164.33	0.57	0.04
Chilomycterus sp.	Burrfish	2	160.72	0.57	0.03
Diapterus auratus	Irish pompano	1	134.59	0.28	0.03
Lagodon rhomboides	Pinfish	1	120.00	0.28	0.03
Orthopristis chrysoptera	Pigfish	3	104.13	0.85	0.02
Micropognias sp.	Croaker	1	98.12	0.28	0.02
Sphyraena borealis	Northern sennet	1	86.95	0.28	0.02
Bivalvia	Clam	1	62.57	0.28	0.01
Protista	Algae	5	45.81	1.42	0.01
Triglidae sp.	Sea robin	1	39.25	0.28	0.01
Anchoa hepsetus	Striped anchovy	2	15.84	0.57	<0.01
Ammodytes sp.	Sand lance	2	15.59	0.57	<0.01
Callinectes sapidus	Blue crab	1	13.13	0.28	<0.01
Engraulidae sp.	Anchovy	1	11.82	0.28	<0.01
Sygnathus louisianae	Chain pipefish	1	10.77	0.28	<0.01
Sygnathus sp.	Pipefish	1	1.73	0.28	<0.01
Total stomachs sampled		448			
Empty stomachs (%)		96 (21.43)			
Stomachs with prey (%)		352 (78.57)			

Table 4. Diet composition of large-medium Atlantic bluefin tuna collected off Cape Lookout, North Carolina throughout the 2004-05 season (December 1-14, December 15-31, and January 1-31). Diet by percent frequency of occurrence (%O) and percent prey weight (%W). Absent entries indicate prey item not found in diet.

	Dec. 1-14, 2004		Dec. 15-31, 2004		Jan. 1-31, 2005		Pooled data	
Prey item	%O	%W	%O	%W	%O	%W	%O	%W
Chordata								
Osteichthyes								
Clupeidae								
Brevoortia tyrannus	95.00	98.13	97.50	99.80	100.00	95.98	96.88	98.97
Mugilidae								
Mugil cephalus	5.00	1.87					1.56	0.69
Pomatomidae								
Pomatomus saltatrix					25.00	3.06	1.56	0.17
Unidentified fish remains	5.00	<0.01	2.50	<0.01	25.00	0.83	4.69	0.05
Crustacea								
Malacostraca								
Portunidae								
Portunus gibbesii			2.50	0.03			1.56	0.02
Portunus spinimanus			2.50	0.09			1.56	0.05
Unidentified crab					25.00	0.13	1.56	0.01
Mollusca								
Cephalopoda								
Loliginidae								
Loligo pealeii			2.50	0.07			1.56	0.04
Total stomachs sampled		24		46		10		80
Empty stomachs (%)		4 (16.7)		6 (13.0)		6 (60.0)		16 (20.0)
Stomachs with prey (%)		20 (83.3)		40 (87.0)		4 (40.0)		64 (80.0)

Table 5. Diet composition of large-medium Atlantic bluefin tuna collected off Cape Lookout, North Carolina throughout the 2005-06 season (December 1-14, December 15-31, and January 1-31). Diet by percent frequency of occurrence (%O) and percent prey weight (%W). Absent entries indicate prey item not found in diet.

	Dec. 1-14, 2005		Dec. 15-31, 2005		Jan. 1-31, 2006		Pooled data	
Prey item	%O	%W	%O	%W	%O	%W	%O	%W
Chordata								
Osteichthyes								
Belonidae								
Strongylura marina	12.50	0.75					4.35	0.13
Clupeidae								
Brevoortia tyrannus	87.50	95.68	70.00	97.70	100.00	93.79	82.61	96.43
Sciaenidae								
Menticirrhus littoralis					20.00	6.21	4.35	1.45
Unidentified fish remains	25.00	1.82	10.00	0.01			13.04	0.33
Crustacea								
Malacostraca								
Portunidae								
Ovalipes sp.			10.00	0.32			4.35	0.19
Portunus spinimanus	12.50	1.54					4.35	0.28
Portunus sp.			10.00	0.07			4.35	0.04
Unidentified crab	12.50	0.21					4.35	0.04
Mollusca								
Cephalopoda								
Unidentified squid			20.00	1.90			8.70	1.11
Total stomachs sampled		10		15		5		30
Empty stomachs (%)		2 (20.0)		5 (33.3)		0 (0.0)		7 (23.3)
Stomachs with prey (%)		8 (80.0)		10 (66.7)		5 (100.0)		23 (76.7)

Table 6. Diet composition of giant Atlantic bluefin tuna collected off Cape Lookout, North Carolina throughout the 2004-05 season (December 1-14, December 15-31, and January 1-31). Diet by percent frequency of occurrence (%O) and percent prey weight (%W). Absent entries indicate prey item not found in diet.

	Dec. 1-14, 2004		Dec. 15-31, 2004		Jan. 1-31, 2005		Pooled data	
Prey item	%O	%W	%O	%W	%O	%W	%O	%W
Chordata								
Osteichthyes								
Ammodytidae								
Ammodytes sp.					3.70	0.08	1.00	0.01
Belonidae								
Strongylura marina	6.25	0.23					1.00	0.01
Clupeidae								
Brevoortia tyrannus	81.25	98.48	87.72	99.13	77.78	98.34	84.00	98.96
Engraulidae								
Anchoa hepsetus			1.75	0.01			1.00	0.01
Sparidae								
Archosargus sp.					3.70	0.61	1.00	0.11
Sygnathidae								
Sygnathus louisianae					3.70	0.06	1.00	0.01
Unidentified fish remains	18.75	0.28	10.53	0.02	18.52	0.35	14.00	0.09
Crustacea								
Malacostraca								
Portunidae								
Ovalipes sp.			5.26	0.21			3.00	0.16
Portunus gibbesii			10.53	0.16	7.41	0.15	8.00	0.15
Portunus spinimanus	6.25	0.65	1.75	0.03	7.41	0.20	4.00	0.09
Portunus sp.	6.25	0.35					1.00	0.02
Portunidae			8.77	0.21	3.70	0.04	6.00	0.17
Unidentified crab			8.77	0.10	3.70	0.02	6.00	0.08
Mollusca								
Bivalvia								
Unidentified clam			1.75	0.08			1.00	0.06

Table 6. Continued

Prey item	Dec. 1-14, 2004		Dec. 15-31, 2004		Jan. 1-31, 2005		Pooled data	
	%O	%W	%O	%W	%O	%W	%O	%W
Cephalopoda								
Loliginidae								
Loligo pealeii			1.75	0.05	3.70	0.15	2.00	0.07
Protista								
Unidentified algae	6.25	0.01					1.00	<0.01
Total stomachs sampled	25		70		44		139	
Empty stomachs (%)	9 (36.0)		13 (18.6)		17 (38.6)		39 (28.1)	
Stomachs with prey (%)	16 (64.0)		57 (81.4)		27 (61.4)		100 (71.9)	

Table 7. Diet composition of giant Atlantic bluefin tuna collected off Cape Lookout, North Carolina throughout the 2005-06 season (December 1-14, December 15-31, and January 1-31). Diet by percent frequency of occurrence (%O) and percent prey weight (%W). Absent entries indicate prey item not found in diet.

	Dec. 1-14, 2005		Dec. 15-31, 2005		Jan. 1-31, 2006		Pooled data	
Prey item	%O	%W	%O	%W	%O	%W	%O	%W
Chordata								
Osteichthyes								
Belonidae								
Strongylura marina	58.33	56.77	2.30	0.04	3.85	0.05	12.41	4.61
Clupeidae								
Brevoortia tyrannus	58.33	37.97	88.51	97.87	88.46	97.19	83.21	92.97
Diodontidae								
Chilomycterus sp.	4.17	0.76			3.85	0.04	1.46	0.07
Engraulidae								
Anchoa hepsetus			1.15	<0.01			0.73	<0.01
Haemulidae								
Orthopristis chrysoptera	12.50	0.53					2.19	0.04
Pomatomidae								
Pomatomus saltatrix			1.15	0.01			0.73	0.01
Sciaenidae								
Cynoscion regalis			2.30	0.56			1.46	0.46
Micropognias sp.	4.17	0.50					0.73	0.04
Sparidae								
Archosargus sp.	4.17	0.11	2.30	0.12			2.19	0.11
Lagodon rhomboides					3.85	0.51	0.73	0.05
Sphyraenidae								
Sphyraena borealis			1.15	0.04			0.73	0.04
Sygnathidae								
Sygnathus sp.	4.17	0.01					0.73	<0.01
Unidentified fish remains	25.00	0.38	12.64	0.36	15.38	0.12	15.33	0.34
Chondrichthyes								
Triakidae								
Mustelus canis			1.15	0.19			0.73	0.16

Table 7. Continued

Prey item	Dec. 1-14, 2005 %O	Dec. 1-14, 2005 %W	Dec. 15-31, 2005 %O	Dec. 15-31, 2005 %W	Jan. 1-31, 2006 %O	Jan. 1-31, 2006 %W	Pooled data %O	Pooled data %W
Crustacea								
Malacostraca								
Portunidae								
Ovalipes sp.	8.33	0.05			11.54	0.34	3.65	0.04
Portunus gibbesii	12.50	0.41	3.45	0.02	15.38	1.04	7.30	0.15
Portunus spinimanus	12.50	0.41			3.85	0.15	2.92	0.05
Portunus sp.	16.67	0.13	2.30	0.01	15.38	0.53	7.30	0.07
Portunidae	4.17	0.02					0.73	<0.01
Unidentified crab			4.60	0.02	3.85	<0.01	3.65	0.02
Mollusca								
Cephalopoda								
Loliginidae								
Loligo pealeii	4.17	0.50	2.30	0.53			2.19	0.48
Unidentified squid	25.00	1.47	4.60	0.21	3.85	0.03	8.03	0.30
Protista								
Unidentified algae			1.15	0.01			0.73	0.01
Total stomachs sampled	25		99		33		157	
Empty stomachs (%)	2 (8.0)		11 (11.1)		7 (21.2)		20 (12.7)	
Stomachs with prey (%)	23 (92.0)		88 (88.9)		26 (78.8)		137 (87.3)	

Table 8. Diet composition of Atlantic bluefin tuna collected off Cape Lookout, North Carolina during the 2002-03, 2003-04, 2004-05, and 2005-06 seasons. Size-class data have been pooled across years (2003-06). Diet by percent frequency of occurrence (%O) and percent prey weight (%W). Absent entries indicate prey item not found in diet.

	Large-mediums		Giants	
Prey Item	%O	%W	%O	%W
Chordata				
Osteichthyes				
Ammodytidae				
Ammodytes sp.			0.79	<0.01
Belonidae				
Strongylura marina	1.00	0.02	7.14	3.16
Clupeidae				
Brevoortia tyrannus	91.00	98.42	82.54	94.71
Diodontidae				
Chilomycterus sp.			0.79	0.04
Engraulidae				
Anchoa hepsetus			0.79	<0.01
Engraulidae sp.			0.40	<0.01
Gerreidae				
Diapterus auratus			0.40	0.04
Haemulidae				
Orthopristis chrysoptera			1.19	0.03
Mugilidae				
Mugil cephalus	1.00	0.57		
Pomatomidae				
Pomatomus saltatrix	1.00	0.14	0.40	0.01
Sciaenidae				
Cynoscion regalis			0.79	0.31
Menticirrhus littoralis	1.00	0.24		
Micropognias sp.			0.40	0.03
Sparidae				
Archosargus sp.			1.59	0.11
Lagodon rhomboides			0.40	0.03
Sphyraenidae				
Sphyraena borealis			0.40	0.02
Sygnathidae				
Sygnathus louisianae			0.40	<0.01
Sygnathus sp.			0.40	<0.01
Triglidae				
Triglidae sp.			0.40	0.01
Unidentified fish remains	10.00	0.19	15.87	0.27
Chondrichthyes				
Triakidae				
Mustelus canis			0.40	0.11

Table 8. Continued.

	Large-mediums		Giants	
Prey Item	%O	%W	%O	%W
Crustacea				
Malacostraca				
Portunidae				
Callinectes sapidus			0.40	<0.01
Ovalipes sp.	1.00	0.03	3.97	0.08
Portunus gibbesii	1.00	0.01	9.13	0.24
Portunus spinimanus	2.00	0.09	3.57	0.07
Portunus sp.	1.00	0.01	4.37	0.05
Portunidae			3.17	0.05
Unidentified crab	3.00	0.04	5.16	0.04
Mollusca				
Bivalvia				
Unidentified clam			0.40	0.02
Cephalopoda				
Loliginidae				
Loligo pealeii	1.00	0.03	1.98	0.35
Unidentified squid	3.00	0.18	4.37	0.20
Protista				
Unidentified algae	2.00	0.03	1.19	0.01
Total stomachs sampled		124		324
Empty stomachs (%)		24 (19.4)		72 (22.2)
Stomachs with prey (%)		100 (80.6)		252 (77.8)

Table 9. Correspondence analysis of Atlantic bluefin tuna collected off Cape Lookout, NC during the 2004-05 and 2005-06 seasons examined for (A) intra-seasonal and (B) inter-annual variation; diet data from all years combined (2003-2006) were used to examine (C) size-class variation. Intra-seasonal time periods (D1 = December 1-14; D2 = December 15-31; and J = January 1-31) were compared for each size-class (large-medium and giant) from both years (2004-05 and 2005-06). Total number of non-empty stomachs analyzed for each comparison is given in parentheses. Values in bold indicate no significant difference at α = 0.05.

Groups compared	%O p-value	%W p-value
(A) Intra-seasonal variation		
Large-medium		
D1 / D2 / J 2004-05 (64)	<0.01	**0.778**
D1 / D2 / J 2005-06 (23)	<0.01	0.010
Giant		
D1 / D2 / J 2004-05 (100)	<0.01	**0.998**
D1 / D2 / J 2005-06 (137)	<0.01	<0.01
(B) Inter-annual variation		
Large-medium		
2004-05 / 2005-06 (87)	<0.01	**0.798**
Giant		
2004-05 / 2005-06 (237)	<0.01	**0.518**
(C) Size-class variation		
Large-medium / Giant (352)	<0.01	**0.690**

Table 10. Range of potential consumption estimates (mt) at various levels of the bluefin tuna population. Days of residency were estimated from the duration of co-occurrence of Atlantic menhaden and bluefin tuna in North Carolina waters during the winter. North Carolina landings were based on mean annual catch from December 2003- January 2005. Bluefin tuna population estimates were based on recent (2002) abundance-at-age data (Restropo et al. 2003); the maximum population of age 6+ bluefin tuna was estimated as 104,535 individuals.

		Days of Residency						
		30	45	60	75	90	105	120
	NC Harvest	37.84	56.76	75.68	94.60	113.52	132.44	151.36
% Population	5%	408.22	612.33	816.44	1020.55	1224.66	1428.77	1632.88
	10%	816.44	1224.66	1632.88	2041.10	2449.32	2857.54	3265.76
	25%	2041.10	3061.65	4082.19	5102.74	6123.29	7143.84	8164.39
	50%	4082.19	6123.29	8164.39	10205.49	12246.58	14287.68	16328.78
	100%	8164.39	12246.58	16328.78	20410.97	24493.17	28575.36	32657.56

Table 11. Parameter estimates of Ecopath trophic groups for the South Atlantic Bight ecosystem. Trophic level, Biomass ($t \cdot m^{-2}$), production to biomass (*P/B* $year^{-1}$), consumption to biomass (*Q/B* $year^{-1}$), and Ecotrophic Efficiency are presented. Values in bold have been estimated by balancing with Ecopath software.

Group	Trophic level	Biomass ($t \cdot km^{-2}$)	*P/B* ($year^{-1}$)	*Q/B* ($year^{-1}$)	Ecotrophic efficiency
Bottlenose dolphin	**4.35**	0.025	0.100	41.700	**0.000**
Large coastal sharks	**4.27**	0.088	0.381	2.087	**0.595**
Small tuna species	**4.14**	**0.081**	0.947	15.402	0.801
Marine birds	**3.88**	0.001	0.100	80.000	**0.000**
Bluefish, Striped Bass, Weakfish	**3.64**	1.238	0.489	5.131	**0.838**
Pelagic piscivores	**3.58**	**1.151**	0.524	10.833	0.883
Cephalopods	**3.45**	**0.082**	2.673	36.500	0.967
Bluefin tuna	**3.29**	**0.003**	0.430	6.356	0.801
Demersal piscivores	**3.27**	**1.995**	0.382	8.948	0.950
Demersal elasmobranchs	**3.25**	0.359	0.312	5.597	**0.545**
Pelagic forage	**3.22**	**7.266**	3.440	21.295	0.984
Demersal forage	**3.21**	**13.276**	0.623	16.406	0.951
Zooplankton	**2.33**	**312.642**	13.000	43.300	0.950
Atlantic menhaden	**2.24**	6.263	2.174	16.425	**0.794**
Invertebrates	**2.11**	**465.372**	0.930	11.056	0.833
Phytoplankton	**1.00**	**38.502**	332.670	-	0.650
Macroalgae+Sea grass	**1.00**	241.450	10.078	-	**0.244**
Detritus	**1.00**	518.000	-	-	**0.911**

Table 12. Consumption estimates ($t \cdot km^{2} \cdot yr^{-1}$) for functional groups in the South Atlantic Bight Ecopath model.

		Predator														
Prey	Functional group	1	2	3	4	5	6	7	8	10	11	13	14	15	16	17
1	Bluefin tuna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Large coastal sharks	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Demersal elasmobranchs	-	0.057	-	-	-	0.001	-	-	-	-	-	-	-	-	-
4	Bluefish, Striped Bass, Weakfish	-	0.003	0.067	-	0.388	0.001	-	-	-	-	-	-	-	0.002	-
5	Bottlenose dolphin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Pelagic piscivores	-	-	-	-	-	0.118	-	-	-	-	-	-	-	0.279	-
7	Pelagic forage	-	-	-	0.416	-	3.799	-	-	-	-	0.040	18.289	0.448	0.705	0.856
8	Atlantic menhaden	0.018	0.009	-	3.613	0.043	7.031	-	-	-	-	0.024	-	-	0.002	-
9	Phytoplankton	-	-	-	-	-	-	-	36.521	6768.709	1520.343	-	-	-	-	-
10	Zooplankton	-	-	-	-	-	-	80.268	18.312	3384.355	374.577	-	3.592	0.031	-	-
11	Invertebrates	-	0.002	1.677	0.100	-	0.779	72.071	-	-	77.288	0.004	190.942	15.223	0.182	2.105
12	Macroalgae + Sea grass	-	-	-	-	-	0.088	2.011	0.514	-	589.408	-	2.830	-	-	-
13	Marine birds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Demersal forage	-	0.080	0.192	1.689	0.528	0.584	0.377	-	-	-	0.008	2.153	2.142	0.014	-
15	Demersal piscivores	-	0.014	0.011	0.534	-	0.048	-	-	-	-	-	-	-	0.041	-
16	Small tuna species	-	0.014	-	-	-	-	-	-	-	-	-	-	-	-	-
17	Cephalopods	-	-	0.012	-	0.097	0.017	-	-	-	-	0.004	-	0.005	0.024	0.046
18	Detritus	-	-	0.053	-	-	-	-	47.528	3384.355	2583.481	-	-	-	-	-
	Sum	0.018	0.183	2.012	6.352	1.056	12.466	154.727	102.875	13537.419	5145.097	0.080	217.806	17.849	1.249	3.007

Table 13. Consumption of Atlantic menhaden by trophic groups in the South Atlantic Bight Ecopath model.

	Consumption of Atlantic menhaden		
Trophic group	($t \cdot km^{-2} \cdot yr^{-1}$)	($t \cdot yr^{-1}$)	(% Total consumption)
Pelagic piscivores	7.031	637008.00	65.47
Bluefish, Striped Bass, Weakfish	3.613	327337.80	33.64
Bottlenose dolphin	0.043	3895.80	0.40
Marine birds	0.024	2174.40	0.22
Bluefin tuna	0.018	1630.80	0.17
Large coastal sharks	0.009	815.40	0.08
Small tuna species	0.002	181.20	0.02
Total	10.740	973044.00	

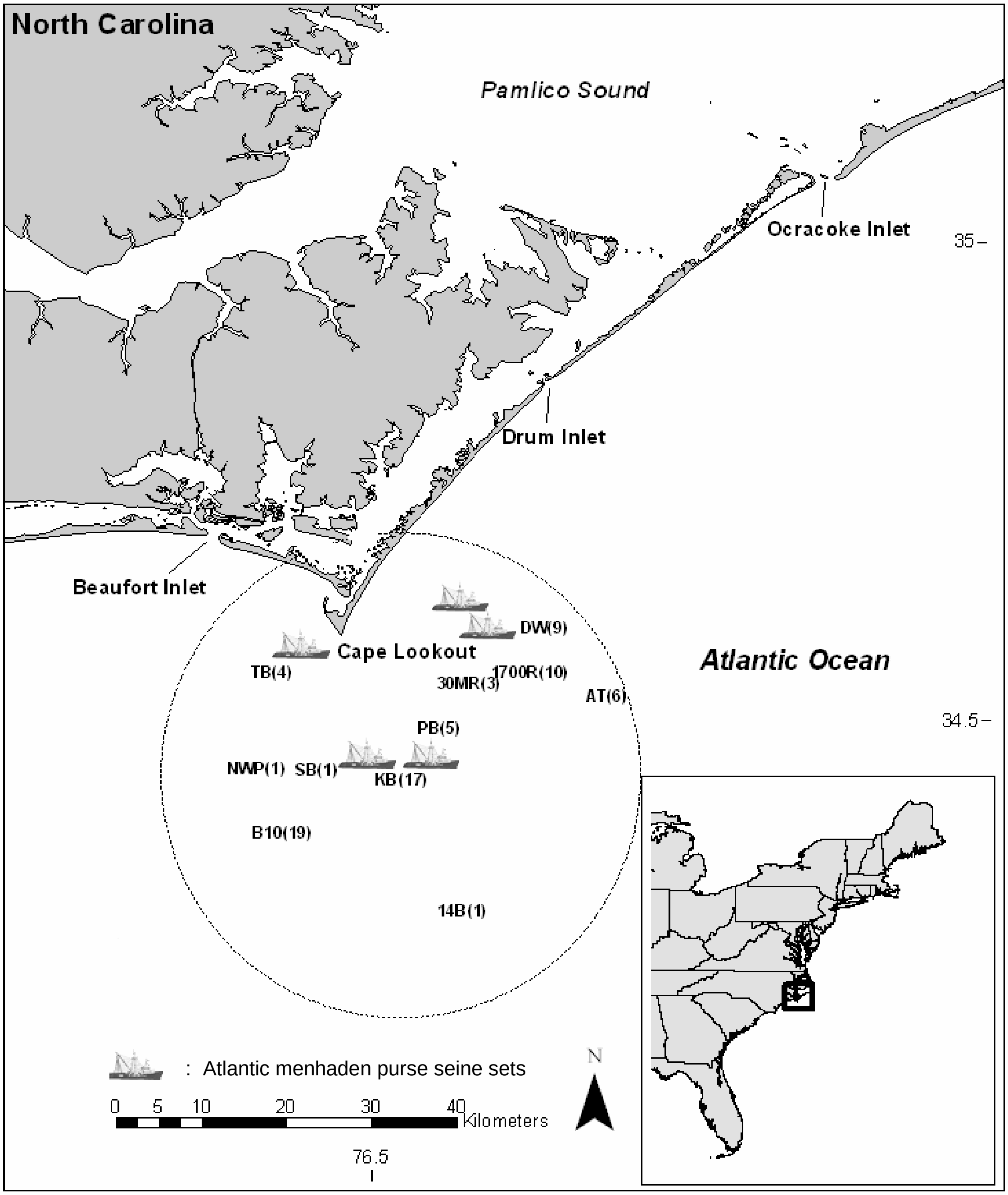


Figure 1. Map of the fishing grounds off Cape Lookout, NC used as a study area. Tuna sample sizes and locations of tuna capture for prey selectivity test are given in parenthesis. Locations are: TB = Trawler buoy; DW = D-Wreck; 30MR = 30-Minute rock; 1700R = 1700 rock; AT = Atlas tanker; PB = Portland buoy; NWP = Northwest places; SB = Sea buoy; KB = Knuckle buoy; B10 = Big ten; and 14B = Fourteen buoy. The large circle recognizes a 28-Km radius from the Knuckle buoy where most bluefin tuna and all purse seine sets were collected.

BLUEFIN TUNA STOMACHS WANTED

All the information below must be __COMPLETELY__ filled out by the fishermen to receive reimbursement. If the donations/payment box is not checked, stomachs will be considered a donation and no reimbursement will be given. North Carolina State University, Center for Marine Science and Technology (CMAST) is studying bluefin tuna feeding in North Carolina waters. We request that you keep bluefin stomachs from legally harvested fish during the 2005-06 winter commercial and recreational fishing seasons. Tear off the waterproof tag and put the tag and stomach in a plastic bag in the cooler (**Stomach contents must remain in the stomach**, and put no other guts in bag). Leave this paper form in the manila envelope on top of cooler. N. C. State University will mail a check for $25 for each stomach received. Call 252-222-6342 or 252-222-6348 if you have questions. Thank you for cooperating.

I would like to: ☐ Donate my tuna stomach

☐ receive $25 payment for my tuna stomach

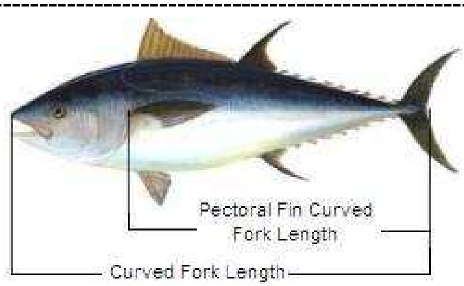
Office use only
Check #____________
Date Issued__________

Fisherman Information (to whom reimbursement is sent)
Name ____
Signature (if payment is requested) ____
Street ____
City, State, Zip ____
Phone ____

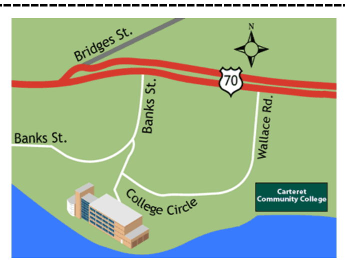
Bluefin Information
Date of Capture ________________________________
Time of Hook-up ______________________________
Time fish was boated ____________________________

Location of Capture (Description) __________________________________ **AND/OR….**
Location of Capture (Lat Degrees or Loran)__________________________
Location of Capture (Long Degrees or Loran)_________________________

Pectoral fin curved fork length "PFCFL" (inches) _________________________ **AND**
Curved fork length "CFL" (inches) _____________________________________**AND**
Fish dressed weight (pounds with head off) _____________________________



Required length measurements



Map to CMAST building

Figure 2. Stomach request data sheet.

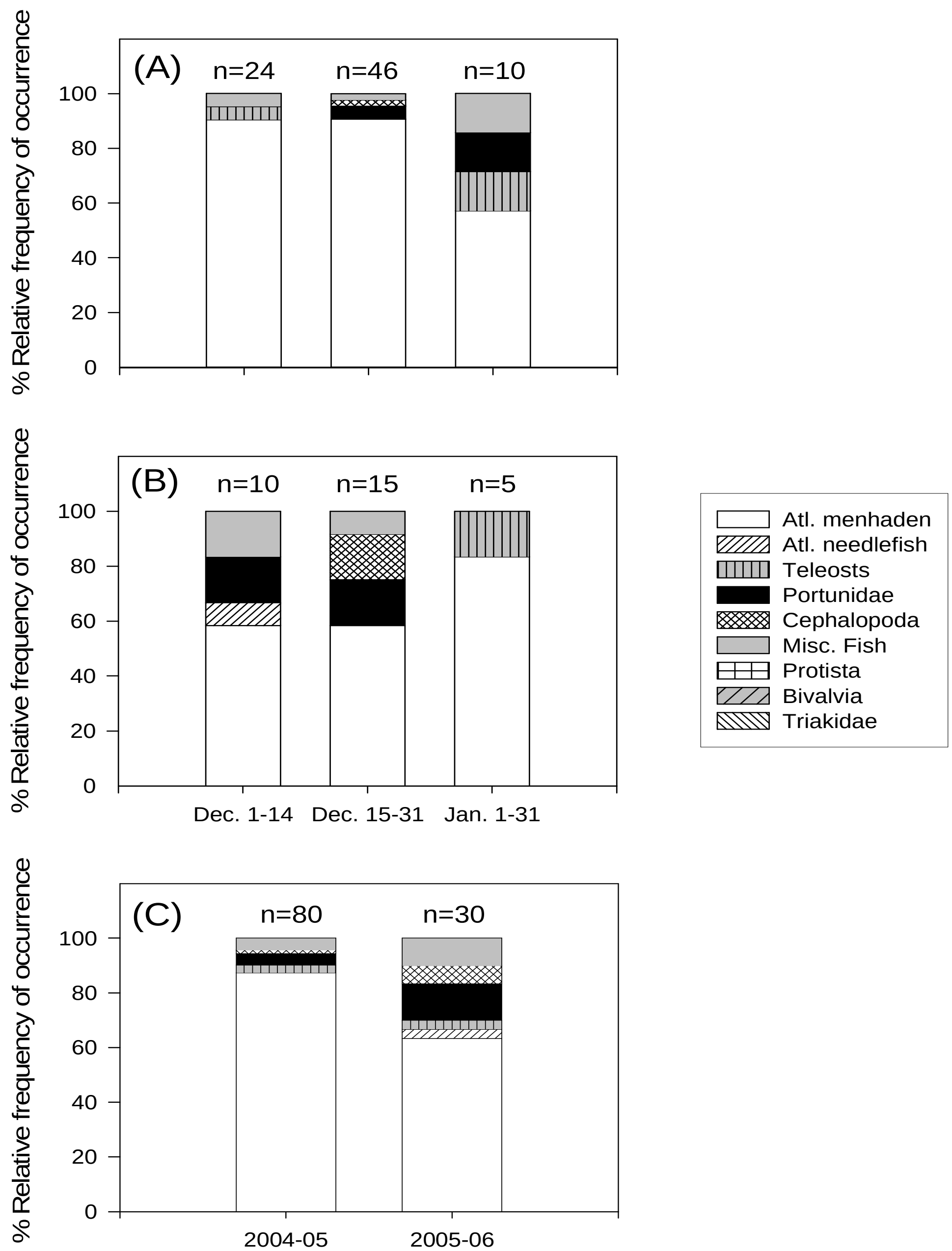


Figure 3. Relative percent frequency of occurrence composition from stomach contents of large-medium sized Atlantic bluefin tuna caught off Cape Lookout, North Carolina during December-January (A) 2004-05, (B) 2005-06, and (C) pooled years. Frequency of occurrence data are normalized to 100%.

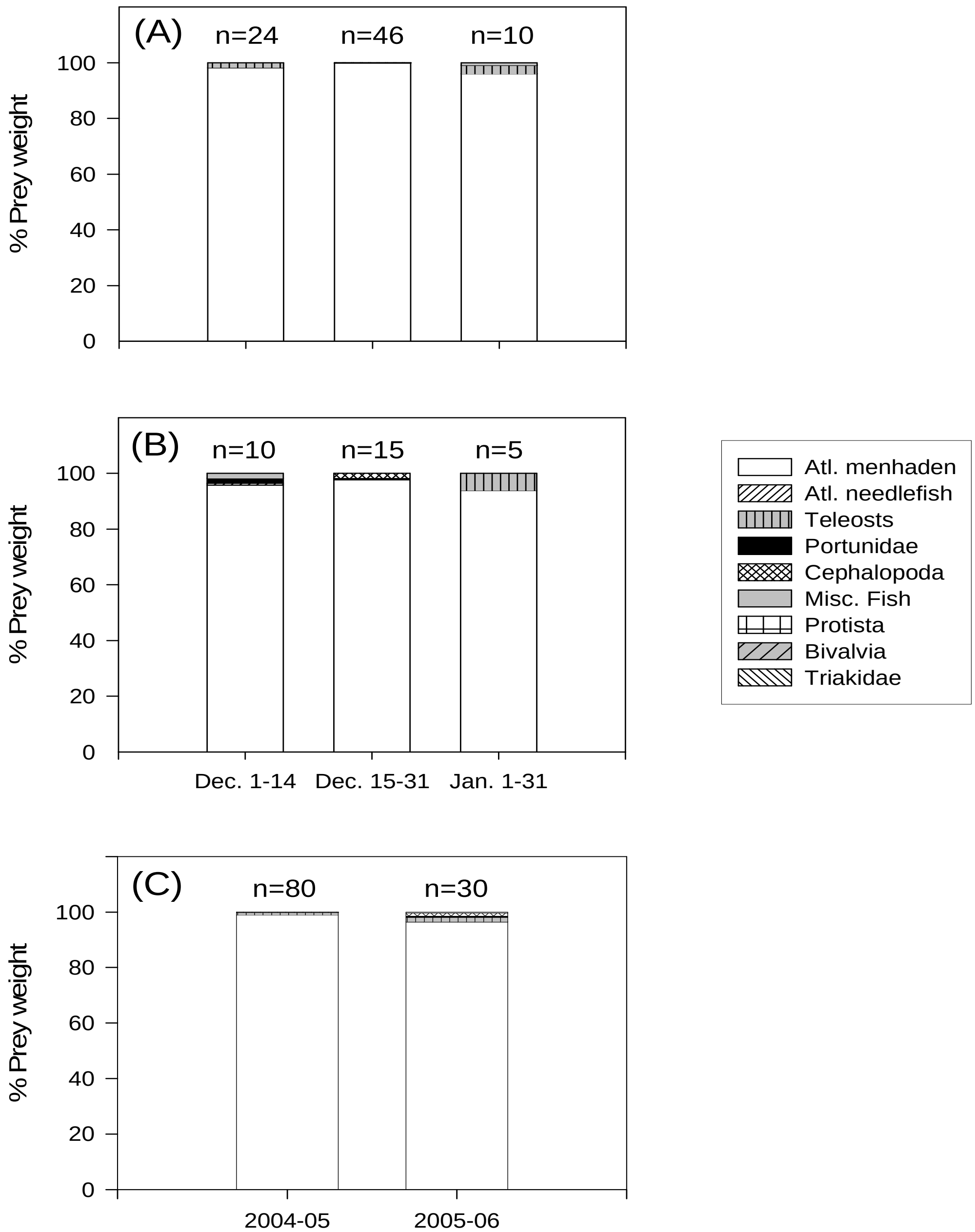


Figure 4. Percent prey weight composition from stomach contents of large-medium sized Atlantic bluefin tuna caught off Cape Lookout, North Carolina during December-January (A) 2004-05, (B) 2005-06, and (C) pooled years.

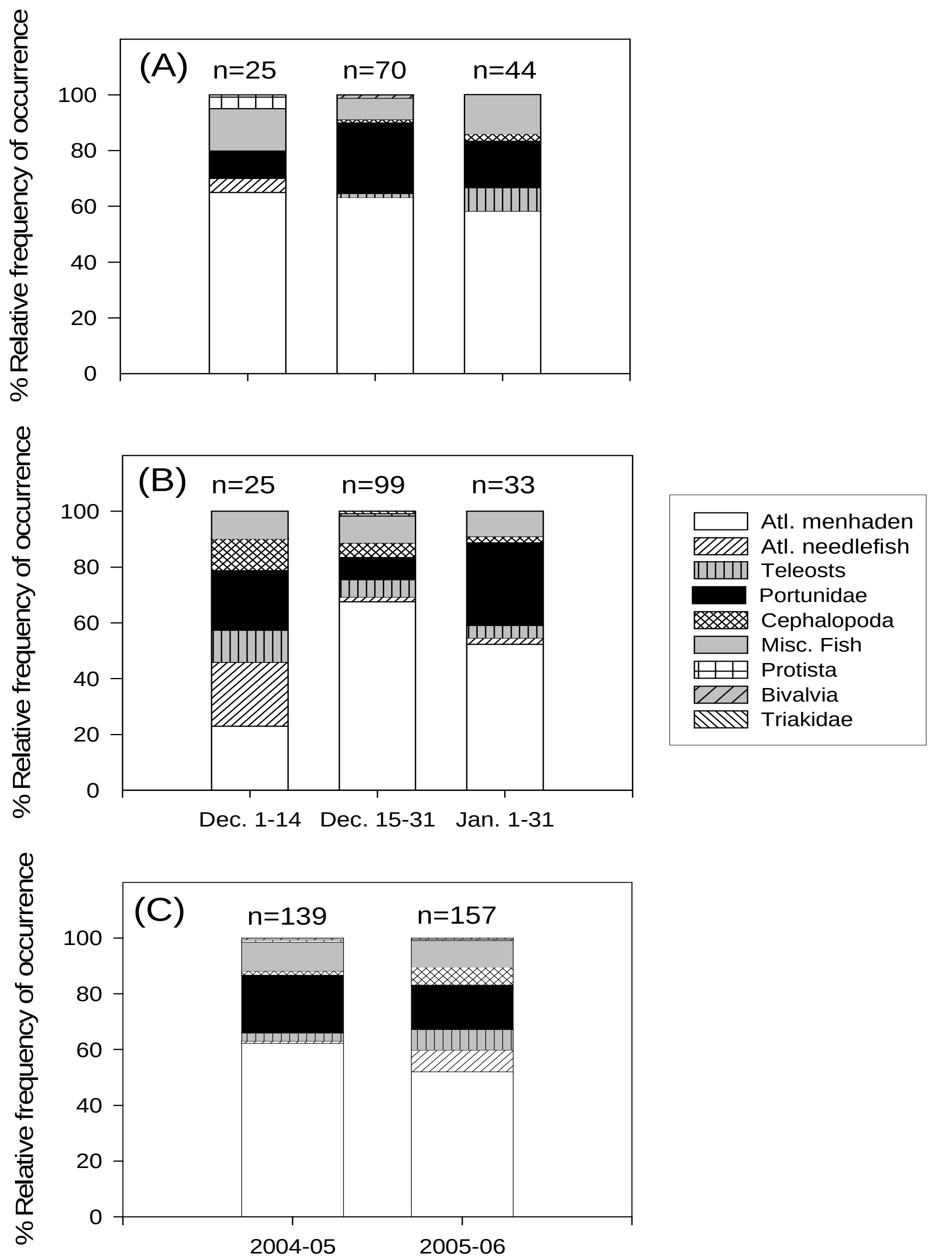


Figure 5. Relative percent frequency of occurrence composition from stomach contents of giant sized Atlantic bluefin tuna caught off Cape Lookout, North Carolina during December-January (A) 2004-05, (B) 2005-06, and (C) pooled years. Frequency of occurrence data are normalized to 100%.

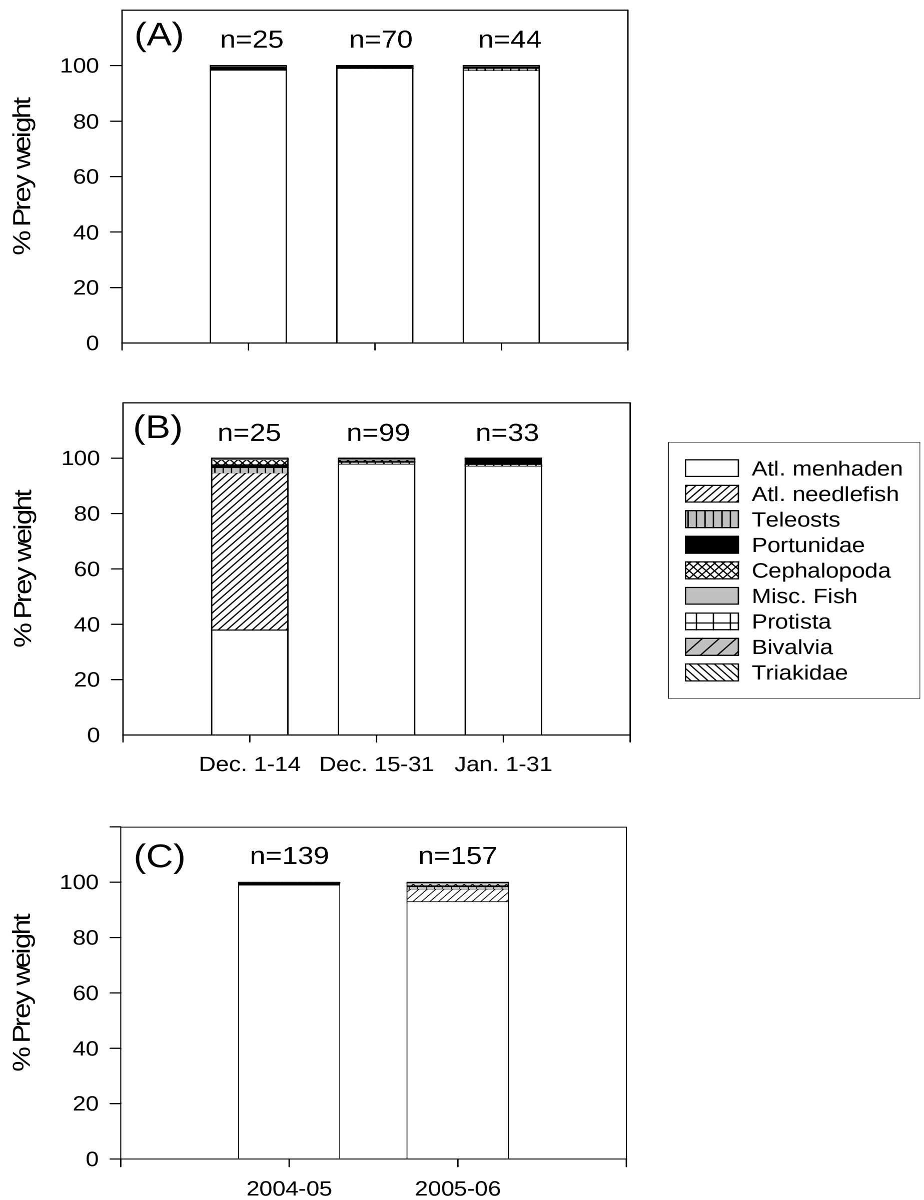


Figure 6. Percent prey weight composition from stomach contents of giant sized Atlantic bluefin tuna caught off Cape Lookout, North Carolina during December-January (A) 2004-05, (B) 2005-06, and (C) pooled years.

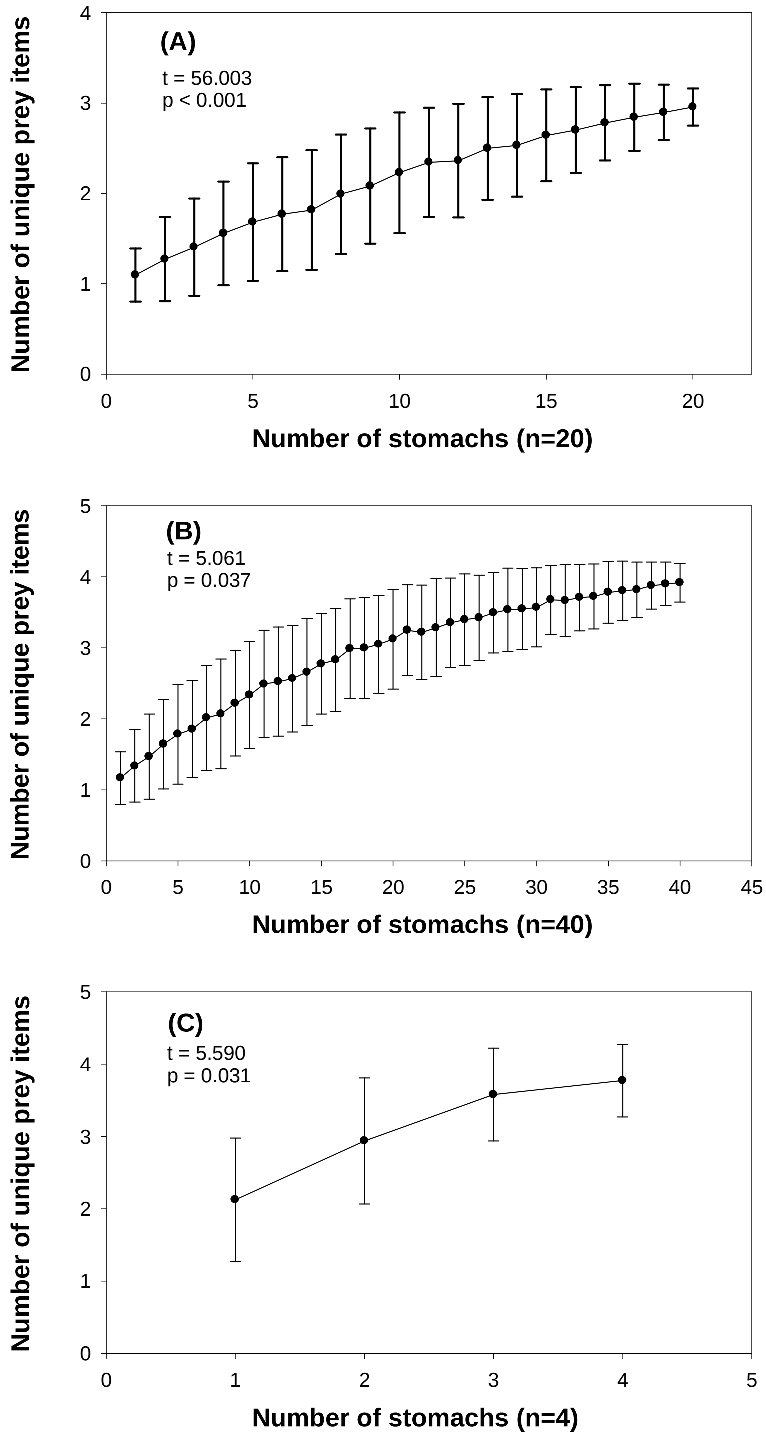


Figure 7. Randomized cumulative prey curves of large-medium Atlantic bluefin tuna collected off Cape Lookout, NC during (A) December 1-14, 2004 (n=20), (B) December 15-31, 2004 (n=40), and (C) January 1-31, 2005 (n=4). Means are plotted ± SD. X-axis is number of stomachs with prey.

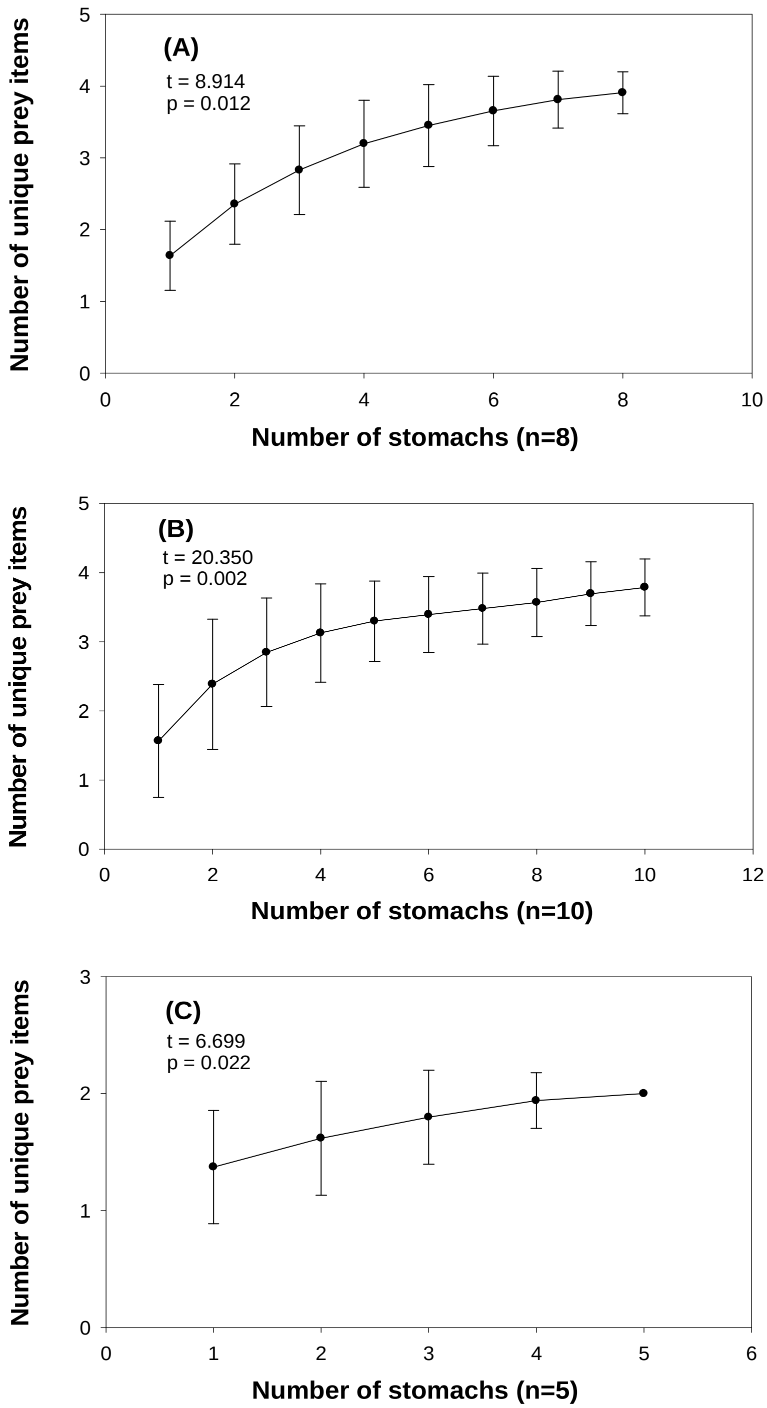


Figure 8. Randomized cumulative prey curves of large-medium Atlantic bluefin tuna collected off Cape Lookout, NC during (A) December 1-14, 2005 (n=8), (B) December 15-31, 2005 (n=10), and (C) January 1-31, 2006 (n=5). Means are plotted ± SD. X-axis is number of stomachs with prey.

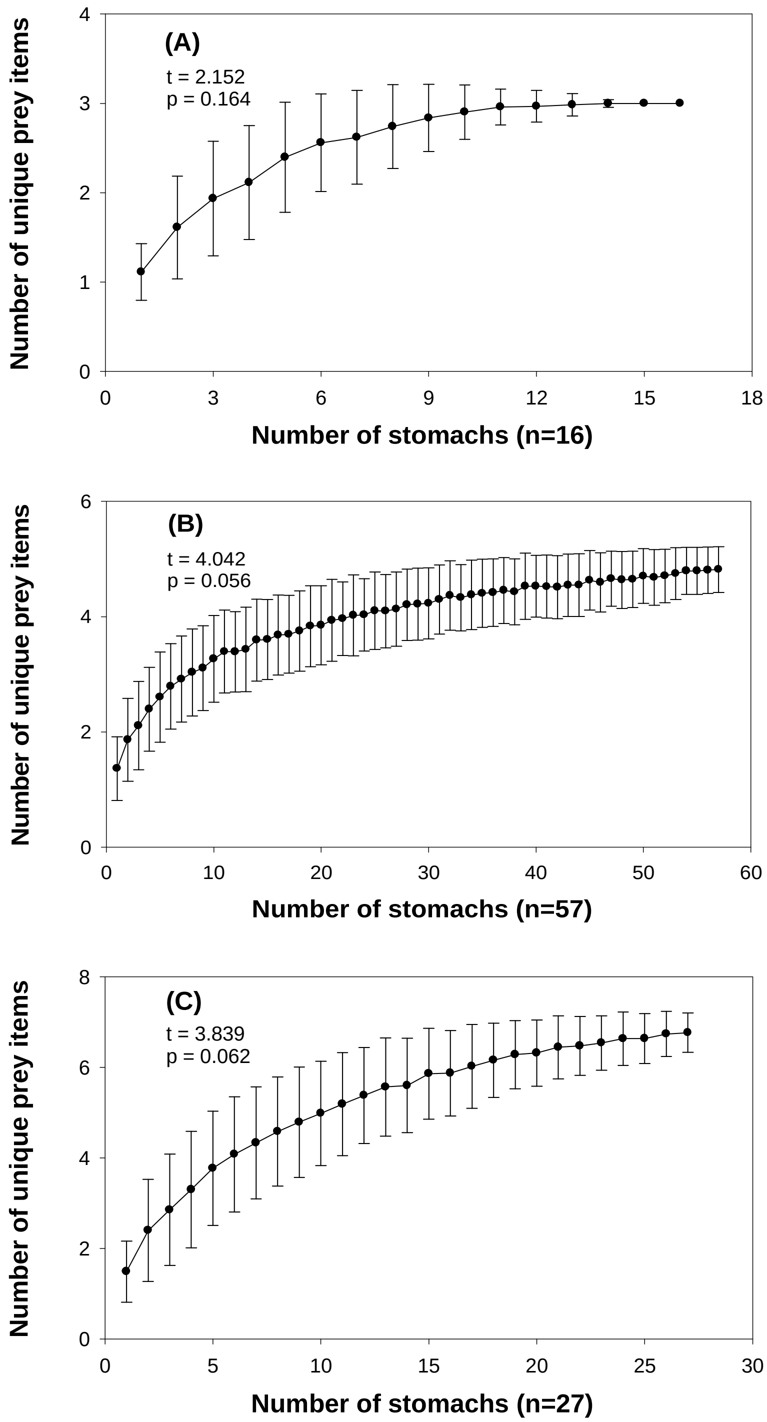


Figure 9. Randomized cumulative prey curves of giant Atlantic bluefin tuna collected off Cape Lookout, NC during (A) December 1-14, 2004 (n=16), (B) December 15-31, 2004 (n=57), and (C) January 1-31, 2005 (n=27). Means are plotted ± SD. X-axis is number of stomachs with prey.

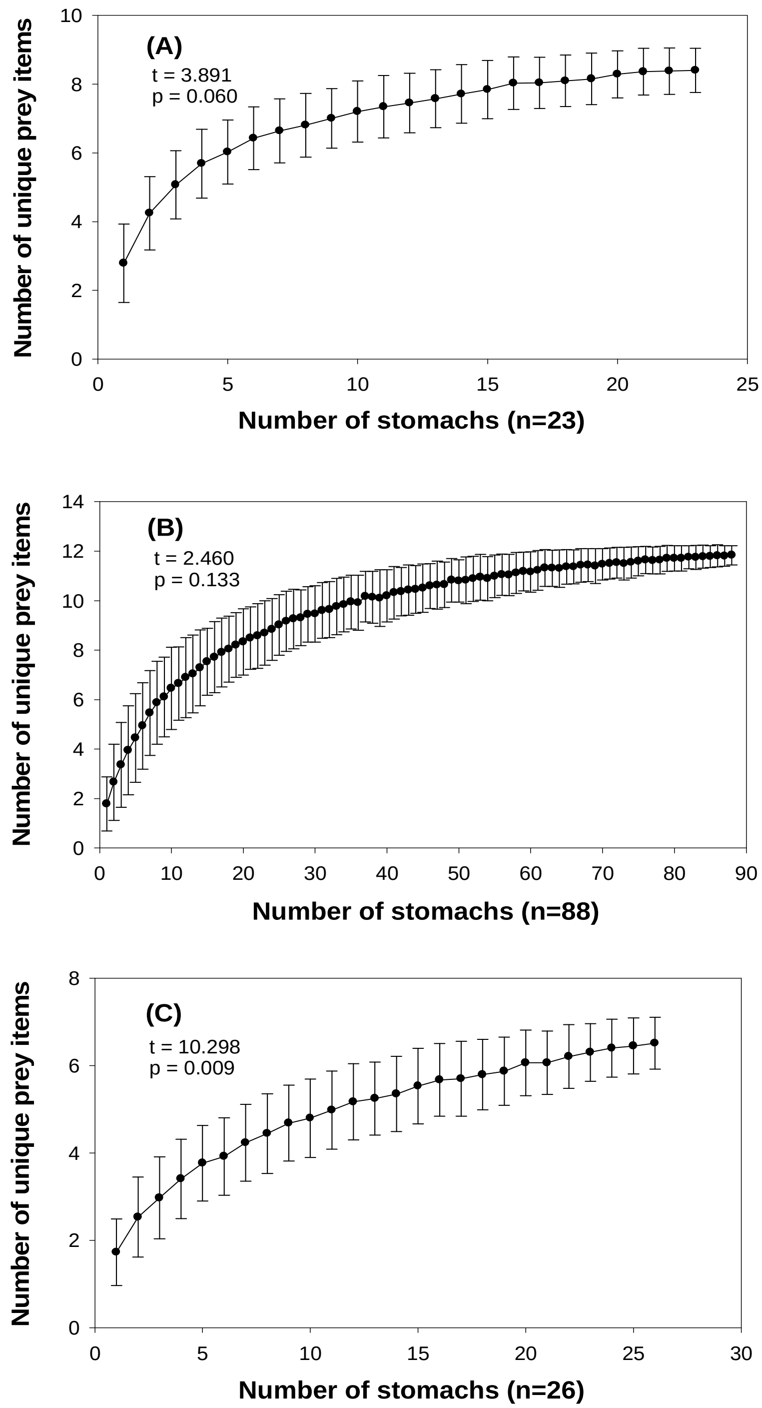


Figure 10. Randomized cumulative prey curves of giant Atlantic bluefin tuna collected off Cape Lookout, NC during (A) December 1-14, 2005 (n=23), (B) December 15-31, 2005 (n=88), and (C) January 1-31, 2006 (n=26). Means are plotted ± SD. X-axis is number of stomachs with prey.

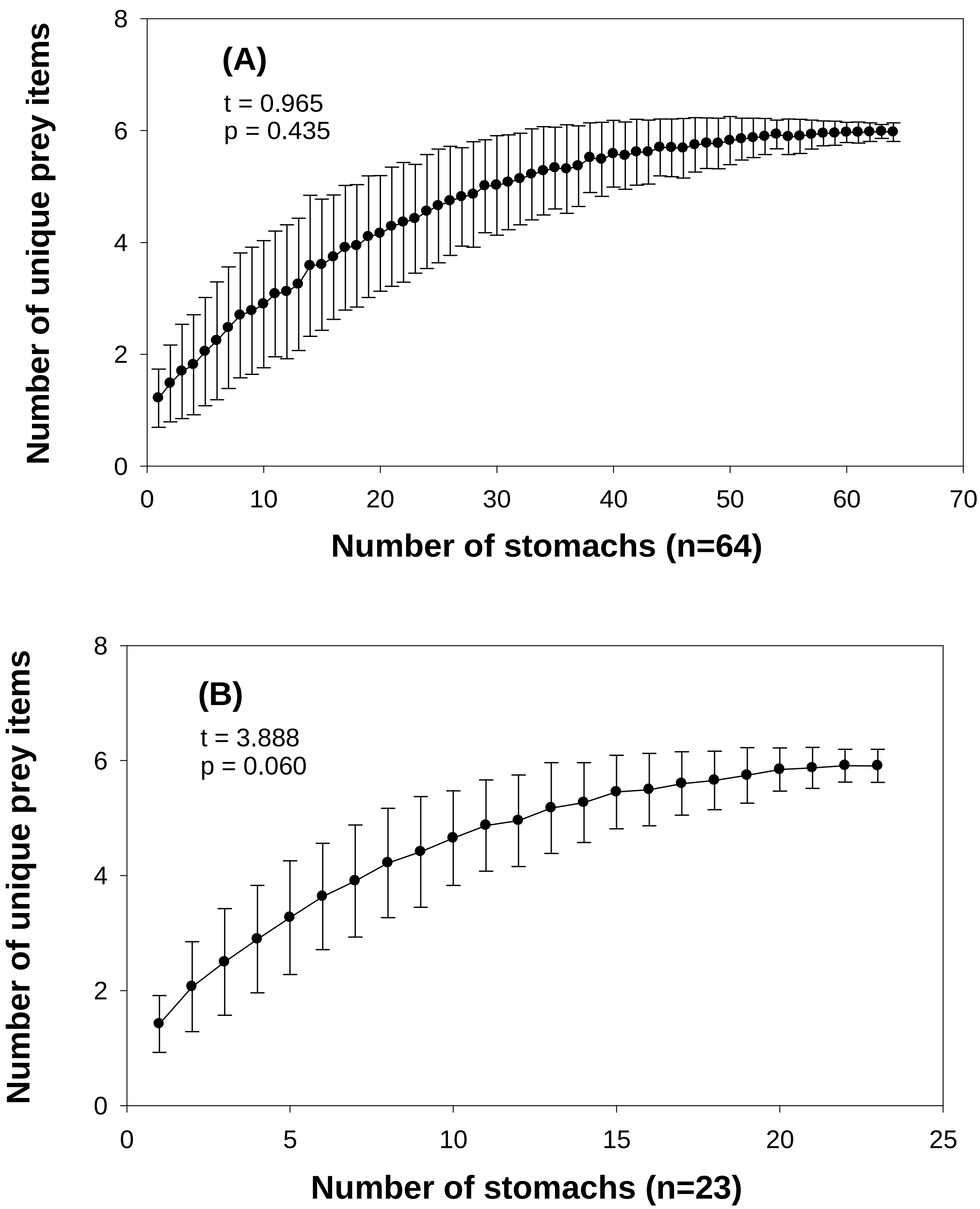


Figure 11. Randomized cumulative prey curves of large-medium Atlantic bluefin tuna collected off Cape Lookout, NC for (A) pooled stomachs collected from the 2004-05 season (n=64) and (B) pooled stomachs collected from the 2005-06 season (n=23). Means are plotted ± SD. X-axis is number of stomachs with prey.

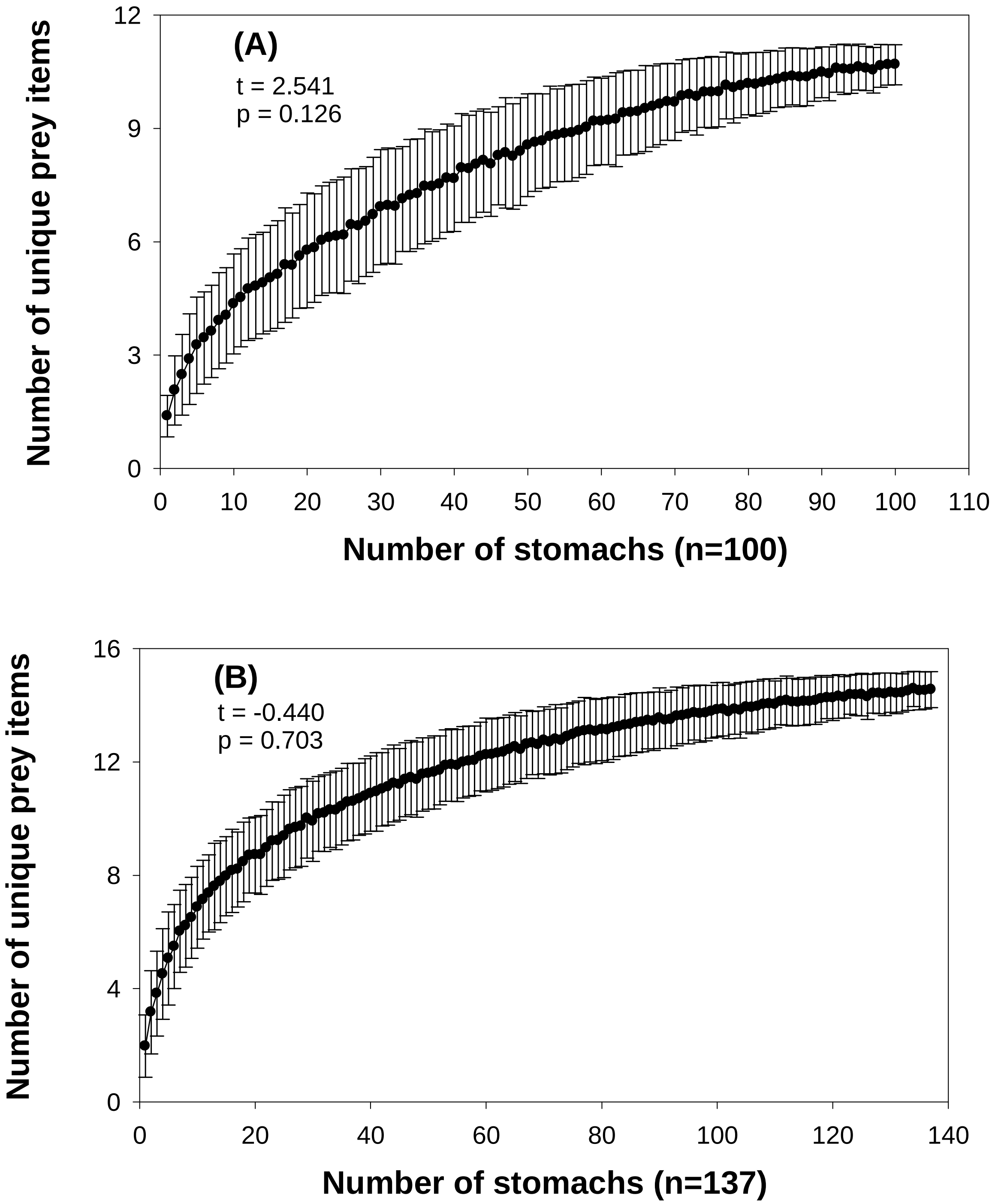


Figure 12. Randomized cumulative prey curves of giant Atlantic bluefin tuna collected off Cape Lookout, NC for (A) pooled stomachs collected from the 2004-05 season (n=100), (B) pooled stomachs collected from the 2005-06 season (n=137). Means are plotted ± SD. X-axis is number of stomachs with prey.

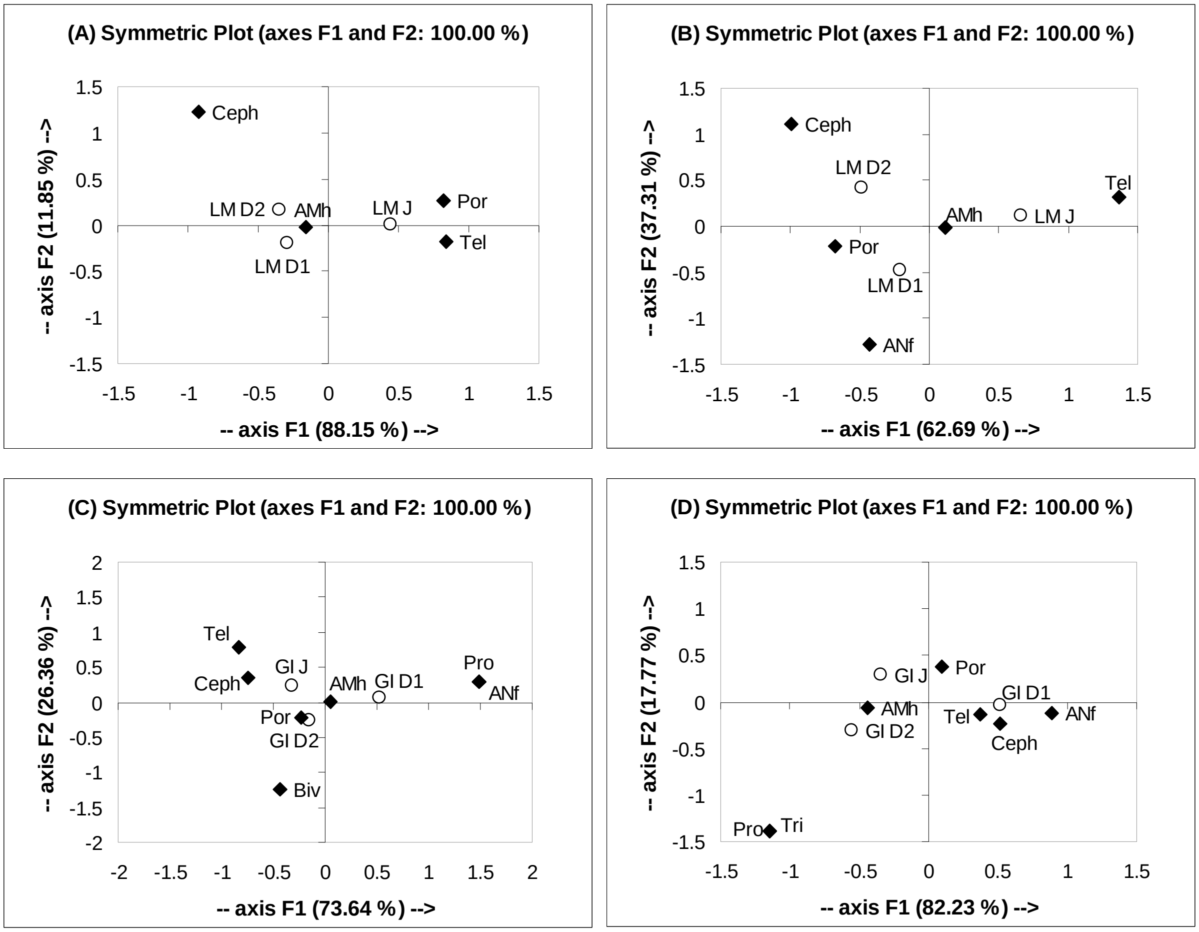


Figure 13. Correspondence analysis plots of intra-seasonal time period and prey category for axes 1 and 2 using %O for large-mediums (LM) collected during (A) 2004-05 and (B) 2005-06, and giants (GI) collected during (C) 2004-05 and (D) 2005-06. Diamonds=prey types, Circles=predator groups. D1 = December 1-14; D2 = December 15-31; J = January 1=31. AMh = Atlantic menhaden; ANf = Atlantic needlefish; Ceph = cephalopoda; Tel = teleostei; Por = portunidae; Pro = protista; Tri = triakidae; and Biv = bivalvia.

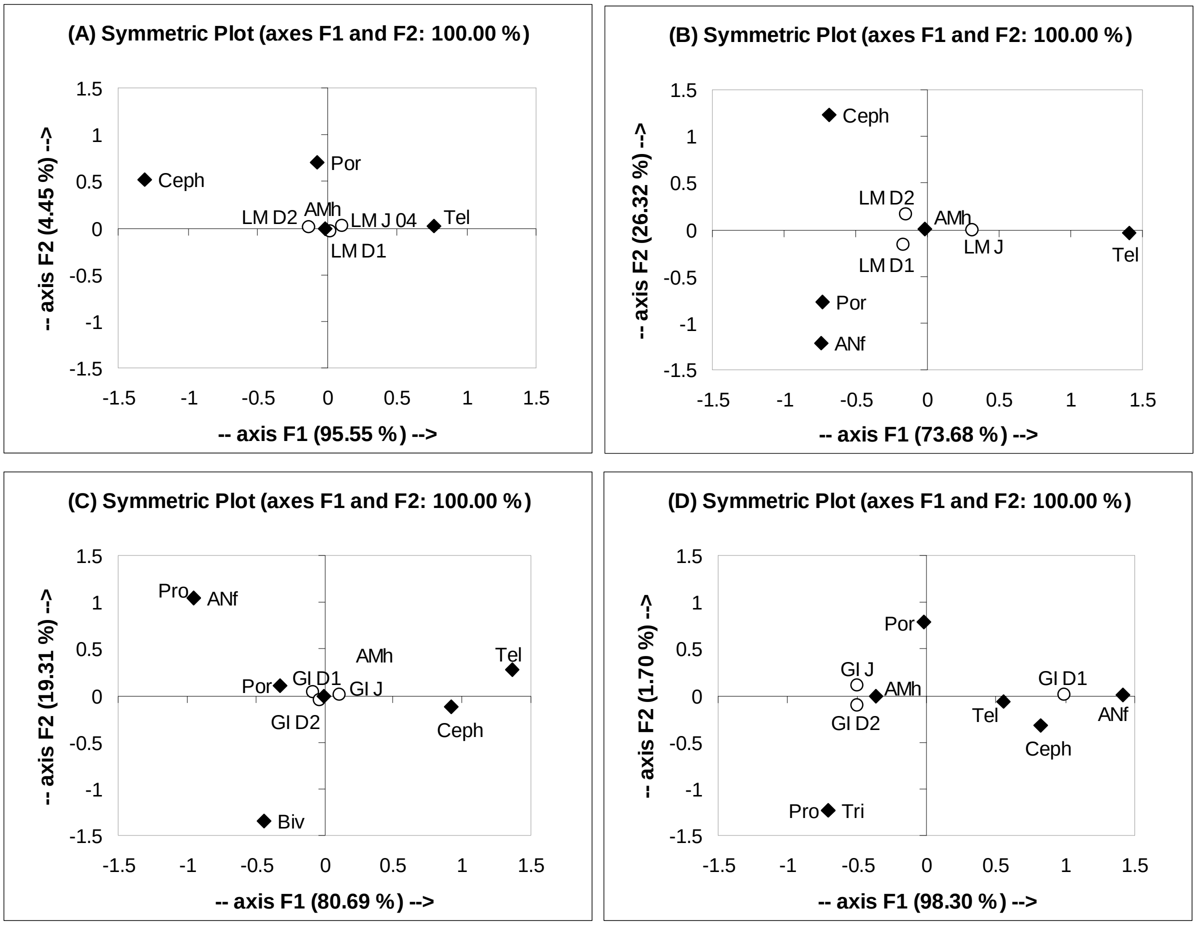


Figure 14. Correspondence analysis plots of intra-seasonal time period and prey category for axes 1 and 2 using %W for large-mediums (LM) collected during (A) 2004-05 and (B) 2005-06, and giants (GI) collected during (C) 2004-05 and (D) 2005-06. Diamonds=prey types, Circles=predator groups. D1 = December 1-14; D2 = December 15-31; J = January 1=31. AMh = Atlantic menhaden; ANf = Atlantic needlefish; Ceph = cephalopoda; Tel = teleostei; Por = portunidae; Pro = protista; Tri = triakidae; and Biv = bivalvia.

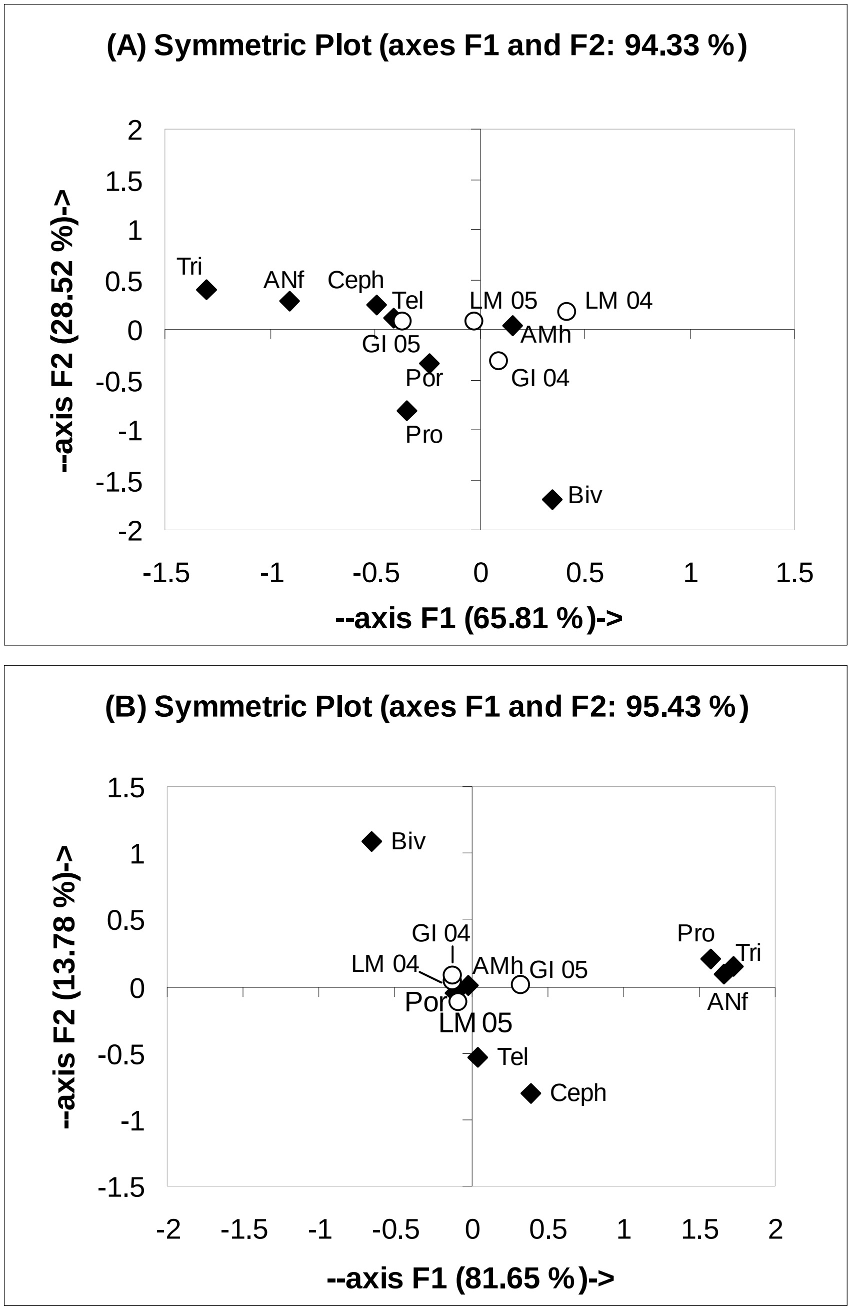


Figure 15. Correspondence analysis plots of size-class, year, and prey category for axes 1 and 2 using indices of (A) percent frequency of occurrence and (B) percent prey by weight for large-medium (LM) and giant (GI) Atlantic bluefin tuna collected during the 2004-05 and 2005-06 seasons. Diamonds=prey types, Circles=predator groups. The labels for the two seasons are: 04 = 2004-05 season and 05 = 2005-06 season. AMh= Atlantic menhaden; ANf = Atlantic needlefish; Ceph = cephalopoda; Tel = teleostei; Por = portunidae; Pro = protista; Tri = triakidae; and Biv = bivalvia.

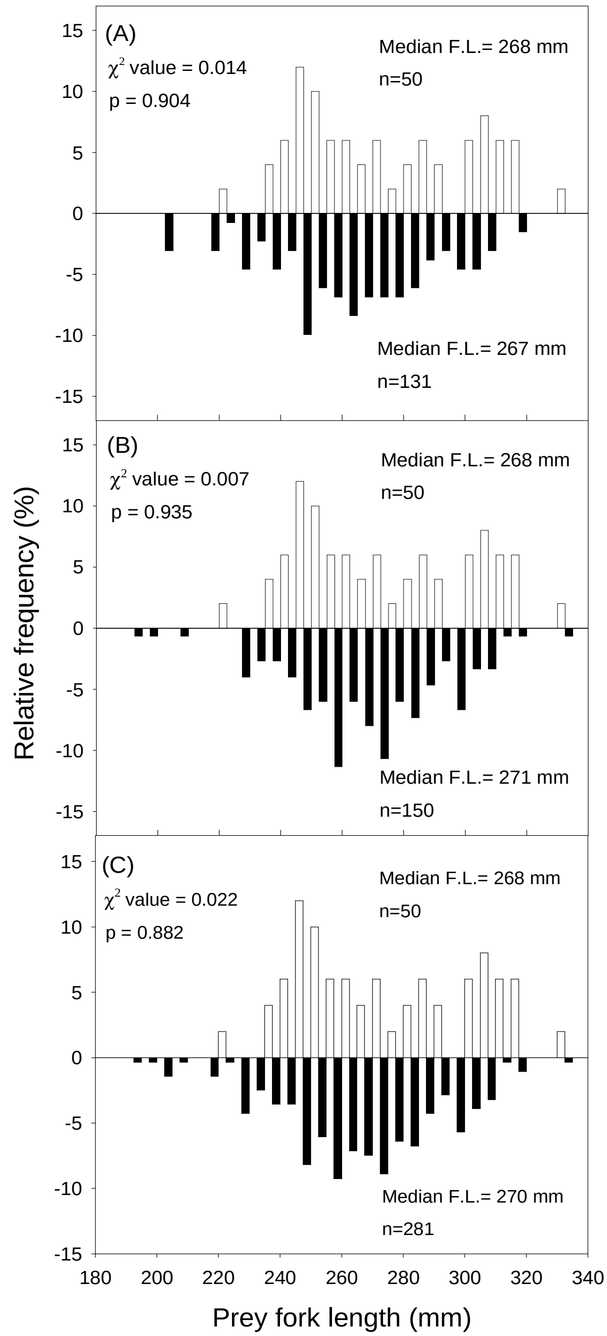


Figure 16. Comparative length-frequency histograms of Atlantic menhaden found in the environment (positive *y*-axis) and in bluefin tuna stomachs (negative *y*-axis) collected off North Carolina during the 2004-05 winter fishery for (A) large-medium, (B) giant, and (C) pooled size-classes. P-values and chi-square statistics were calculated using chi-square median tests (significance-level = 0.05). Sample sizes from purse seine and stomach content analysis are given for all measured prey during each comparison.

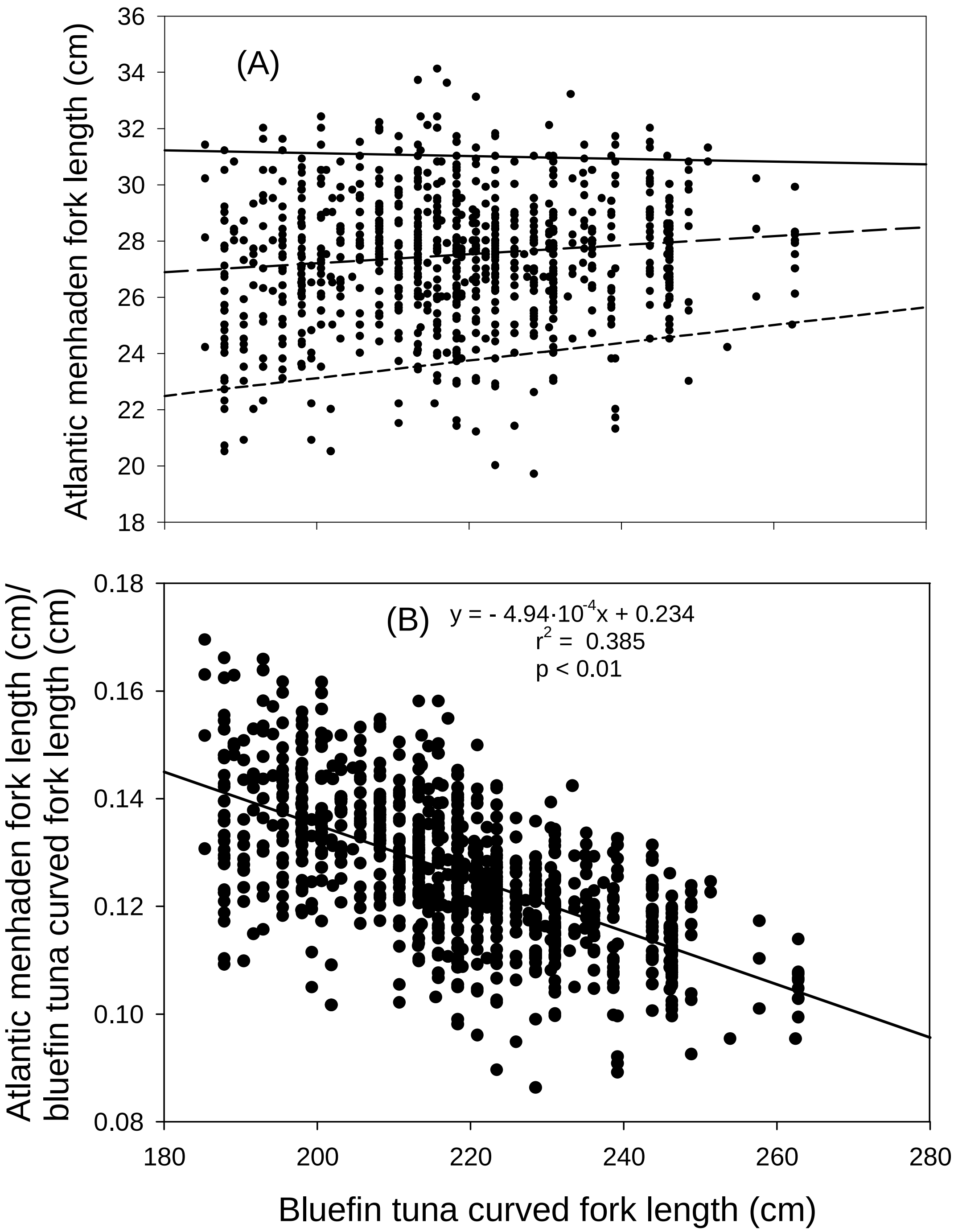


Figure 17. Atlantic menhaden consumed by bluefin tuna examined by (A) quantile regression analysis. Lines in regression analysis illustrate changes of minimum (y=0.032x + 16.820; p<0.01), median (y=0.016x + 23.991; p<0.01), and maximum (y=-0.005x + 32.125; p=0.83) prey consumed with increasing predator size. (B) Relative prey sizes of Atlantic menhaden compared to bluefin tuna fork length using linear regression analysis.

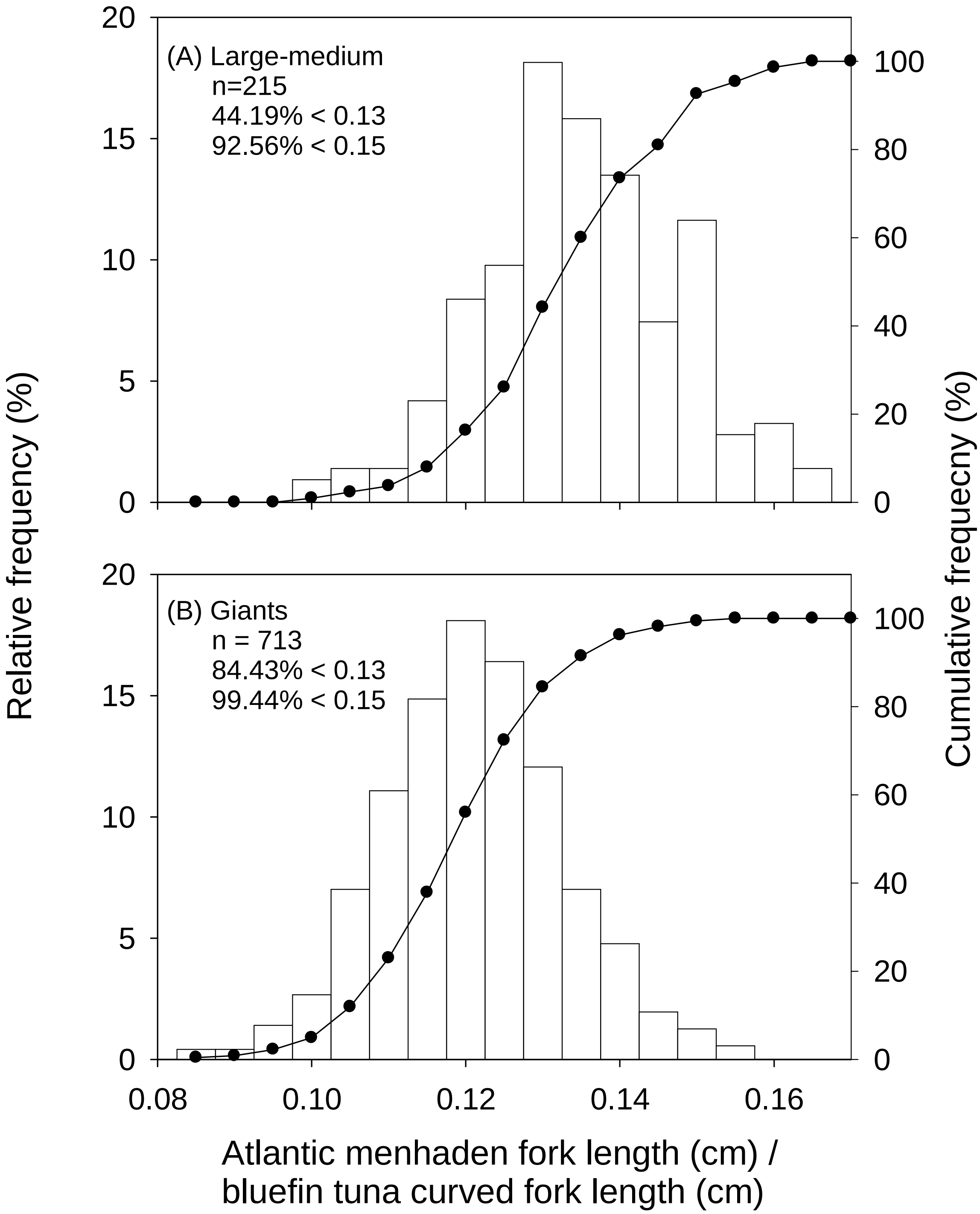


Figure 18. Distributions of Atlantic menhaden fork length-bluefin tuna curved fork length ratios for (A) large-medium and (B) giant bluefin tuna. Open bars show relative frequencies at 0.5% intervals. Circles represent cumulative frequencies at 0.5% intervals

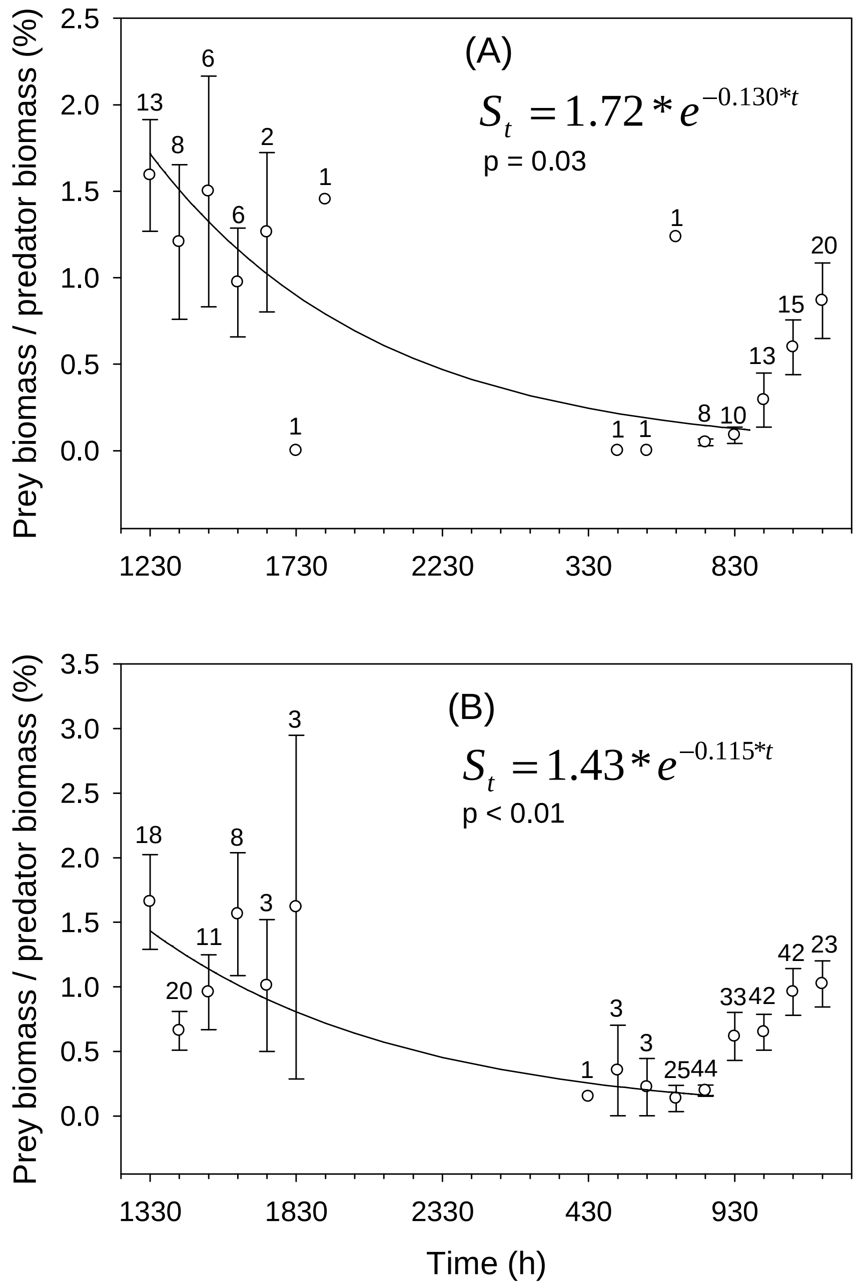


Figure 19. Diel patterns of gut fullness (kg kg^{-1}·100) for (A) large-medium and (B) giant bluefin tuna collected off Cape Lookout, North Carolina during the 2004-05 and 2005-06 winter seasons. Mean gut fullness values (± SE) for each size-class are plotted. Gastric evacuation patterns were estimated using an exponential model; exponential equations and the corresponding curves are provided.

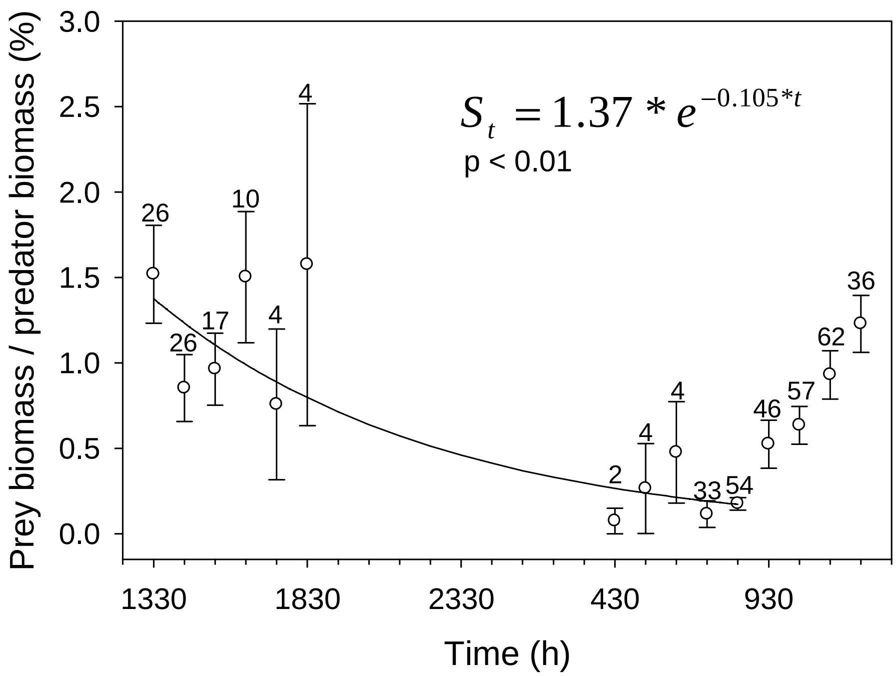


Figure 20. Diel pattern of gut fullness (kg kg^{-1}·100) for combined size-classes of Atlantic bluefin tuna collected off Cape Lookout, North Carolina during the 2004-05 and 2005-06 winter seasons. Mean gut fullness values (± SE) for each size-class are plotted. Gastric evacuation patterns were estimated using an exponential model; the exponential equation and corresponding curve are provided.

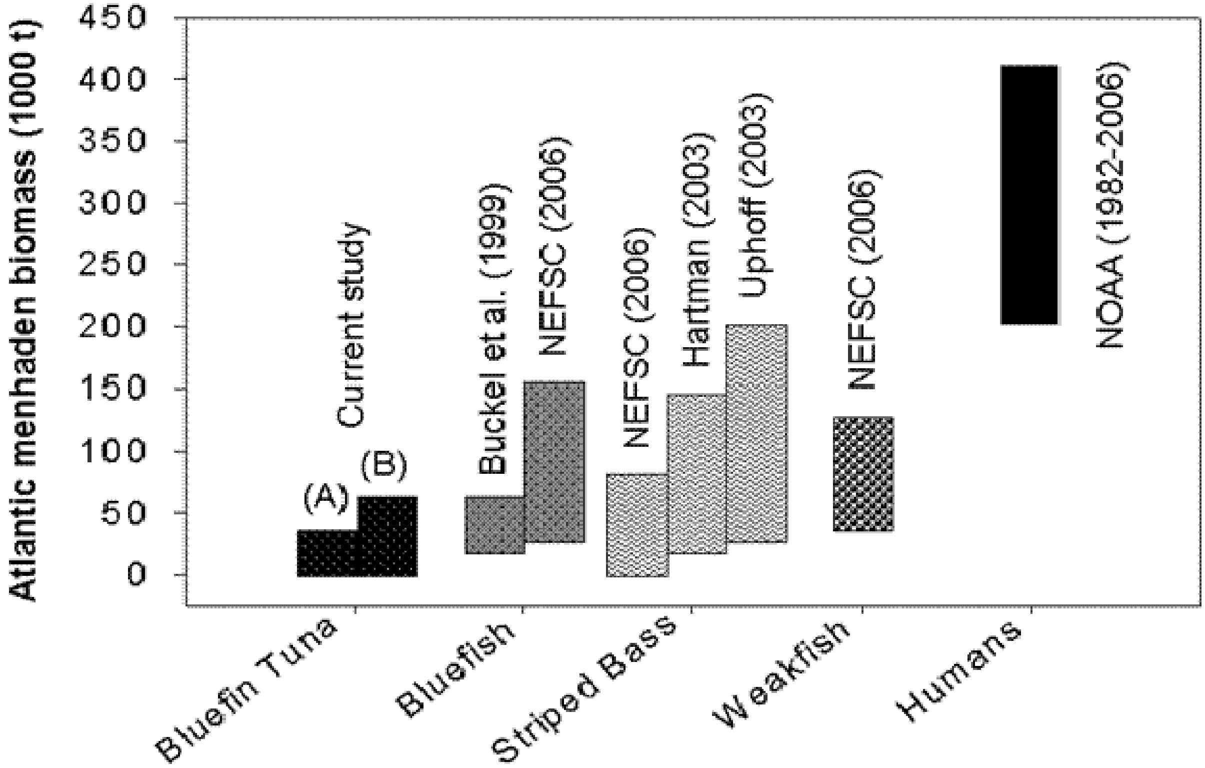


Figure 21. Estimated population-level consumption of Atlantic menhaden by recognized predators; bottom and top of bars represent minimum and maximum estimated consumption levels. References given cite published consumption estimates for a specific predator. Bluefin tuna consumption estimates from the current study are represented by (A) current bluefin tuna population levels and (B) a rebuilt western-Atlantic bluefin tuna population to 1975 biomass levels.

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Appendix

Appendix: Ecopath model construction

A.1 *Assembling functional groups*

The first step in assembling functional groups was to compile a list of species, families, orders, or other levels (e.g., "groupers") from several primary sources. Sources included the Southeast Area Monitoring and Assessment Program (SEAMAP 2004), Fishbase (Froese and Pauly 2007), Robins et al.'s (1986) A Field Guide to Atlantic Coast Fishes, Mackinson's (2000) Ecopath model of the West Florida Shelf ecosystem, and Okey and Pugliese's (2001) preliminary Ecopth model for the SAB. This list was then grouped into 18 functional groups based on ecological, biological, and trophic characteristics; functional groups from the current model followed those suggested by the previous Ecopath models (Okey and Pugliese 2001; Mackinson et al. 2000). However, several commercially and recreationally important species (e.g., bluefin tuna and Atlantic menhaden) were considered separately since their predator-prey interactions were of primary concern for the current study. The groups (species, families, orders, etc.) that make up the 18 functional groups will be referred to as "individual groups" below and are presented on Table A1.

A.2 *Biomass estimates*

The total biomass for a functional group was attained by summing the biomass estimates of individual groups. Biomass estimates of "Bottlenose dolphin," "Macroalgae + Sea grass," and "Small tuna species" were taken from references given in Mackinson et al. (2000). Biomass values of individual groups in the "Large coastal sharks" and "Demersal elasmobranch" functional groups were obtained from both Mackinson (2000) and SEAMAP

(2004) trawl data. “Marine birds” and “Detritus” biomass estimates were acquired from Vidal-Hernandez and Nesbitt (2000) and Okey and Pugliese (2001), respectively.

Biomass for the “Bluefish, Striped Bass, Weakfish” group was obtained from various literature sources. Weakfish biomass was estimated from SEAMAP (2004) trawl data. Due to the migratory nature of bluefish and striped bass, biomass was estimated based on the proportion of the population that is believed to occur in the South Atlantic Bight on an annual time-step. For bluefish, it was assumed that 50% of the population biomass (see Buckel et al. (1999)) occurred in the SAB on an annual basis. It was assumed that 80% of the striped bass biomass estimated by ASMFC (2005b) was believed to reside in the SAB for one-third of the year; this is equivalent to ~27% of the striped bass biomass present in the SAB for the entire year.

“Atlantic menhaden” biomass was estimated from the ASMFC (2006) stock assessment. For the current Ecopath model, 50% of the population (age 0+) was assumed to occur in the SAB annually.

Biomass values for the remaining nine functional groups (“Pelagic piscivores”, “Cephalopods”, “Bluefin tuna”, “Demersal piscivore”, “Pelagic forage”, “Demersal forage”, “Zooplankton”, “Invertebrates”, and “Phytoplankton”) were initially estimated as the sum of the biomass values for each individual group (see Table A1) making up a functional group; estimates of biomass at the individual group level were used in weighting individual *P/B* and *Q/B* parameters to estimate a mean for the functional group. However, the under representation of individual groups within some of the functional groups creates substantial uncertainty associated with these biomass values and the model did not balance during initial iterations (see section A.7 below). Therefore, I allowed Ecopath software to estimate the potential biomasses for these functional groups during the mass-balancing process.

A.3 *Production and consumption*

Whenever possible, previously calculated *P/B* and *Q/B* (e.g., Mackinson et al. 2000; Okey and Pugliese 2001) parameters for functional groups within the SAB were used; eleven out of 36 of these two parameters were derived from these two models (see Table A1). Estimates of *P/B* and *Q/B* for the remaining functional groups were obtained from various literature resources. The *P/B* ratio is analogous to the instantaneous mortality rate (*Z*). Values of *Z* were obtained from stock assessments and fisheries management plans (FMP) for *Morone saxatilis, Cynoscion regalis, Scomberomorus cavalla*, and "Atlantic menhaden"; instantaneous mortality rates for *Scomberomorus maculates, Centropristis striata, and Mustelus canis* were obtained from Fishbase (Froese and Pauly 2007) (Table A1). All other *P/B* parameters were acquired from other ecosystem-based models (Ulanowicz et al. 1998; Mackinson et al. 2000; Okey and Pugliese 2001; and Christensen et al. 2005); *P/B* for "Bluefin tuna" was estimated by Mackinson (2000) as 0.43. Thirty-one out of 66 *Q/B* estimates for individual groups were derived from Fishbase (Froese and Pauly 2007) following the multiple regression equation defined by Palomares and Pauly (1989) (Table A1). The remaining *Q/B* estimates for individual groups were obtained from either other Ecopath models (Mackinson et al. 2000; Okey and Pugliese 2001) or from estimates of daily ration from the literature. The latter group included *Carcharhinus plumbeus, Negaprion brevirostris*, *Ginglymostoma cirratum*, *Morone saxatilis*, *Pomatomus saltatrix*, and "Atlantic menhaden" (see Table A1). An estimate of *Q/B* for "Bluefin tuna" was derived from daily ration estimates from this study. Estimates of *P/B* and *Q/B* ratios for functional groups were weighted based on the potential biomasses of individual groups within each functional group. Of all the parameters, I felt the most confident with the *P/B* and *Q/B* values used during model development; therefore, I did not allow Ecopath to estimate either of these parameters for any functional group during the mass-balancing process

A.4 *Diet composition*

Diet composition data for individual groups within a functional group were obtained after extensive review of available literature (see Table A1 for sources). Since Ecopath is a biomass-based model, diet composition was determined using the index of %W. Diet data by %W was unavailable for one species of “Large coastal sharks”, *Carcharhinus leucas*, and the functional group “Marine birds”; thus, diet composition for each of these groups was assumed to be proportional to either percent by number or percent occurrence, respectively. Diet composition for functional groups was determined by weighting the diets of individual groups based on their proportion of the total biomass (Table A2). In instances where unique prey items (e.g., plastic) were identified but are not described by the trophic groupings of the present Ecopath model, such values were eliminated from further analysis; all diets were normalized to 100%.

A.5 *Ecotrophic efficiency*

The ecotrophic efficiency (*EE*) is defined as the amount of total production from a single functional group that is utilized by all other functional groups and human harvest. For functional groups where the *B*, *P/B*, and *Q/B* are known, Ecopath estimated the *EE*. In the initial iteration of the model, only the *EE* of “Bluefin tuna” was assumed known (estimated in Okey and Pugliese’s (2001) Ecopath model as 0.801). However, the initial attempt at mass-balancing gave estimates of *EE* values that were too high for several groups. Therefore, I used previously determined *EE* values (see Table A1) and allowed Ecopath to estimate biomass values for these groups to balance the model (see section A.7 below).

A.6 *Fishery harvests*

Commercial and recreational fishery catches (http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html; http://www.st.nmfs.gov/st1/recreational/queries/catch/snapshot.html) for harvested species (landed during 2005) were summed by trophic groupings (see Table A3).

A.7 *Balancing the model*

The initial Ecopath model was unbalanced for nine of the 18 functional groups (i.e., values of *EE* were higher than 1.00 for “Small tuna species,” “Pelagic piscivores,” “Cephalopods,” “Demersal piscivores,” “Pelagic forage,” “Demersal forage,” “Zooplankton,” “Invertebrates,” and “Detritus”). The *EE* values greater than 1.00 require either reduced consumption (*Q/B*) of predators on that group, increased production (*P/B*), or increased biomass values in order for the model to balance; out of the three parameters to manipulate, I was the least confident in the biomass values for these groups. Therefore, I used previously estimated *EE* values for these groups from Okey and Pugliese (2001) and allowed Ecopath to estimate biomass values for all unbalanced groups. However, Ecopath does not allow the user to predict the *EE* of “Detritus”; thus, “Detritus” biomass remained constant during model iterations. The second iteration of the model predicted the *EE* of "Phytoplankton" and "Detritus" were greater than 1.00. Once again, I used a previously estimated *EE* value from Okey and Pugliese (2001) for "Phytoplankton" to predict the biomass of "Phytoplankton" in the SAB. The next step towards mass-balancing required the minimization of cannibalism within a trophic group; the effect of cannibalism was minimized to a maximum value of 20% for functional groups (as recommended by Ecopath) where cannibalism is a major component of the diet; these groups were "Cephalopods," "Invertebrates," and "Pelagic piscivores". The Ecopath model balanced after these changes.

Table A1. Sources of basic parameter estimates for trophic groups within the South Atlantic Bight Ecopath model. Values of Q/B and P/B in bold represent the weighted mean for trophic groups based on biomass estimates of individual species.

Group	Biomass (t/km^2)	Reference	*Q/B* (year^{-1})	Reference	*P/B* (year^{-1})	Reference	*EE*	Reference	Diet composition (see Table A2 for values)
Bottlenose dolphin	**0.025**		**41.700**		**0.100**				
Tursiops truncatus	0.025	Mullin and Hogard (2000) from Mackinson et al. (2000)	41.700	Mackinson et al. (2000)	0.100	Browder (1993); Matkin and Hobbs (1999) from Mackinson et al. (2000)			Gannon and Waples (2004)
Large coastal sharks	**0.088**		**2.087**		**0.381**				
Carcharhinus plumbeus	0.030	Mackinson (2000)	3.139	Stillwell and Kohler (1982)	0.263	Mackinson (2000)			NOAA trawl data 1977-1980 from Bowman et al. (2000)
Carcharhinus limbatus	0.003	Mackinson (2000)	3.500	Pred. Palomares and Pauly (1989)	0.466	Mackinson (2000)			Bethea et al. (2004) (juveniles)
Carcharhinus falciformis	2.300E^{-04}	Mackinson (2000)	1.800	Pred. Palomares and Pauly (1989)	0.280	Mackinson (2000)			
Carcharhinus brevipinna	1.000E^{-05}	Mackinson (2000)	3.100	Pred. Palomares and Pauly (1989)	0.440	Mackinson (2000)			Bethea et al. (2004)
Carcharias taurus	0.038	SEAMAP trawl (2004)	1.500	Pred. Palomares and Pauly (1989)	0.620	Mackinson (2000)			Gelsleichter et al. (1999)
Carcharhinus leucas	0.002	Mackinson (2000)	1.700	Pred. Palomares and Pauly (1989)	0.210	Mackinson (2000)			Snelson et al. (1984)
Carcharhinus obscurus	0.001	Mackinson (2000)	2.100	Pred. Palomares and Pauly (1989)					NOAA trawl data 1977-1980 from Bowman et al. (2000)
Negaprion brevirostris	3.000E^{-05}	Mackinson (2000)	7.300	Cortés and Gruber (1990)	0.750	Mackinson (2000)			Cortés and Gruber (1990)
Ginglymostoma cirratum	0.013	SEAMAP trawl (2004)	1.095	Clark (1963)					
Sphyrna mokarran	0.001	Mackinson (2000)	1.200	Pred. Palomares and Pauly (1989)	0.250	Mackinson (2000)			
Sphyrna lewini	4.100E^{-04}	SEAMAP trawl (2004)	2.300	Pred. Palomares and Pauly (1989)	0.430	Mackinson (2000)			NOAA trawl data 1977-1980 from Bowman et al. (2000)
Small tuna species			**15.402**		**0.947**		**0.801**	Okey and Pugliese (2001)	
Euthynnus alletteratus	0.009	Mackinson (2000)	15.110	Pred. Palomares and Pauly (1989)	0.900	Mackinson (2000)			Manooch et al. (1985)

Table A1 (Cont'd)

Group	Biomass (t/km²)	Reference	*Q/B* (year⁻¹)	Reference	*P/B* (year⁻¹)	Reference	*EE*	Reference	Diet composition (see Table A2 for values)
Katsuwonus pelamis	0.002	Mackinson (2000)	23.894	Brown et al. (1991) from Mackinson (2000)	1.140	Mackinson (2000)			Ankenbrandt (1985)
Thunnus atlanticus	0.010	Mackinson (2000)	15.455	Browder model from Mackinson (2000)	0.870	Mackinson (2000)			Collette and Nauen (1983)
Thunnus albacares	0.004	Mackinson (2000)	12.221	Brown et al. (1991) from Mackinson (2000)	1.200	Mackinson (2000)			Satoh et al. (2004)
Thunnus obesus	$4.000E^{-05}$	Mackinson (2000)	7.900	Pred. Palomares and Pauly (1989)	0.640	Mackinson (2000)			Satoh et al. (2004)
Thunnus alalunga		Mackinson (2000)	9.400	Pred. Palomares and Pauly (1989)	0.780	Mackinson (2000)			Satoh et al. (2004)
Marine birds	**0.001**		**80.000**		**0.100**				
	0.001	Vidal-Hernandez and Nesbitt (2000) from Okey and Pugliese (2001)	80.000	Nilsson and Nilsson (1976); and Vidal-Hernandez & Nesbitt (2000) from Okey and Pugliese (2001)	0.100	Acosta et al. (1998) from Okey and Pugliese (2001)			Fogarty et al. (1981)
Bluefish, Striped Bass, Weakfish	**1.238**		**6.712**		**0.489**				
Morone saxatilis	0.265	ASMFC (2005b)	1.633	Hartman (2003)	0.410	ASMFC (2005b) $Z=F_{2004NC}+M_{2004NC}$			NOAA trawl data 1977-1980 from Bowman et al. (2000)
Pomatomus saltatrix	0.623	Buckel et al. (1999)	7.700	Buckel et al. (1999)	0.545	Christensen et al. (2005)			Hartman and Brandt (1995)
Cynoscion regalis	0.350	SEAMAP trawl (2004)	3.200	Pred. Palomares and Pauly (1989)	0.450	Spear et al. (2003) M=0.2; and Smith et al. (2000) F=0.25 from Christensen et al (2005)			Hartman and Brandt (1995)

Table A1 (Cont'd)

Group	Biomass (t/km^2)	Reference	*Q/B* (year^{-1})	Reference	*P/B* (year^{-1})	Reference	*EE*	Reference	Diet composition (see Table A2 for values)
Pelagic piscivores			**10.833**		**0.524**		**0.883**	Okey and Pugliese (2001)	
Rachycentron canadum	0.001	Mackinson (2000)	7.300	Brown et al. (1991) from Mackinson (2000)	0.700	Mackinson (2000)			Arendt et al. (2001)
Megalops atlanticus	4.50E-^{04}	Schmidt (1979); FLDEP (1997)	6.300	FLDEP (1997)	1.060	Browder model from Mackinson (2000)			Goode(1879); FLDEP (1997) from Ulanowicz et al. (1998)
Sciaenops ocellatus	0.014	Mackinson (2000)	3.900	Pred. Palomares and Pauly (1989)	0.350	GoM model from Mackinson (2000)			Nate Bacheler (NCSU, unpublished)
Sphyraenidae sp.	0.051	Schmidt (1979); Hoss et al. (1996); Venier (1997); and Matheson et al. (1999) from Ulanowicz et al. (1998)	3.700	Pred. Palomares and Pauly (1989)	1.420	Arreguin-Sanchez et al. (1993); de la Cruz-Aguero et al. (1993); and Vega-Cendejas et al. (1993) from Ulanowicz et al. (1998)			Schmidt (1989); and FLDEP (1997) from Ulanowicz et al. (1998)
Scomberomorus cavalla	0.225	SAFMC (SEDAR 2004)	12.600	Pred. Palomares and Pauly (1989)	0.300	SAFMC (SEDAR 2004)			NOAA trawl data 1977-1980 from Bowman et al. (2000); Devane (1978)
Scomberomorus maculatus	0.012	SEAMAP trawl (2004)	16.700	Pred. Palomares and Pauly (1989)	1.110	Fishbase Z=F+M			Robins et al. (1986); and FLDEP (1997) from Ulanowicz et al. (1998)
Belonidae sp.	2.032E-04	SEAMAP trawl (2004)	7.200	Arreguin-Sanchez et al. (1993); de la Cruz-Aguero (1993); and Vega-Cendejas et al. (1993) from Ulanowicz et al. (1998)	0.300	Schmidt (1979); Sogard et al. (1989); and Thayer et al. (1987) from Ulanowicz et al. (1998)			Carr and Adams (1973); Robins et al. (1986); and Ley et al.(1994) from Ulanowicz et al. (1998)
Cephalopods			**36.500**		**2.673**		**0.967**	Okey and Pugliese (2001)	
Loligo sp.	0.267	Mendoza (1993) from Mackinson et al. (2000)	36.500	Mendoza (1993) from Mackinson et al. (2000)	2.673	Mendoza (1993); Pauly et al. (1993) from Mackinson et al. (2000)			NOAA trawl data 1977-1980 from Bowman et al. (2000)

Table A1 (Cont'd)

Group	Biomass (t/km^2)	Reference	*Q/B* (year^{-1})	Reference	*P/B* (year^{-1})	Reference	*EE*	Reference	Diet composition (see Table A2 for values)
Bluefin tuna			**6.356**		**0.430**		**0.801**	Okey and Pugliese (2001)	
Thunnus thynnus			6.356	Current study	0.430	Mackinson (2000)			Current study
Demersal piscivores			**8.948**		**0.382**		**0.950**	Okey and Pugliese (2001)	
Flounders	0.006	Schmidt (1979); Sogard et al. (1989); Hoss et al. (1996)	9.460	Mackinson (2000)	0.300	Mackinson (2000) from Okey and Pugliese (2001)			Carr and Adams (1973); de la Cruz-Aguero (1993); and FLDEP (1997) from Ulanowicz et al. (1998)
Synodus foetens	0.138	SEAMAP (2000) trawl from Mackinson (2000)	9.500	Pred. Palomares and Pauly (1989)	0.300	GoM model from Mackinson (2000)			Livingston (1984)
Groupers	0.001	Schmidt (1979); Sogard et al. (1989); Rutherford et al. 1989, Hoss et al. (1996); and Matheson et al. (1999) from Ulanowicz et al. (1998)	8.400	Mackinson (2000) from Okey and Pugliese (2001)	0.700	Mackinson (2000) from Okey and Pugliese (2001)			Robins et al. (1986); FLDEP (1997); and Smith (1997) from Ulanowicz et al. (1998)
Lutjanidae sp.	0.024	Schmidt (1979); Sogard et al. (1989); Rutherford et al. 1989, Hoss et al. (1996); and Matheson et al. (1999) from Ulanowicz et al. (1998)	5.830	Arreguin-Sanchez et al. (1993); de la Cruz-Aguero (1993); and Vega-Cendejas et al. (1993) from Ulanowicz et al. (1998)	0.813	Arreguin-Sanchez et al. (1993); de la Cruz-Aguero et al. (1993); and Vega-Cendejas et al. (1993) from Ulanowicz et al. (1998)			Robins et al. (1986); Hettler (1989); FLDEP (1997)
Centropristis striata	0.001	SEAMAP trawl (2004)	4.400	Pred . Palomares and Pauly (1989)	1.380	Fishbase Z=F+M			NOAA trawl data 1977-1980 from Bowman et al. (2000)
Centropristis philadelphica	1.904E-04	SEAMAP trawl (2004)	13.600	Pred. Palomares and Pauly (1989)	1.120	Mackinson (2000)			

Table A1 (Cont'd)

Group	Biomass (t/km^2)	Reference	*Q/B* (year^{-1})	Reference	*P/B* (year^{-1})	Reference	*EE*	Reference	Diet composition (see Table A2 for values)
Demersal elasmobranchs	**0.359**		**5.597**		**0.312**				
Squalus acanthias	0.008	SEAMAP trawl (2004)	4.770	Pred. Palomares and Pauly (1989)					
Mustelus canis	0.144	SEAMAP trawl (2004)	2.600	Pred. Palomares and Pauly (1989)	0.380	Fishbase Z=F+M			Gelsleichter et al. (1999)
Rhinoptera bonasus	0.158	SEAMAP (2000) trawl from Mackinson (2000)	6.400	Pred. Palomares and Pauly (1989)	0.240	Pred. M (Pauly, 1980) from Mackinson (2000)			NOAA trawl data 1977-1980 from Bowman et al. (2000)
Raja eglanteria	0.050	SEAMAP (2000) trawl from Mackinson (2000)	11.800	Pred. Palomares and Pauly (1989)	0.390	Pred. M (Pauly, 1980) from Mackinson (2000)			Collins et al. (2007)
Pelagic forage			**21.295**		**3.440**		**0.984**	Okey and Pugliese (2001)	
Anchoa mitchilli	0.177	Brown et al. (1991) from Mackinson (2000)	19.700	Arreguin-Sanchez et al. (1993) from Ulanowicz et al. (1998)	3.940	Arreguin-Sanchez et al. (1993) from Ulanowicz et al. (1998)			Sheridan (1978); Livingston (1984)
Anchoa hepsetus	0.028	SEAMAP trawl (2004)	19.700	Arreguin-Sanchez et al. (1993) from Ulanowicz et al. (1998)	3.940	Arreguin-Sanchez et al. (1993) from Ulanowicz et al. (1998)			Motta et al. (1993); and Smith (1997) from Ulanowicz et al. (1998)
Atherinidae sp.			8.400	Arreguin-Sanchez et al. (1993); de la Cruz-Aguero (1993); and Vega-Cendejas et al. (1993) from Ulanowicz et al. (1998)	1.420	Arreguin-Sanchez et al. (1993); de la Cruz-Aguero (1993); and Vega-Cendejas et al. (1993) from Ulanowicz et al. (1998)			Carr and Adams (1973); Adams (1976); and Robins et al. (1986) from Ulanowicz et al. (1998)
Alosa spp.	0.005	SEAMAP (2000) trawl from Mackinson (2000)	10.910	Pred. Palomares and Pauly (1989)	0.600				NOAA trawl data 1977-1980 from Bowman et al. (2000)

Table A1 (Cont'd)

Group	Biomass (t/km^2)	Reference	*Q/B* ($year^{-1}$)	Reference	*P/B* ($year^{-1}$)	Reference	*EE*	Reference	Diet composition (see Table A2 for values)
Harengula jaguana	0.001	SEAMAP trawl (2004)	23.700	Pred. Palomares and Pauly (1989)	1.570	GoM model from Mackinson (2000)			Motta et al. (1993); and Smith (1997) from Ulanowicz et al. (1998)
Sardinella aurita	0.001	SEAMAP trawl (2004)	24.600	Pred. Palomares and Pauly (1989)	0.950	GoM model from Mackinson (2000)			Motta et al. (1993); and Smith (1997) from Ulanowicz et al. (1998)
Opisthonema oglinum	0.046	SEAMAP trawl (2004)	29.400	Pred. Palomares and Pauly (1989)	1.600	GoM model from Mackinson (2000)			Motta et al. (1993); and Smith (1997) from Ulanowicz et al. (1998)
Demersal forage			**16.406**		**0.623**		**0.951**	Okey and Pugliese (2001)	
Leiostomus xanthurus	0.720	SEAMAP trawl (2004)	17.900	Pred. Palomares and Pauly (1989)	0.350	GoM model from Mackinson (2000)			NOAA trawl data 1977-1980 from Bowman et al. (2000)
Micropogonias undulatus	0.510	SEAMAP trawl (2004)	22.900	Pred. Palomares and Pauly (1989)	0.350	GoM model from Mackinson (2000)			Carr and Adams (1973); Livingston (1984); de la Cruz-Aguero (1993); Chavez et al. (1993); and FLDEP (1997) from Ulanowicz et al. (1998)
Lagodon rhomboides	0.065	SEAMAP trawl (2004)	11.600	Chavez et al. (1993); and Vega-Cendejas et al. (1993) from Ulanowicz et al. (1998)	1.245	Chavez et al. (1993); and Vega-Cendejas et al. (1993) from Ulanowicz et al. (1998)			Carr and Adams (1973); Livingston (1984); Huh and Kitting (1985); and Motta et al. (1995) from Ulanowicz et al. (1998)
Orthopristis chrysoptera	0.487	SEAMAP (2000) trawl from Mackinson (2000)	8.300	Pred. Palomares and Pauly (1989)	1.250	GoM model from Mackinson (2000)			NOAA trawl data 1977-1980 from Bowman et al. (2000)
Menticirrhus sp.	0.033	SEAMAP (2000) trawl from Mackinson (2000)	12.500	Pred. Palomares and Pauly (1989)	0.350	GoM model from Mackinson (2000)			Carr and Adams (1973); Livingston (1984); de la Cruz-Aguero (1993); Chavez et al. (1993); and FLDEP (1997) from Ulanowicz et al. (1998)

Table A1 (Cont'd)

Group	Biomass (t/km²)	Reference	*Q/B* (year⁻¹)	Reference	*P/B* (year⁻¹)	Reference	*EE*	Reference	Diet composition (see Table A2 for values)
Zooplankton			**43.300**		**13.000**		**0.950**	Okey and Pugliese (2001)	
Zooplankton	36.500	Sutton and Burghart (2000) from Okey and Pugliese (2001)	43.300	Sutton and Burghart (2000) from Okey and Pugliese (2001)	13.000	Sutton and Burghart (2000) from Okey and Pugliese (2001)			Mackinson (2000)
Atlantic menhaden	**6.263**		**16.425**		**2.174**				
Brevoortia tyrannus	6.263	ASMFC (2006)	16.425	Rippetoe (1993)	2.174	ASMFC (2006)			Lewis and Peters (1994)
Invertebrates			**11.056**		**0.930**		**0.833**	Okey and Pugliese (2001)	
Marine crabs	9.261	Okey and Pugliese (2001)	8.500	Arreguin-Sanchez et al. (1993) from Okey and Pugliese (2001)	1.380	Ehrhardt and Restrepo (1989) from Okey and Pugliese (2001)			Freire and González-Gurriarán (1995); Mantelatto and Christofoletti (2001)
Shrimp	0.550	Mackinson et al. (2000)	19.200	Arreguin-Sanchez et al. (1993) from Okey and Pugliese (2001)	3.160	Parrack (1981); Arreguin-Sanchez et al. (1993); Okey and Nance (2000) from Okey and Pugliese (2001)			http://www.dnr.sc.gov/marine/pub/seascience/shrimp.html
Echinoderms	25.000	Okey (2000a) from Okey and Pugliese (2001)	3.700	Pauly et al. (1993) from Okey and Pugliese (2001)	1.200	Lewis (1981); Schwinghamer et al. (1986) from Opitz (1993) from Mackinson et al. (2001)			http://www.oceaninn.com/guides/echino.htm
Bivalves	55.000	Arnold et al. (2000) from Okey and Pugliese (2001)	23.000	Guénette (1996) from Mackinson et al. (2001)	1.220	Arnold et al. (2000)			Mackinson (2000)

Table A1 (Cont'd)

Group	Biomass (t/km^2)	Reference	*Q/B* (year^{-1})	Reference	*P/B* (year^{-1})	Reference	*EE*	Reference	Diet composition (see Table A2 for values)
Sessile epibenthos	219.000	Mackinson et al. (2000)	9.000	Based on Wilkinson (1987) & Sorokin (1987) in Opitz (1993) from Mackinson et al. (2001)	0.800	Odum and Odum (1955); Sorokin (1987) in Opitz (1993) from Mackinson et al. (2001)			Mackinson et al. (2000)
Stomatopods	0.994	Mackinson et al. (2000)	7.430	Meyer and Caldwell (2000) from Mackinson et al. (2001)	1.340	Meyer and Caldwell (2000) from Mackinson et al. (2001)			Mackinson et al. (2000)
Phytoplankton					**332.670**		**0.650**	Okey and Pugliese (2001)	
Pytoplankton	5.645	Okey and Pugliese (2001)			332.670	Cahoon and Cooke (1992) from Okey and Pugliese (2001)			
Macroalgae + Sea grass	**241.450**				**10.078**				
Macroalgae	36.050	Mackinson et al. (2000)			4.000	Luning (1990) from Okey and Pugilese (2001)			
Sea grass	175.620	Mackinson et al. (2000)			9.010	Mackinson et al. (2000)			
Microphytobenthos	29.780	Mackinson et al. (2000)			23.730	Mackinson et al. (2000)			
Detritus	**518.000**								
Detritus	518.000	Okey (2000b) from Okey and Pugliese (2001)							

Table A2. Diet composition matrix for functional groups within the South Atlantic Bight Ecopath model. Values are weighted based on biomass estimates of individual groups within each functional group (see Table A1 for individual group references); all values have been normalized to 100%.

		Predator														
Prey	Functional group	1	2	3	4	5	6	7	8	10	11	13	14	15	16	17
1	Bluefin tuna															
2	Large coastal sharks		0.020													
3	Demersal elasmobranchs	0.001	0.309				3.900E-05									
4	Bluefish, Striped Bass, Weakfish	0.003	0.019	0.033		0.367	8.600E-05								0.002	
5	Bottlenose dolphin															
6	Pelagic piscivores	0.025					0.106								0.223	
7	Pelagic forage	0.002	0.002		0.066		0.275					0.500	0.084	0.025	0.564	0.266
8	Atlantic menhaden	0.955	0.048		0.569	0.041	0.509					0.300			0.002	
9	Phytoplankton								0.355	0.500	0.276					
10	Zooplankton							0.519	0.178	0.250	0.068		0.016	0.002		
11	Invertebrates	0.005	0.010	0.834	0.016		0.056	0.466			0.081	0.050	0.877	0.853	0.146	0.654
12	Macroalgae + Sea grass	1.000E-04	5.400E-05				0.006	0.013	0.005		0.107		0.013			
13	Marine birds															
14	Demersal forage	0.007	0.436	0.095	0.266	0.500	0.042	0.002				0.100	0.010	0.120	0.011	
15	Demersal piscivores		0.077	0.006	0.084		0.003								0.032	
16	Small tuna species		0.078												4.00E-04	
17	Cephalopods	0.003	0.002	0.006		0.092	0.001					0.050		2.900E-04	0.019	0.08
18	Detritus			0.026					0.462	0.250	0.469					

Table A3. Fisheries landings for functional groups within the SAB Ecopath model. Landings data from commercial, recreational, and combined fisheries are given (mt·km^{-2}). Total landings (mt) are based on combined fisheries landings for the total area (90,600 km^2) within the SAB.

	Landings			
Functional group	Commercial (mt·km^{-2})	Recreational (mt·km^{-2})	Combined (mt·km^{-2})	Total (mt)
Bluefin tuna	0.001		0.001	94.60
Large coastal sharks	0.013	0.003	0.016	1469.26
Demersal elasmobranchs	0.003	0.001	0.004	340.47
Bluefish, Striped Bass, Weakfish	0.021	0.025	0.046	4177.98
Pelagic piscivores	0.042	0.093	0.135	12212.48
Pelagic forage	0.028	0.027	0.055	5014.68
Atlantic menhaden	0.067		0.067	6051.80
Inverts	0.283		0.283	25650.60
Demersal forage	0.078	0.025	0.103	9331.33
Demersal piscivores	0.049	0.027	0.077	6936.20
Small tuna species	0.007	0.040	0.047	4236.82
Cephalopods	0.008		0.008	684.50