Feeding ecology of Atlantic bluefin tuna (*Thunnus thynnus*) in North Carolina: diet, daily ration, and consumption of Atlantic menhaden (*Brevoortia tyrannus*)

Christopher M. Butler (contact author)
Paul J. Rudershausen
Jeffrey A. Buckel
Email address for contact author: c.m.butler@usm.edu
Department of Biology
Center for Marine Sciences and Technology
North Carolina State University
303 College Circle
Morehead City, North Carolina 28557
Present Address (for C. M. Butler): Center for Fisheries Research & Development
Gulf Coast Research Laboratory
The University of Southern Mississippi
703 East Beach Drive
Ocean Springs, Mississippi 39564

Abstract—Diet, gastric evacuation rates, daily ration, and population-level prey demand of bluefin tuna (*Thunnus thynnus*) were estimated in the continental shelf waters off North Carolina. Bluefin tuna stomachs were collected from commercial fishermen during the late fall and winter months of 2003–04, 2004–05, and 2005–06. Diel patterns in mean gut fullness values were used to estimate gastric evacuation rates. Daily ration determined from mean gut fullness values and gastric evacuation rates was used, along with bluefin tuna population size and residency times, to estimate population-level consumption by bluefin tuna on Atlantic menhaden (*Brevoortia tyrannus*). Bluefin tuna diet (n=448) was dominated by Atlantic menhaden; other teleosts, portunid crabs, and squid were of mostly minor importance. The time required to empty the stomach after peak gut fullness was estimated to be ~20 hours. Daily ration estimates were approximately 2% of body weight per day. At current western Atlantic population levels, bluefin tuna predation on Atlantic menhaden is minimal compared to predation by other known predators and the numbers taken in commercial harvest. Bluefin tuna appear to occupy coastal waters in North Carolina during winter to prey upon Atlantic menhaden. Thus, changes in the Atlantic menhaden stock status or distribution would alter the winter foraging locations of bluefin tuna.

Manuscript submitted 13 January 2009.
Manuscript accepted 21 October 2009.
Fish. Bull. 56–69 (2010).

Ecosystem-based management of marine fisheries, as a complementary approach to single-species stock assessments, is now recommended (Latour et al., 2003). Ecosystem-based models incorporate ecological interactions to evaluate the potential flows of energy and biomass among interacting populations within an exploited ecosystem (Pauly et al., 2000). Some of these models allow comparisons between removals by natural predators and fisheries to help address tradeoffs (e.g., harvesting fewer prey to provide potential prey biomass for more predators) when fisheries for both predator and prey exist (Overholtz et al., 2008).

Atlantic menhaden (*Brevoortia tyrannus*) play a vital ecological role in estuarine and coastal habitats along the East Coast of the United States (Quinlan et al., 1999). From 2002 to 2006, Atlantic menhaden comprised between 27.0% to 30.5% of the total U.S. commercial landings in the Atlantic and represented one of the larger commercial fisheries in the United States (NOAA[1]). On the U.S. East Coast, there is much controversy over the Atlantic menhaden fishery and whether or not it should be reduced or shut down to prevent reductions in the availability of prey biomass. Atlantic menhaden are considered a primary forage species for several commercially and recreationally important predators including striped bass (*Morone saxatilis*), bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) (NEFSC[2]). In addition to these three predators, 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.

The bluefin tuna is a highly migratory pelagic species that is distributed throughout the North Atlantic Ocean. In western North Atlantic waters, bluefin tuna are found from Nova Scotia to Brazil (Block et al., 2001). Migrations are related to annual spawning and feeding events

[1] National Oceanic and Atmospheric Administration (NOAA). 2007. Annual Commercial Landing Statistics. [Available from http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html, accessed August 16, 2008.]

[2] NEFSC (Northeast Fisheries Science Center). 2006. 42nd northeast regional stock assessment workshop (42nd SAW) stock assessment report, part B: Expanded multispecies virtual population analysis (MSVPA-X) stock assessment model. U.S. Dep. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 06-09b, 308 p.

(Rooker et al., 2007; Teo et al., 2007). Beginning in late November, bluefin tuna migrate into North Carolina coastal waters and feed upon local prey resources (Kade, 2000; Boustany, 2006). Atlantic menhaden aggregate off North Carolina to spawn during winter (Checkley et al., 1999) and may be the primary prey of bluefin tuna.

When compared to other teleosts, bluefin tuna have standard metabolic rates that are among the highest of any fish species (Dickson and Graham, 2004; Blank et al., 2007). These high metabolic demands require them to consume large amounts of prey. Thus, bluefin tuna have the potential to influence the abundance of other species within an ecosystem. Overholtz (2006) modeled predation demand of bluefin tuna on Atlantic herring (*Clupea harengus*) in the Northwest Atlantic during summer months. Consumption of Atlantic herring by bluefin tuna was highest in 1970, declined to a low in 1982, and increased through 2002. To our knowledge, the predatory impact of bluefin tuna on Atlantic menhaden during winter has not been examined.

Here, we describe the diets of bluefin tuna (>185 cm curved fork length) off North Carolina during winter. We also estimate field-derived gastric evacuation rates and daily ration; daily ration is used to estimate the population-level consumption of bluefin tuna on Atlantic menhaden. Lastly, we compare the population-level consumption of Atlantic menhaden by bluefin tuna with the predatory demand from other known Atlantic menhaden predators. The latter question was addressed at both current and rebuilt bluefin tuna populations to investigate predator and prey management implications.

Materials and methods

Study area

From 2003 to 2006, we sampled stomachs from commercially caught bluefin tuna landed in Beaufort and Morehead City, North Carolina. The fishery operated from November through January (length of season varied by year) within a 28-km radius (centered at approximately 34°26′N lat., 76°28′W long.) south of Cape Lookout shoals. Bluefin tuna were predominantly captured by trolling, where a dead-baited hook (with or without a lure) is pulled behind a moving vessel to imitate live prey. Generally, ballyhoo (*Hemiramphus brasiliensis*) was used as bait.

Collection of samples

Bluefin tuna stomachs were collected during the winters of 2003–04 (n=42), 2004–05 (n=219), and 2005–06 (n=187) off the coast of North Carolina; during the first winter a pilot collection was undertaken and the results were included only in the overall diet analysis. For most bluefin tuna, stomachs and other viscera were removed at sea by the fishermen. Upon excision, all stomachs were stored on ice until they could be collected by researchers. In addition to the stomach, the fisherman was responsible for providing information on time and location of capture, curved fork length (*CFL*, cm), and dressed weight (*DW*, kg). Curved fork length 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 by using the allometric relationship of *CFL* to *DW* defined from the current study (n=379) as

$$DW = 7.625 \times 10^{-6} \cdot CFL^{3.088},\ r^2 = 0.871.$$

Dressed weights were converted to round weights (i.e., the total weight of a live fish; *RW*, kg) by using the regression equation (n=685) developed by Baglin (1980):

$$RW = -7.922 + 1.296 \cdot DW,\ r^2 = 0.874.$$

Diet analysis

Individual stomach samples 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 possible taxon. Identifiable prey items were grouped by taxa and wet weight (g) was recorded. Teleosts or invertebrates that could not be identified were measured and recorded as unidentified species (e.g., “unidentified fish remains”).

Diets were expressed by indices of percent frequency of occurrence (*%O*) and percent weight (*%W*) (Hyslop, 1980). Percent frequency of occurrence was calculated as the number of bluefin tuna that had ingested a specific prey item divided by the total number of bluefin tuna that contained prey. Percent weight was estimated as the total wet weight of a specific prey type divided by the total wet weight of all prey across the total number of stomachs samples.

Cumulative prey curves were constructed *a posteriori* by within-winter period (early December, late December, and January), year (2004–05 and 2005–06), and size class (large medium [individuals between 185.4 and 205.7 cm *CFL*] and giant [individuals >205.7 cm *CFL*]) to determine if the sample sizes were sufficient to describe bluefin tuna diets (Ferry and Cailliet, 1996). Prey species were grouped by family and the mean and standard deviation of the cumulative number of unique prey was calculated by randomly resampling the number of stomachs that contained prey 500 times (Bizzarro et al., 2007). The cumulative mean number of unique prey taxa calculated from randomized stomach samples was then plotted against the number of stomachs examined (Ferry and Cailliet, 1996). Sample size sufficiency for each prey curve was tested by the linear regression method (Bizzarro et al., 2007), where the slope from a regression of the mean number of unique prey items from the last four stomach samples was compared to a slope of zero (Student’s t-test of the equality of two population regression coefficients; Zar, 1999). Sample size sufficiency was reached if the difference between the slopes was not significantly different ($P>0.05$).

The effects of within-winter period, year, and size class on bluefin tuna diets were determined by using row × column ($R \times C$) tests of independence and using counts of stomachs with a particular prey species (Sokal and Rohlf, 1981). Prey species were grouped by family for $R \times C$ tests and degrees of freedom were calculated as (*rows*–1) (*columns*–1).

Gastric evacuation rate and daily ration

Individual stomach fullness (kg prey/kg predator) values were highest in early afternoon and lowest during the early morning for both large medium and giant bluefin tuna. These high and low periods were used as beginning and ending points, respectively, to estimate gastric evacuation rates. Stomach fullness values were assigned to one-hour time periods (with the exception of the first and final hours when stomachs were at values before maximum and after minimum stomach fullness, respectively) to examine diel feeding patterns; data from 2004–05 (n=64) and 2005–06 (n=114) were pooled for this analysis to increase sample size. Gastric evacuation rates (GER) of bluefin tuna were estimated using an exponential decay model (Elliott and Persson, 1978),

$$S_t = S_0 \cdot e^{-GER \cdot t}, \tag{1}$$

where S_t = the individual stomach fullness at time t;
S_0 = the stomach fullness at time t=0;
GER = the instantaneous rate of gastric evacuation (rate per hr); and
t = the time in hours after peak gut fullness.

The number of fish used in this analysis was lower than the total collected because time of capture was not always provided by the fishing crew. Although other evacuation rate models have been used with tuna (e.g., linear, Olson and Boggs, 1986), we chose the exponential model because we could not test between multiple evacuation models given the gap in stomach contents data at night. Additionally, an exponential decline may better describe the evacuation rates of fish which require rapid digestion rates because of high metabolic demands (Bromley, 1994). The difference ($GER_{difference}$) between $GER_{large\ medium}$ and GER_{giant} was estimated by using the nonlinear (NLIN) procedure of SAS (SAS, 1996). If the confidence interval of $GER_{difference}$ contained the value of zero then it was assumed that $GER_{large\ medium}$ and GER_{giant} were not significantly different.

Daily ration (kg prey/kg predator/day) estimates of large medium, giant, and pooled bluefin tuna size classes were calculated by using the Eggers (1977) approach,

$$DR = 24 \cdot \overline{S} \cdot GER, \tag{2}$$

where DR = the daily ration estimate; and
$\overline{S}$ = the mean stomach fullness of the hourly means.

For time points at which no stomachs were collected (1900–0300 Eastern Standard Time [EST]), stomach fullness values were estimated from the gastric evacuation model (described above).

Population-level consumption

Annual population-level consumption of Atlantic menhaden by bluefin tuna during their residency in North Carolina (C_{Pop}) was estimated as

$$C_{Pop} = B_{BFT} \cdot P_{NC} \cdot DR \cdot W_{Mh} \cdot T_{NC}, \tag{3}$$

where B_{BFT} = bluefin tuna biomass (kg);
P_{NC} = proportion of the bluefin tuna population in North Carolina during the winter;
DR = the estimate of bluefin tuna daily ration (kg prey/kg predator/day) in this study;
W_{Mh} = the proportion by weight of Atlantic menhaden in bluefin tuna stomachs; and
T_{NC} = the time (days) that bluefin tuna and Atlantic menhaden are both present in the coastal waters of North Carolina.

In order to determine the precision of C_{Pop}, a distribution of C_{Pop} estimates was obtained by using simulation software (@RISK, vers. 5.0, Palisade Corp.). The Monte Carlo simulation approach is described in Overholtz (2006); briefly, a distribution was created for each variable in the C_{Pop} equation above. Then, a random draw was made from each distribution and a new estimate of C_{Pop} was made. This process was repeated 5000 times. The range of C_{Pop} estimates was then compared to the range of consumption estimates previously published on other known Atlantic menhaden predators (e.g., bluefish, striped bass, weakfish, and the Atlantic Coast commercial harvest). The consumption estimates presented are annual and cover the entire U.S. East Coast. Given past bluefin tuna diet studies conducted on summer and fall feeding grounds (e.g., Chase 2002), we assume that Atlantic menhaden are not a major prey of bluefin tuna in other areas at other times of the year. Thus, our estimates off North Carolina during winter are likely indicative of the annual coastwide consumption of Atlantic menhaden by bluefin tuna.

Bluefin tuna captured in North Carolina were estimated to be predominantly age 6+ fish based on size-at-age regressions (Murray-Brown et al.[3]). The most recent (2005) population estimate was 94,836 age-6+ bluefin tuna (ICCAT, 2007). These values were coupled with individual mean weight-at-age[3] estimates to calculate the total biomass (B_{BFT}) of age 6+ bluefin tuna from the western Atlantic. A pert distribution of the mean, minimum, and maximum B_{BFT} values was constructed by using one standard deviation below and above the

[3] Murray-Brown, M., S. McLaughlin, and C. Lopez. 2007. History of United States Atlantic bluefin tuna size class classification and changes. NOAA Fisheries Final Report, 14 p. U.S. Dep. Commerce, Silver Spring, MD.

calculated mean biomass; the assumed coefficient of variation was 30% (Overholtz, 2006).

It is unknown what proportion of the age-6+ bluefin tuna biomass occurs off North Carolina during winter. Therefore, we used data from a preliminary Ecopath model of the South Atlantic Bight which indicated that biomass levels ranged between 5% and 25% of the total age-6+ western Atlantic bluefin tuna population (Butler, 2007). A uniform distribution with this range of P_{NC} values was used for the Monte Carlo simulation.

A pert distribution (Overholtz, 2006) was used to model the estimate of DR from the current study. Minimum and maximum estimates of DR were calculated as one standard deviation above and below the mean, respectively (Overholtz, 2006); the standard deviation of DR was calculated by the Delta method (Williams et al., 2002).

The proportion by weight of Atlantic menhaden in bluefin tuna diet (W_{Mh}) was modeled by a uniform distribution where the minimum and maximum values were the lowest and highest W_{Mh} values observed annually in this and Kade's (2000) study. A uniform distribution was chosen because it allows an equal probability of occurrence for the estimated proportion by weight value (i.e., W_{Mh}) between the minimum and maximum observed values.

The maximum number of days (T_{NC}) that both Atlantic menhaden and bluefin tuna overlap in North Carolina is unknown. Adult Atlantic menhaden form large spawning congregations in the shelf waters off North Carolina from November through March (Checkley et al., 1999). Bluefin tuna are commercially harvested off North Carolina beginning in late November until the end of January. However, Boustany (2006) has shown that bluefin tuna fitted with pop-up satellite tags may extend their residency in these waters until late May. Thus, the maximum T_{NC} was assumed to be 120 days (i.e., late November through late March) and a minimum was chosen arbitrarily at 30 days. A uniform distribution covering this range was used for the simulations.

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 in 1975 (ICCAT, 2007). Thus, a new distribution of C_{Pop} for a "restored" population was determined by using abundance-at-age data from 1975 for age-6+ bluefin tuna to calculate a new distribution of B_{BFT}. All other distributions for the "restored" analysis were identical to the distributions used for the current population model.

Results

Diet analysis

The stomach contents of 448 bluefin tuna were examined. Of these, 124 (100 nonempty) were large medium and 324 (252 nonempty) were giant tuna. Samples were further categorized by year and within-winter time period (i.e., 1–14 December, 15–31 December, and 1–31 January). The two December time periods were chosen because of good sample sizes throughout December and perceived changes in diets within that month. January was not split into two time periods because most January fish were caught within the first two weeks of the month during each year of the study.

Overall, stomachs of 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. Atlantic menhaden (*Brevoortia tyrannus*) was the most common prey item by $\%O$ for both large medium (Table 1) and giant bluefin tuna (Table 2). By weight, Atlantic menhaden similarly dominated the diets of both size classes (Tables 1 and 2). Although Atlantic needlefish (*Strongylura marina*) were not important to large medium bluefin tuna, they were the second most identifiable prey item of giants (7.14% O, 3.16% W), mainly in one year (2005–06). Despite the occurrence of individual portunids and cephalopods in both size classes, they contributed little in terms of biomass. Other prey included several teleost species, elasmobranchs, bivalves, and algae that were rare items and that contributed little to the diet.

Sample sizes were adequate to describe the within-winter diet of giant bluefin tuna, as well as between winters for both size classes and size class comparisons. All within-winter periods for giant bluefin tuna, with the exception of January 2006, reached an asymptote (Table 3). Both large medium and giant size classes reached asymptotes when data were pooled by winter (Table 3). However, the within-winter analyses of large medium bluefin tuna were likely biased because of the low sample sizes. Randomized cumulative prey curves did not reach an asymptote for any of the within-winter periods for large medium bluefin tuna (Table 3). Given the difficulty in collecting large numbers of stomachs over short periods, the lack of a defined asymptote is not uncommon in diet studies of other apex species (Bethea et al., 2004).

Atlantic menhaden was the dominant prey of large medium bluefin tuna throughout the winter in both years (Fig. 1, A and B). Diets of large medium bluefin tuna were independent of within-winter time period (Table 4). Although Atlantic menhaden varied in importance, variability in other prey groups (e.g., portunids, teleosts) likely drove the within-winter effect of the giant size class (Fig. 2, A and B; Table 4). The diets of large medium bluefin tuna were dominated by Atlantic menhaden in both winters (Fig. 1C; Table 4). The diet of giant bluefin tuna did differ between years (Table 4) owing to the increased occurrence of Atlantic needlefish and cephalopods in 2005–06 (Fig. 2C). Overall, the two size classes differed in diets (Table 4). This result was likely driven by the higher occurrence of non-Atlantic menhaden prey types in giants than in large medium bluefin tuna (Figs. 1C and 2C).

Table 1

Stomach contents of large medium (185.4–205.7 cm curved fork length [CFL]) Atlantic bluefin tuna (*Thunnus thynnus*) caught off Cape Lookout, North Carolina, during Dec. 2003–Jan. 2004, Dec. 2004–Jan. 2005, and Dec. 2005–Jan. 2006. Diet is presented as percent frequency of occurrence (%*O*) and percent prey weight (%*W*).

	Dec. 2003–Jan. 2004		Dec. 2004–Jan. 2005		Dec. 2005–Jan. 2006		Pooled years	
Prey item	%*O*	%*W*	%*O*	%*W*	%*O*	%*W*	%*O*	%*W*
Chordata								
Brevoortia tyrannus	76.92	89.41	96.88	98.97	82.61	96.43	91.00	98.42
Menticirrhus littoralis					4.35	1.45	1.00	0.24
Mugil cephalus			1.56	0.69			1.00	0.57
Pomatomus saltatrix			1.56	0.17			1.00	0.14
Strongylura marina					4.35	0.13	1.00	0.02
Unidentified fish remains	30.77	6.78	4.69	0.05	13.04	0.33	10.00	0.19
Crustacea								
Ovalipes sp.					4.35	0.19	1.00	0.03
Portunus gibbesii			1.56	0.02			1.00	0.01
Portunus spinimanus			1.56	0.05	4.35	0.28	2.00	0.09
Portunus spp.					4.35	0.04	1.00	0.01
Unidentified crab	7.69	1.91	1.56	0.01	4.35	0.04	3.00	0.04
Mollusca								
Loligo pealeii			1.56	0.04	8.70	1.11	1.00	0.03
Unidentified squid	7.69	0.02					3.00	0.18
Protista								
Unidentified algae	15.38	1.87					2.00	0.03
Total prey biomass (kg)	1.45		83.04		16.37		100.86	
Total stomachs sampled	14		80		30		124	
Stomachs with prey (%)	13 (92.9)		64 (80.0)		23 (76.7)		100 (80.6)	
Empty stomachs (%)	1 (7.1)		16 (20.0)		7 (23.3)		24 (19.4)	
Mean length of bluefin tuna (cm)	198.57		194.59		197.18		195.66	
Standard error	1.27		0.62		1.14		0.52	
Mean weight of bluefin tuna (kg)	119.02		108.66		113.03		110.89	
Standard error	2.89		1.72		3.03		1.40	

When examined by %*W*, diets were almost always dominated by Atlantic menhaden (Fig. 1, D–F and Fig. 2, D–F). The only exception was the 1–14 December 2005 within-winter period when Atlantic needlefish accounted for approximately 60% of diet by weight for giant tuna. When pooled, diets varied little between winters (for either large medium or giant bluefin tuna) or between size classes (Figs. 1F and 2F).

Gastric evacuation rates and daily ration

During winter in North Carolina, large medium and giant bluefin tuna appear to feed predominantly during diurnal time periods (Fig. 3, A and B). A small number of fish were caught on trolled baits several hours before sunrise, and those stomachs collected during presunrise hours were typically empty or contained food in the final stages of digestion (e.g., scales, bones, eye lenses, and pyloric stomachs of Atlantic menhaden), indicating that digestion occurred throughout the night and that feeding had not resumed until just before sunrise. Sample sizes for each size class were largest after sunrise (approximately 0700 EST) and remained high throughout the morning as gut fullness increased. Large medium bluefin tuna reached maximum gut fullness between 1200 and 1300 EST (time point zero on Fig. 3A). The estimate of *GER* (±standard error [SE]) for the large medium bluefin tuna size class was 0.13 ±0.05/hr. Giant bluefin tuna attained a maximum gut fullness between 1300 and 1400 EST (time point zero on Fig. 3B), and had a *GER* (±SE) of 0.12 ±0.04/hr. The confidence interval of $GER_{difference}$ contained the value of zero, and therefore there was no significant difference between $GER_{large\ medium}$ and GER_{giant}. Thus, a combined (large medium and giant) *GER* value (Fig. 3C) was used to estimate *DR*. The *GER* (±SE) was 0.12 ±0.03/hr for the combined analysis (Fig. 3C).

The mean (±SE) *DR* estimate of bluefin tuna in NC was 2.03% ±0.59. When multiplied by the mean weight of bluefin tuna collected during our study, the absolute daily consumption by an individual bluefin tuna in North Carolina during winter was 3.18 kg/day.

Table 2

Stomach contents of giant (>205.7 cm curve fork length [CFL]) Atlantic bluefin tuna (*Thunnus thynnus*) caught off Cape Lookout, North Carolina, during Dec. 2003–Jan. 2004, Dec. 2004–Jan. 2005, and Dec. 2005–Jan. 2006. Diet is presented as percent frequency of occurrence (%*O*) and percent prey weight (%*W*).

	Dec. 2003–Jan. 2004		Dec. 2004–Jan. 2005		Dec. 2005–Jan. 2006		Pooled years	
Prey item	%*O*	%*W*	%*O*	%*W*	%*O*	%*W*	%*O*	%*W*
Chordata								
Ammodytes sp.			1.00	0.01			0.79	<0.01
Anchoa hepsetus			1.00	0.01	0.73	<0.01	0.79	<0.01
Archosargus sp.			1.00	0.11	2.19	0.11	1.59	0.11
Brevoortia tyrannus	60.00	91.39	84.00	98.96	83.21	92.97	82.54	94.71
Chilomycterus sp.					1.46	0.07	0.79	0.04
Cynoscion regalis					1.46	0.46	0.79	0.31
Diapterus auratus	6.67	1.78					0.40	0.04
Engraulidae	6.67	0.16					0.40	<0.01
Lagodon rhomboides					0.73	0.05	0.40	0.03
Micropogonias sp.					0.73	0.04	0.40	0.03
Mustelus canis					0.73	0.16	0.40	0.11
Orthopristis chrysoptera					2.19	0.04	1.19	0.03
Pomatomus saltatrix					0.73	0.01	0.40	0.01
Sphyraena borealis					0.73	0.04	0.40	0.02
Strongylura marina			1.00	0.01	12.41	4.61	7.14	3.16
Syngnathus louisianae			1.00	0.01			0.40	<0.01
Syngnathus sp.					0.73	<0.01	0.40	<0.01
Triglidae	6.67	0.52					0.40	0.01
Unidentified fish remains	40.00	0.74	14.00	0.09	15.33	0.34	15.87	0.27
Crustacea								
Callinectes sapidus	6.67	0.17					0.40	<0.01
Ovalipes sp.	13.33	0.37	3.00	0.16	3.65	0.04	3.97	0.08
Portunidae	6.67	0.10	6.00	0.17	0.73	<0.01	3.17	0.05
Portunus gibbesii	13.33	4.28	8.00	0.15	7.30	0.15	9.13	0.24
Portunus spinimanus	6.67	0.33	4.00	0.09	2.92	0.05	3.57	0.07
Portunus spp.			1.00	0.02	7.30	0.07	4.37	0.05
Unidentified crab	13.33	0.12	6.00	0.08	3.65	0.02	5.16	0.04
Mollusca								
Loligo pealeii			2.00	0.07	2.19	0.48	1.98	0.35
Unidentified squid					8.03	0.30	4.37	0.20
Unidentified clam			1.00	0.06			0.40	0.02
Protista								
Unidentified algae	6.67	0.03	1.00	<0.01	0.73	0.01	1.19	0.01
Total prey biomass (kg)	7.54		106.23		245.43		359.20	
Total stomachs sampled	28		139		157		324	
Stomachs with prey (%)	15 (53.6)		100 (71.9)		137 (87.3)		252 (77.8)	
Empty stomachs (%)	13 (46.4)		39 (28.1)		20 (12.7)		72 (22.2)	
Mean length of bluefin tuna (cm)	217.56		223.14		225.92		224.01	
Standard Error	1.89		0.93		1.12		0.71	
Mean weight of bluefin tuna (kg)	155.12		172.09		179.17		174.66	
Standard Error	5.25		2.70		3.37		2.08	

Population-level consumption

Using bluefin tuna abundance data from 2005, we estimated that C_{Pop} ranged from 189 to 13,385 metric tons (t) (mean=3,021 t; Fig. 4A). For a completely restored bluefin tuna population, estimates ranged from 986 to 42,858 t (mean=10,020 t; Fig. 4B). At 2005 population levels, the maximum estimate of C_{Pop} was below the majority of estimates of annual predatory demand by other predators of Atlantic menhaden; other predators were bluefish, striped bass, and weakfish (Fig. 5). However, the maximum estimate of C_{Pop} by a fully restored

Table 3

Results from randomized cumulative prey curves for large medium and giant bluefin tuna (*Thunnus thynnus*) collected off Cape Lookout, North Carolina, during the 2004–05 and 2005–06 season. Values in bold indicate sufficient sample sizes to describe bluefin tuna diet at α=0.05. Sample sizes (n), sampling statistics (t), and P-values are presented.

Large medium	n	t	P-value	Giant	n	t	P-value
2004–05				2004–05			
1–14 Dec.	20	56.003	<0.001	1–14 Dec.	**16**	**2.152**	**0.164**
15–31 Dec.	40	5.061	0.037	15–31 Dec.	**57**	**4.042**	**0.056**
1–31 Jan.	4	5.590	0.031	1–31 Jan.	**27**	**3.839**	**0.062**
Pooled data	**64**	**0.965**	**0.435**	Pooled data	**100**	**2.541**	**0.126**
2005–06				2005–06			
1–14 Dec.	8	8.914	0.012	1–14 Dec.	**24**	**3.891**	**0.060**
15–31 Dec.	10	20.350	0.002	15–31 Dec.	**87**	**2.460**	**0.133**
1–31 Jan.	5	6.699	0.022	1–31 Jan.	26	10.298	0.009
Pooled data	**23**	**3.888**	**0.060**	Pooled data	**137**	**–0.440**	**0.703**

bluefin tuna population fell within the ranges of predatory demand of these other predators (Fig. 5). None of the consumption estimates of natural Atlantic menhaden predators approached the annual harvest from the commercial fishery.

Table 4

Chi-square values for comparisons of the effects of within-winter, year, and size class on dietary composition of Atlantic bluefin tuna (*Thunnus thynnus*) collected off Cape Lookout, North Carolina, during 2004–05 and 2005–06 as determined by R×C tests of independence (Sokal and Rohlf, 1981) of frequency (count) data. Degrees of freedom were calculated as (*rows*–1)(*columns*–1). Within-winter time periods (D1=1–14 December; D2=15–31 December; and J=1–31 January) and years were compared for each size class (large medium and giant tuna) from both years. The total number of nonempty stomachs analyzed for each comparison is given within parentheses.

Groups compared	χ^2 value	Degrees of freedom	P-value
Within-winter			
Large medium tuna			
D1 / D2 / J 2004–05 (64)	10.864	10	0.210
D1 / D2 / J 2005–06 (23)	11.140	10	0.347
Giant tuna			
D1 / D2 / J 2004–05 (100)	16.182	14	0.303
D1 / D2 / J 2005–06 (137)	51.976	14	<0.001
Year			
Large medium tuna			
2004–05 / 2005–06 (87)	9.570	5	0.088
Giant tuna			
2004–05 / 2005–06 (237)	19.736	8	0.011
Size class			
Large medium /Giant (352)	15.637	8	0.048

Discussion

Importance of Atlantic menhaden to bluefin tuna

Atlantic menhaden was the primary prey for both large medium and giant bluefin tuna during multiple winters in North Carolina; this focus on a single prey type is unusual for a marine apex predator. Although other prey were frequently present (e.g., portunid crabs), they contributed little in terms of biomass. With the exception of Kade (2000), Atlantic menhaden has not been considered a dominant prey of bluefin tuna along the U.S. East Coast (Chase, 2002). Kade's (2000) result for 1999 and now our results for subsequent years have confirmed that bluefin tuna are a consistent and potentially important predator of Atlantic menhaden during winter. Although these are the first quantitative studies to identify this predator-prey linkage, historic anecdotal information described bluefin tuna feeding on schools of Atlantic menhaden off New England in the 1800s (Goode, 1879).

The composition of bluefin tuna diet depends on prey availability and predator body size (Chase, 2002). In North Carolina, diets of large medium and giant bluefin tuna were dominated by Atlantic menhaden. Thus, there was no shift in diet with the increase in bluefin tuna length. Chase (2002) reviewed previous bluefin tuna diet studies and came to the conclusion that the diet of bluefin tuna from any particular study location is dominated by "a single, pelagic, schooling prey species." Atlantic menhaden appear to match this prey description during winter in North Carolina.

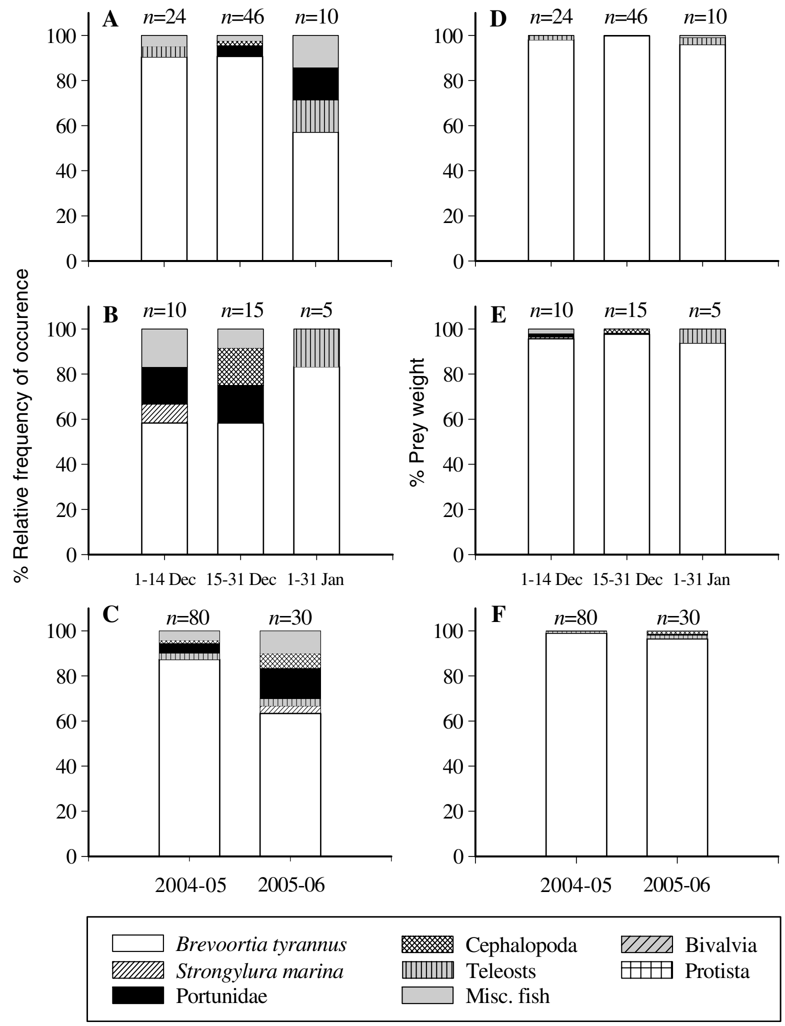

Figure 1

Stomach content composition of large medium Atlantic bluefin tuna (*Thunnus thynnus*) examined by using relative percent frequency of occurrence (**A–C**) and percent prey weight (**D–F**). Stomachs were collected from fish captured near Cape Lookout, North Carolina, during December–January 2004–05 (**A** and **D**), December–January 2005–06 (**B** and **E**), and pooled years (**C** and **F**). Frequency of occurrence data are normalized to 100%.

We regularly observed squid (*Loligo* spp.) and portunid crabs in bluefin tuna stomachs. Squid has been suggested as the second-most important prey item, behind teleosts, in several bluefin tuna diet studies (Dragovich, 1970; Eggleston and Bochenek, 1990; and Kade, 2000). Portunid crabs have previously been documented by Kade (2000), and authors such as Krumholz (1959), Dragovich (1970), and Chase (2002) have found minor amounts of crustaceans in the diet of bluefin tuna of various size classes and at various locations. The inclusion of cephalopods and crustaceans at certain times of the year may be a result of increases in their relative abundance. Juanes et al. (2001) found this to be the explanation for bluefish, a primary piscivore that included invertebrate prey in its diet when invertebrates were relatively abundant in the environment. No quantitative information exists on the distribution and abundance of potential prey. Thus, we were unable to make any conclusions about prey-type selectivity.

Gastric evacuation and daily ration

Bluefin tuna in North Carolina were caught from approximately two hours before sunrise to late afternoon or evening. Time of catch could match bluefin tuna feeding periods or could be an artifact of fishing times.

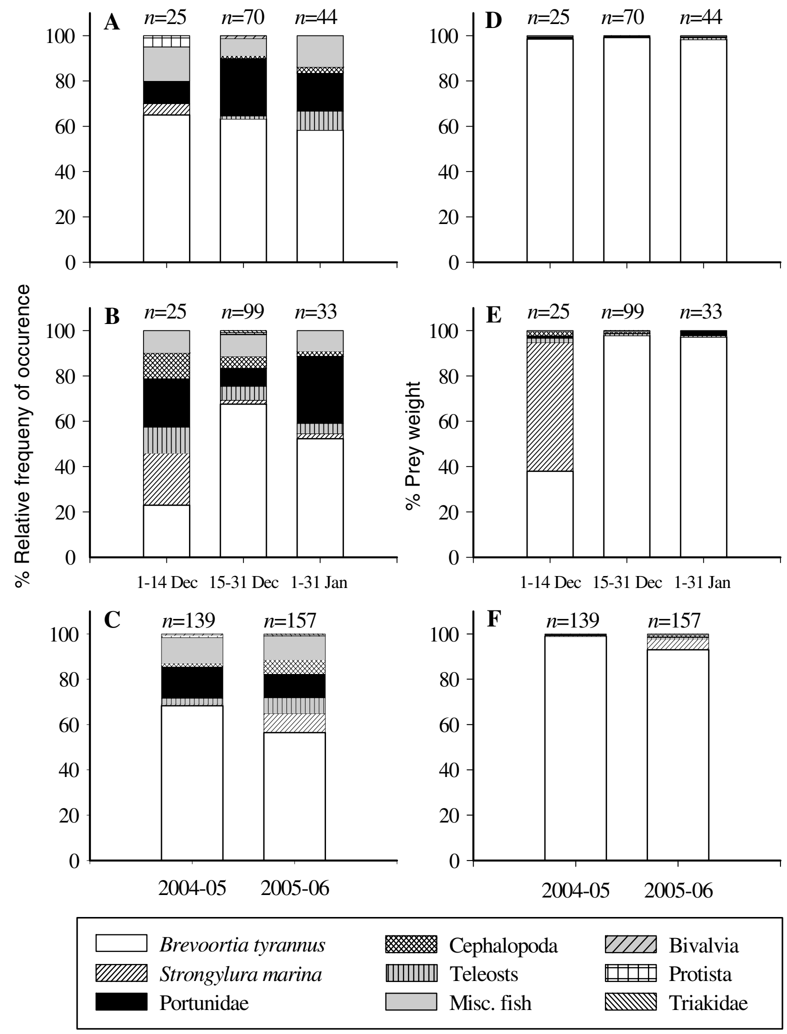

Figure 2

Stomach content composition of giant Atlantic bluefin tuna (*Thunnus thynnus*) examined using relative percent frequency of occurrence (**A–C**) and percent prey weight (**D–F**). Stomachs were collected from fish captured near Cape Lookout, North Carolina, during December–January 2004–05 (**A** and **D**), December–January 2005–06 (**B** and **E**), and pooled years (**C** and **F**). Frequency of occurrence data are normalized to 100%.

We suggest the former given that there has been little success at catching bluefin tuna at night during winter in North Carolina (G. Leone, personal commun.[4]). This finding is further corroborated by observed diurnal feeding patterns in other tuna species such as southern bluefin (*Thunnus maccoyii* [Young et al., 1997]), yellowfin (*Thunnus albacares* [Josse et al., 1998]), longtail (*Thunnus tonggol* [Griffiths et al., 2007]), blackfin (*Thunnus atlanticus* [Josse et al., 1998]), and skipjack (*Katsuwonus pelamis* [Magnuson, 1969]). Additionally, increased foraging activity has been observed during crepuscular hours in New England for Atlantic bluefin tuna (Lutcavage et al., 2000) and for Pacific bluefin tuna (*Thunnus orientalis*) in Alaska (Hobson, 1986). Given the feeding behavior of other tuna species, the absence of tuna catch at night, and the stage of digested items observed in presunrise stomach samples, we conclude that most feeding in North Carolina occurs during presunrise and diurnal hours.

To our knowledge, this is the first field estimate of *GER* for Atlantic bluefin tuna. Young et al. (1997) estimated an exponential *GER* 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 *GER* was calculated in their study, it is not comparable

[4] Leone, George. 2007. Morgan Harvest Inc., Morehead City, NC 28557.

to our estimate. The only other *GER* for a tuna species that we are aware of is that of Olson and Boggs (1986). Those authors found that under laboratory conditions, the *GER* of yellowfin tuna was best represented by a linear evacuation model and depended on the type, surface area, and digestibility of the prey consumed. Their results showed that mackerel, which contained the highest lipid level of the prey types they examined, were the most digestion-resistant and consequently took the longest (~18.5 hours) to evacuate. Because the diets of bluefin tuna in our study were dominated by Atlantic menhaden by weight, our *GER* estimates are representative of Atlantic menhaden prey and should be used with caution if applied to bluefin tuna that feed on other prey, particularly prey that may differ in digestibility (e.g., prey with an exoskeleton, and having differing lipid levels).

In the present study, several key assumptions were made to estimate *GER*. Because no fish were landed from 1900 to 0300 EST, we assumed that feeding was negligible at night. If bluefin tuna do feed throughout the night, then our *GER* and mean gut fullness values (estimated over a 24-hour period) could potentially be biased low (i.e., peak gut fullness would occur later in night with a shorter [and faster] time to digest prey). We also had to assume that stomachs were not completely emptied several hours before the first presunrise samples were collected. Given that many of the samples collected during presunrise hours contained prey in the final stages of digestion, this appears to be a valid assumption. If digestion was completed before the time of sunrise collections (shortening the time between peak and valley), then our current estimates of *GER* would be biased low (i.e., we would again be assuming a longer time to digest prey than what is actually true).

Estimates of digestion times in pen-held and wild Atlantic bluefin tuna corroborate our estimates of *GER*. Butler and Mason (1978) used stomach content analysis on pen-held giant bluefin tuna (>200 kg) that were fed a variety of "forage fish" species and determined that it took 18–20 hours to completely empty a full stomach (other than viscous liquid). Using acoustic telemetry, Stevens et al. (1978) fed mackerel to captive giant bluefin tuna (>200 kg) and identified gradual increases of stomach temperatures which lasted 14 to 20 hours following a feeding event. Similarly, Carey et al. (1984) used acoustic transmitters in pen-held fish to measure stomach contractions and temperature increases after bluefin tuna feeding events (prey=mackerel and herring) and concluded it took 18 to 21 hours before liquefied food was moved out of the stomach and into the intestine and pyloric caeca These studies indicate that complete evacuation time is not reached in less than 18 to 20 hours and support our estimated digestion time of ~20 hours (i.e., from peak gut fullness to gut fullness near zero).

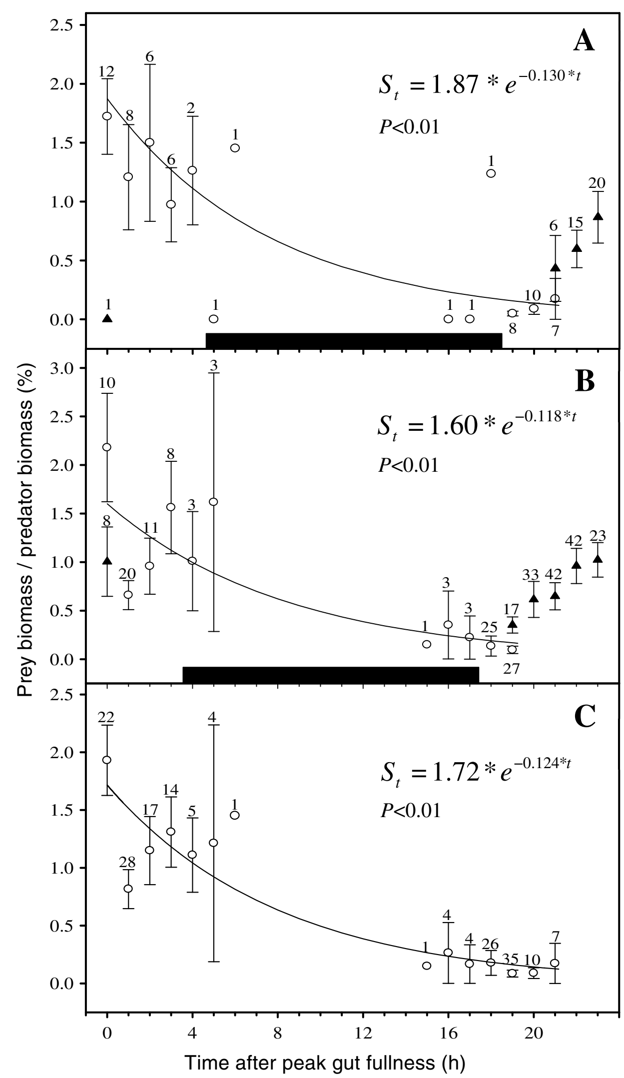

Figure 3

Diel patterns of mean gut fullness (kg prey/kg predator · 100%; ± standard error) for (**A**) large medium, (**B**) giant, and (**C**) pooled bluefin tuna (*Thunnus thynnus*) collected off Cape Lookout, North Carolina, during the winters of 2004–05 and 2005–06. Open circles represent values used to estimate gastric evacuation; filled triangles represent values that were not used during gastric evacuation estimates (see *Methods* section for description of data selection). The fit of the exponential gastric evacuation model ($S_t = S_0 \cdot e^{-GER \cdot t}$) is represented by the solid line, where S_t is the individual stomach fullness (kg prey/kg predator) at time t; S_0 is the stomach fullness at time t=0; *GER* is the instantaneous rate of gastric evacuation (rate per hr); and t is the time in hours after peak gut fullness. Samples sizes are listed above the mean gut fullness value. Time point 0=1200–1300 hours for (**A**) and 0=1300–1400 hours for (**B**); average time between sunset and sunrise is represented by solid horizontal bar.

The *DR* of giant bluefin tuna has been estimated in several studies by various methods. Palomares and Pauly (1989) estimated a *DR* of 1.08% body mass per day for maximum-size (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. Andreas Walli[5] estimated a *DR* of 1.1% [±0.3%] body mass per day based on heat incremented feeding of archival-tagged bluefin tuna tracked throughout the western Atlantic. Although the mean *DR* estimate (2.03% ±0.59%) from the current study is somewhat greater than that of previous studies, our estimate is potentially negatively biased for two reasons. First, we used the longest time between periods of peak stomach fullness and empty stomachs. Increasing the time required for gastric emptying effectively decreases the estimate of the amount of food consumed on a daily basis. Second, stomach fullness could be decreased by regurgitation during hook-and-line capture and digestion could be continued after death.

[5] Walli, Andreas. 2006. Unpubl. data. Stanford Univ., Stanford, CA 94305.

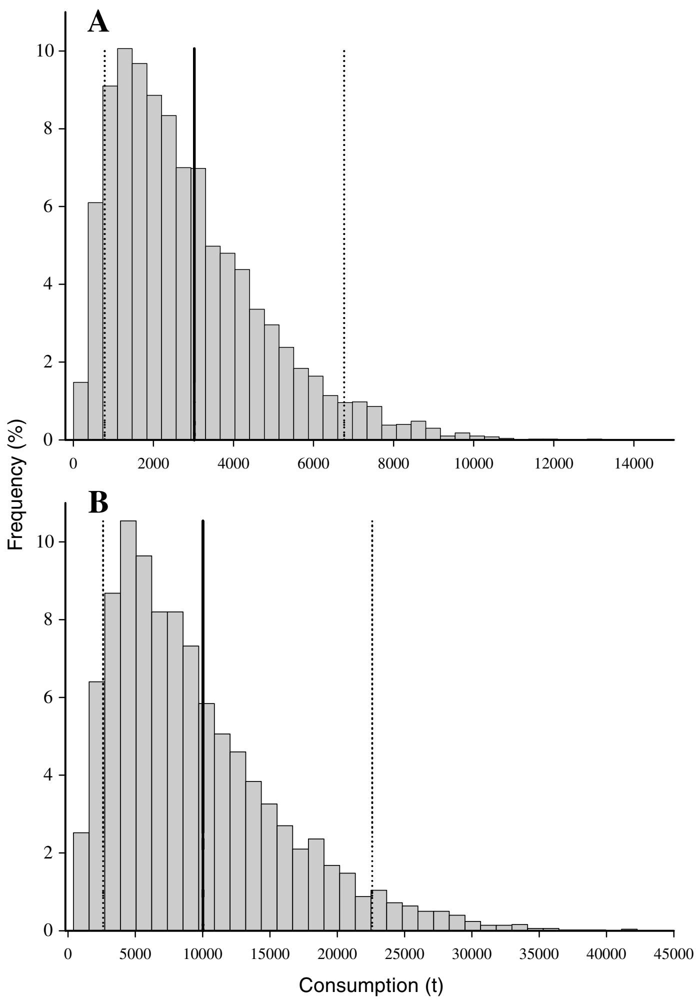

Figure 4

Frequency of Monte Carlo simulation results for consumption estimates (metric tons, t) of Atlantic menhaden (*Brevoortia tyrannus*) by (**A**) the current (2005) population of age-6+ western Atlantic bluefin tuna (*Thunnus thynnus*) and (**B**) a restored (to 1975 levels) western Atlantic bluefin tuna population of age-6+ fish. Mean (solid line) and 90% confidence intervals (dotted lines) are presented.

Predatory impact

An understanding of predator-prey interactions is necessary for ecosystem-based assessment models. Bluefish, striped bass, weakfish, and fishermen are considered the dominant predators of Atlantic menhaden in current multispecies assessment models (NEFSC[2]). The assumption that bluefin tuna are not a dominant predator of Atlantic menhaden along the U.S. East Coast appears correct given the small amount of Atlantic menhaden consumed by bluefin tuna in relation to other Atlantic menhaden predators. However, the goal of ICCAT is to rebuild the biomass of western Atlantic bluefin tuna population to its 1975 level by 2018 (ICCAT, 2007). If the population is rebuilt, our estimates of consumption indicate that bluefin tuna should be considered in future multispecies modeling efforts where Atlantic menhaden are a focal prey. Similarly, Overholtz (2006) suggested that a recovery of the western bluefin tuna stock would make bluefin tuna a dominant predator of Atlantic herring in the Georges Bank region.

Similar to results for bluefish (Buckel et al., 1999; NEFSC[2]), striped bass (Hartman, 2003; Uphoff, 2003; NEFSC, 2006[2]), and weakfish (NEFSC[2]), our estimates of Atlantic menhaden consumption by bluefin tuna were lower than any of the annual coastwide estimates of Atlantic menhaden commercial harvests during the last 25 years[1]. However, with continued attempts at rebuilding populations of bluefin tuna, bluefish, striped bass, and weakfish stocks, predation mortality may become a more important component of the overall mortality rate of Atlantic menhaden. For future modeling efforts, it is important to note that sizes of Atlantic menhaden consumed by bluefin tuna were larger than previously reported sizes of Atlantic menhaden prey found in bluefish, striped bass, and weakfish (Butler, 2007). Additionally, competition for Atlantic menhaden resources during winter may be most important off of NC during winter, and future efforts to investigate this will require information on the spatial distribution of these predators during winter.

There were several sources of uncertainty in our analysis of predatory demand. First, our study was dependent on the commercial bluefin tuna fishery which is limited to only those fish greater than 185 cm (*CFL*). Although infrequent, smaller bluefin are captured locally during the winter. If smaller size classes of bluefin tuna are consuming Atlantic menhaden during winter or at other times of the year, then they too should be considered in future consumption estimates. Currently, there is no evidence for this during non-winter months (Eggleston and Bochenek, 1990). 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 (ICCAT, 2007) assumed a mixing rate of 1–2% between the east and west bluefin tuna stocks. Rooker et al. (2008) found that as many as 40% of the age 5+ bluefin tuna captured in the Mid-Atlantic bight were from the eastern stock. Bluefin tuna mixing rates for the U.S. South-Atlantic bight during the winter could be used to assign additional biomass from the eastern stock to the B_{BFT} variable described above.

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, the continental shelf of NC serves as a spawning ground for several estuarine-dependent species, including Atlantic menhaden. The diets of large medium and giant bluefin tuna have been dominated by Atlantic menhaden during recent winters (Kade, 2000; this study) and likely in earlier years. Therefore, the migrations to and residence times of bluefin tuna in NC will likely be dependent on the abundance of Atlantic menhaden. Within-winter 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.

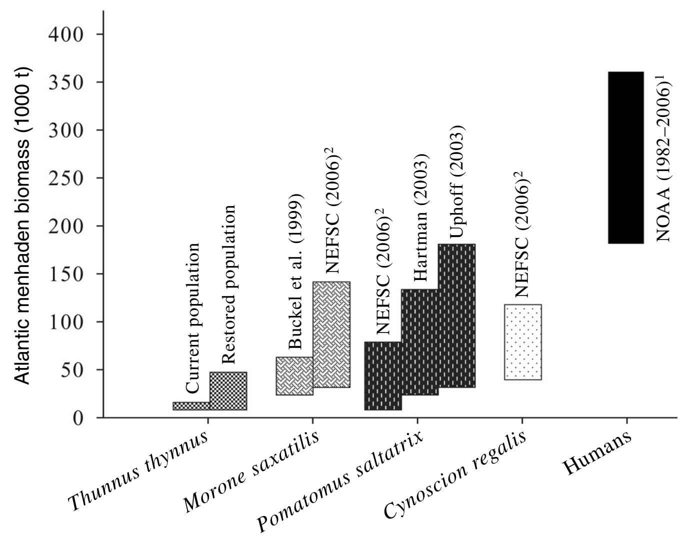

Figure 5

Estimated population-level consumption (metric tons, t) of Atlantic menhaden (*Brevoortia tyrannus*) by other important predators (see references provided on figure for further details from other studies); bottom and top of bars represent minimum and maximum estimated consumption (harvest) levels. Bluefin tuna (*Thunnus thynnus*) consumption estimates from this study are represented by the current (2005) abundance estimate for age-6+ western Atlantic bluefin tuna and a restored (to 1975 levels) age-6+ western Atlantic bluefin tuna population.

Acknowledgments

This study was funded by a NC Sea Grant Fishery Resource Grant 04-EP-04. We would like to thank the commercial fishermen and tuna buyers who participated in the study, especially G. Leone, A. Ng, and J. Cox. We would like to give special thanks to J. Miller and J. Osborne for their assistance with data analyses and manuscript editing, D. Bethea and J. Bizzarro for their help with cumulative prey curve analysis, J. Morley for his assistance with prey identification, and J. Merrell for his help with data collection. We also thank J. Smith, N. McNeill, B. Block, A. Boustany, A. Walli, B. Chase, A. Bianchi, and E. Loew for providing either data or knowledge pertinent to the current research. The comments from three anonymous reviewers substantially improved this paper.

Literature cited

Aguado-Giménez, F., and B. García-García.
2005. Growth, food intake and feed conversion rates in captive Atlantic bluefin tuna (*Thunnus thynnus* Linnaeus, 1758) under fattening conditions. Aquac. Res. 36:610–614.

Baglin, R. E., Jr.
1980. Length-weight relationships of western Atlantic bluefin tuna, *Thunnus thynnus*. Fish. Bull. 77:995–1000.

Bethea, D. M., J. A. Buckel, and J. K. Carlson.
2004. Foraging ecology of the early life stages of four sympatric shark species. Mar. Ecol. Prog. Ser. 268:245–264.

Bizzarro, J. J., H. J. Robinson, C. S. Rinewalt, and D. A. Ebert.
2007. Comparative feeding ecology of four sympatric skate species off central California. Environ. Biol. Fishes 80(2–3):197–200.

Blank, J. M., C. J. Farwell, J. M. Morrissette, R. J. Schallert, and B. A. Block.
2007. Influence of swimming speed on metabolic rates of juvenile pacific bluefin tuna and yellowfin tuna. Phys. Biochem. Zool. 80:167–177.

Block, B. A., H. Dewar, S. B. Blackwell, T. D. Williams, E. D. Prince, C. J. Farwell, A. Boustany, S. L. H. Teo, A. Seitz, A. Walli, and D. Fudge.
2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 293:1310–1314.

Boustany, A. M.
2006. An examination of population structure, movement patterns and environmental preferences in northern bluefin tuna. Ph.D. diss., 158 p. Stanford Univ., Stanford, CA.

Bromley, P. J.
1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. Rev. Fish Biol. Fish. 4:33–66.

Buckel, J. A., M. J. Fogarty, and D. O. Conover.
1999. Mutual prey of fish and humans: a comparison of biomass consumed by bluefish, *Pomatomus saltatrix*, with that harvested by fisheries. Fish. Bull. 97:776–785.

Butler, C. M.
2007. Atlantic bluefin tuna (*Thunnus thynnus*) feeding ecology and potential ecosystem effects during winter in North Carolina. M.S. thesis, 106 p. North Carolina State Univ., Raleigh, NC.

Butler, M. J. A., and J. A. Mason.
1978. Behavioral studies on impounded bluefin tuna. Col. Vol. Sci. Pap. ICCAT, 7(2):379–382.

Carey, F. G., J. W. Kanwisher, and E. D. Stevens.
1984. Bluefin tuna warm their viscera during digestion. J. Exp. Biol. 109:1–20.

Chase, B. C.
2002. Differences in diet of Atlantic bluefin tuna (*Thunnus thynnus*) at five seasonal feeding grounds on the New England continental shelf. Fish. Bull. 100:168–180.

Checkley, D. M., Jr., P. B. Ortner, F. E. Werner, L. R. Settle, and S. R. Cummings.
1999. Spawning habitat of the Atlantic menhaden in Onslow Bay, North Carolina. Fish. Oceanogr. 8 (suppl. 2):22–36.

Dickson, K. A., and J. B Graham.
2004. Evolution and consequences of endothermy in fishes. Physiol. Biochem. Zool. 77:998–1018.

Dragovich, A.
1970. The food of bluefin tuna (*Thunnus thynnus*) in the western North Atlantic Ocean. Trans. Am. Fish. Soc. 99:726–731.

Eggers, D.M.
1977. Factors in interpreting data obtained by diel sampling of fish stomachs. J. Fish. Res. Board Can. 34:290–294.

Eggleston, D. B., and E. Bochenek.
1990. Stomach contents and parasite infestation of school bluefin tuna *Thunnus thynnus* collected from the Middle Atlantic Bight, Virginia. Fish. Bull. 88:389–395.

Elliott, J. M., and L. Persson.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977–991.

Ferry, L. A., and G. M. Cailliet.
1996. Sample size and data: Are we characterizing and comparing diet properly? *In* Feeding ecology and nutrition in fish; proceedings of the symposium on feeding ecology and nutrition in fish; Int. Congress Biology of Fishes (D. Makinlay, and K. Shearer, eds.), p. 70–81. Am. Fish. Soc., San Francisco, CA.

Goode, G.B.
1879. The natural and economical history of the American menhaden. U.S. Comm. Fish and Fish., pt. 5, Rep. Comm. 1877 (append. A):1–529.

Griffiths, S. P., G. C. Fry, F. J. Manson, and R. D. Pillans.
2007. Feeding dynamics, consumption rates and daily ration of longtail tuna (*Thunnus tonggol*) in Australian waters, with emphasis on the consumption of commercially important prawns. Mar. Freshw. Res. 58:376–397.

Hartman, K. J.
2003. Population-level consumption by Atlantic coastal striped bass and the influence of population recovery upon prey communities. Fish. Manag. Ecol. 10:281–288.

Hobson, E. S.
1986. Predation on the Pacific sand lance, *Ammodytes hexapterus* (Pisces, Ammodytidae), during the transition between day and night in southeastern Alaska. Copeia 1986:223–226.

Hyslop, E. J.
1980. Stomach contents analysis – a review of methods and their application. J. Fish. Biol. 17:411–429.

ICCAT (International Commission for the Conservation of Atlantic Tunas).
2007. Report of the 2006 Atlantic bluefin tuna stock assessment session. Col. Vol. Sci. Pap. ICCAT, 60:652–880

Josse, E., P. Bach, and L. Dagorn.
1998. Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. Hydrobiologia 371/372:61–69.

Juanes, F., J. A. Buckel, and F. S. Scharf.
2001. Predatory behavior and selectivity of a primary piscivore: comparing fish and non-fish prey. Mar. Ecol. Prog. Ser. 217:157–165.

Kade, T. C.
2000. The natural and social science implications of bluefin tuna migrations off the coast of North Carolina. M. S. thesis, 86 p. Duke Univ. Marine Laboratory, Beaufort, NC.

Krumholz, L. A.
1959. Stomach contents and organ weights of some bluefin tuna, *Thunnus thynnus* (Linnaeus), near Bimini, Bahamas. Zoologica 44:127–131.

Latour, R. J., M. J. Brush, and C. F. Bonzek.
2003. Toward ecosystem-based fisheries management: Strategies for multispecies modeling and associated data requirements. Fisheries 28:10–22.

Lutcavage, M. E., R. W. Brill, G. B. Skomal, B. C. Chase, J. L. Goldstein, and J. Tutein.
2000. Tracking adult North Atlantic bluefin tuna (*Thunnus thynnus*) in the northwestern Atlantic using ultrasonic telemetry. Mar. Biol. 137:347–358.

Magnuson, J. J.
1969. Digestion and food consumption by skipjack tuna (*Katsuwonus pelamis*). Trans. Am. Fish. Soc. 98:379–392.

Olson, R. J., and C. H. Boggs.
1986. Apex predation by yellowfin tuna (*Thunnus albacares*): Independent estimates from gastric evacuation and stomach contents, bioenergetics, and cesium concentrations. Can. J. Fish. Aquat. Sci. 43:1760–1775.

Overholtz, W. J.
2006. Estimates of consumption of Atlantic herring (*Clupea harengus*) by bluefin tuna (*Thunnus thynnus*) during 1970–2002: an approach incorporating uncertainty. J. Northw. Atl. Fish. Sci. 36:55–63.

Overholtz, W. J., L. D. Jacobson, and J. S. Link.
2008. An ecosystem approach for assessment advice and biological reference points for the Gulf of Maine-Georges Bank Atlantic herring complex. N. Am. J. Fish. Manag. 28:247–257.

Palomares, M. L., and D. Pauly.
1989. A multiple regression model for predicting the food consumption of marine fish populations. Aust. J. Mar. Freshw. Res. 40:259–273.

Pauly, D., V. Christensen, and C. J. Walters.
2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57:697–706.

Quinlan, J. A., B. O. Blanton, T. J. Miller, and F. E. Werner.
1999. From spawning grounds to the estuary: using linked individual-based and hydrodynamic models to interpret patterns and processes in the oceanic phase of Atlantic menhaden *Brevoortia tyrannus* life history. Fish. Oceanogr. 8:224–246.

Rooker, J. R., J. R. Alvarado Bremer, B. A. Block, H. Dewar, G. de Metrio, A. Corriero, R. T. Kraus, E. D. Prince, E. Rodríquez-Marín, and D. H. Secor.
2007. Life history and stock structure of Atlantic bluefin tuna (*Thunnus thynnus*). Rev. Fish. Sci. 15:265–310.

Rooker, J. R., D. H. Secor, G. DeMetrio, R. Schloesser, B. A. Block, and J. D. Neilson.
2008. Natal homing and connectivity in Atlantic bluefin tuna populations. Science 322:742–744.

SAS Institute.
1996. SAS/STAT user's guide, vers. 6, 4th ed., vol. 2. SAS Inst. Inc., Cary, NC.

Sokal, R. R., and F. J. Rohlf.
1981. Biometry: The principles and practice of statistics in biological research, 2nd ed., 880 p. W.H. Freeman, New York, NY.

Stevens, E. D., F. G. Carey, and J. Kanwisher.
1978. Changes in visceral temperature of Atlantic bluefin tuna. Col. Vol. Sci. Pap. ICCAT, 7(2):383–388.

Teo, S. L. H., A. Boustany, H. Dewar, M. J. W. Stokesbury, K. C. Weng, S. Beemer, A. C. Seitz, C. J. Farwell, E. D. Prince, and B. A. Block.
2007. Annual migrations, diving behavior, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds. Mar. Biol. 238:1–18.

Uphoff, J. H., Jr.
2003. Predator-prey analysis of striped bass and Atlantic menhaden in upper Chesapeake Bay. Fish. Manag. Ecol. 10:313–322.

Williams, B. K., J. D. Nichols, and M. J. Conroy.
2002. Analysis and management of animal populations, 1040 p. Academic Press, San Diego, CA.

Young, J. W., T. D. Lamb, D. Le, R. W. Bradford, and A. W. Whitelaw.
1997. Feeding ecology and interannual variations in diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. Environ. Biol. Fishes 50:275–291.

Zar, J. H.
1999. Biostatistical analysis, 4th ed., 929 p. Prentice-Hall, Upper Saddle River, NJ.