

Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds

John M. Logan · Enrique Rodríguez-Marín · Nicolas Goñi · Santiago Barreiro · Haritz Arrizabalaga · Walter Golet · Molly Lutcavage

Received: 12 August 2009 / Accepted: 5 September 2010 / Published online: 18 September 2010
© US Government 2010

Abstract Atlantic bluefin tuna (*Thunnus thynnus*) are highly migratory predators whose abundance, distribution, and somatic condition have changed over the past decades. Prey community composition and abundance have also varied in several foraging grounds. To better understand underlying food webs and regional energy sources, we performed stomach content and stable isotope analyses on mainly juvenile (60–150 cm curved fork length) bluefin

tuna captured in foraging grounds in the western (Mid-Atlantic Bight) and eastern (Bay of Biscay) Atlantic Ocean. In the Mid-Atlantic Bight, bluefin tuna diet was mainly sand lance (*Ammodytes* spp., 29% prey weight), consistent with historic findings. In the Bay of Biscay, krill (*Meganyctiphanes norvegica*) and anchovy (*Engraulis encrasicolus*) made up 39% prey weight, with relative consumption of each reflecting annual changes in prey abundance. Consumption of anchovies apparently declined after the local collapse of this prey resource. In both regions, stable isotope analysis results showed that juvenile bluefin tuna fed at a lower trophic position than indicated by stomach content analysis. In the Mid-Atlantic Bight, stable isotope analyses suggested that >30% of the diet was prey from lower trophic levels that composed <10% of the prey weights based upon traditional stomach content analyses. Trophic position was similar to juvenile fish sampled in the NW Atlantic but lower than juveniles sampled in the Mediterranean Sea in previous studies. Our findings indicate that juvenile bluefin tuna targeted a relatively small range of prey species and regional foraging patterns remained consistent over time in the Mid-Atlantic Bight but changed in relation to local prey availability in the Bay of Biscay.

Communicated by M. A. Peck.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-010-1543-0) contains supplementary material, which is available to authorized users.

J. M. Logan · W. Golet · M. Lutcavage
Large Pelagics Research Center,
Department of Biological Sciences,
University of New Hampshire, Durham, NH 03824, USA

J. M. Logan (✉)
Massachusetts Division of Marine Fisheries,
1213 Purchase Street, New Bedford, MA 02740, USA
e-mail: john.logan@state.ma.us

E. Rodríguez-Marín · S. Barreiro
Instituto Español de Oceanografía (IEO), Centro Oceanográfico
de Santander, Apartado 240, 39080 Santander, Spain

N. Goñi · H. Arrizabalaga
AZTI Tecnalia, Herrera Kaia Portualdea z/g, 20110 Pasaia,
Gipuzkoa, Spain

Present Address:
M. Lutcavage
Large Pelagics Research Center, Department of Natural
Resources Conservation, University of Massachusetts Amherst,
108 East. Main Street, Gloucester, MA 01930, USA

Introduction

Atlantic bluefin tuna (ABFT; *Thunnus thynnus*) are top pelagic predators in coastal and open ocean food webs (Matthews et al. 1977; Chase 2002). Since 1980, distinct changes have occurred in the relative abundance, distribution, fisheries, and somatic condition of ABFT (Mather et al. 1995; Fromentin and Powers 2005; Golet et al. 2007). Recent stock assessments estimate ABFT spawning stock

biomass to be <40% of historical levels (ICCAT 2009). The abundance and distribution of bluefin tuna prey have also changed in key areas of their foraging habitats, including the Mid-Atlantic Bight (MAB) and Bay of Biscay (BYB) (Nelson and Ross 1991; Ibaibarriaga et al. 2008). Any reductions in the abundance of top predators have the potential to alter food web dynamics and trophic structure in marine systems (Paine 1966; Hinke et al. 2004), while changes in the prey community can also affect marine top predators (Rosen and Trites 2000).

Coastal waters of the BYB and MAB are productive foraging grounds for young and adolescent ABFT (Ortiz de Zárate and Cort 1986; Eggleston and Bochenek 1990). Commercial (BYB) and recreational fisheries (MAB) target regional ABFT aggregations that arrive from late May to early June and remain through autumn (Mather et al. 1995; Rodríguez-Marín et al. 2003). In addition to dispersing along a north–south gradient in their coastal foraging grounds, young, most likely immature (i.e., 1–3 years) ABFT also undertake trans-Atlantic migrations, presumably to feed (Mather et al. 1995). Consequently, individual fish may forage in widely separated regions during their first years of life, although inter-annual mixing rates may be highly variable (Rooker et al. 2007).

Previous studies of juvenile ABFT diet have used either stomach content analysis (SCA) (Ortiz de Zárate and Cort 1986; Eggleston and Bochenek 1990; Chase 2002; Sinopoli et al. 2004) or stable isotope analysis (SIA) (Estrada et al. 2005; Sara and Sara 2007). Traditional SCA techniques can provide detailed information on diet composition, prey size distribution, and consumption rate estimates over a short timescale (Chippis and Garvey 2007). SIA data track diet over longer timescales, depending on compound or tissue turnover rates (Gannes et al. 1998). Nitrogen isotope values ($\delta^{15}\text{N}$) indicate trophic position, while carbon isotopes ($\delta^{13}\text{C}$) reflect sources of primary production (Peterson and Fry 1987). Comparison of isotope values from multiple tissues with different turnover rates can provide information about arrival times to sampling areas (Fry et al. 2003). In fish tissue, ratios of total carbon to nitrogen (C:N) are linearly related to lipid content (Post et al. 2007) and can be used to track changes in body condition (Estrada et al. 2005).

We used a combined SCA and SIA approach to assess dietary preferences of mainly juvenile ABFT (~60–150 cm curved fork length, CFL) on foraging grounds in the western (MAB) and eastern (BYB) Atlantic Ocean. Our study examines current foraging patterns and compares them with earlier works to more thoroughly identify diet preferences, to assess possible trophic changes, and to establish current information on ABFT trophic relationships for use in ecosystem studies.

Methods

Study sites

ABFT were sampled from the Mid-Atlantic Bight (~36°30'N–37°30'N, 74°30'W–75°30'W) and Bay of Biscay (~43°40'N–45°30'N, 2°00'W–3°50'W). MAB foraging grounds are located ~30–60 km off the eastern shore of Virginia, USA and are characterized by sandy substrate and water depths of 30–40 m (Bochenek 1989). The BYB is an open oceanic bay partly enclosed by shelf regions along the western coast of France and the northern coast of Spain. Samples were collected from the southeastern region off the coast of Spain, where the continental shelf is very narrow. Most ABFT from this region were sampled off the edge of the shelf (Rodríguez-Marín et al. 2003).

Sample collection and preservation

Biological samples were obtained from surface troll fisheries in the MAB and BYB, as well as baitboat, pelagic trawl, and recreational fisheries in the latter (Table 1). The baitboat fishery was the primary source of samples in the BYB (~80%). Stomachs were removed from ABFT at sea during the scientific surveys, but most BYB samples (2001–2004) were collected from commercial landings in which ABFT were stored on ice for 1–2 days. Whole stomachs, dorsal white muscle, and liver samples were removed from each fish at sea or at dockside cleaning stations, placed on ice, then stored frozen until analysis at -23°C (MAB) or -28°C (BYB). The majority of BYB stomach samples were analyzed fresh (without freezing). Curved fork length (CFL), measured in a line along the contour of the body from the tip of the upper jaw to the fork of the caudal fin, was determined ($\pm\text{cm}$) for each fish.

Prey samples for SIA were collected from scientific trawl surveys (BYB, fall 2006) and stomach contents of ABFT and other large pelagic fishes (MAB, summer 2005, 2006). Cephalopod, teleost, and swimming crab (*Polybius henslowii*) prey samples consisted of muscle sub-samples, while for all other crustacean prey, whole organisms were analyzed. All prey samples were stored frozen prior to analysis.

Samples of ABFT were grouped by size (age) or sampling season. Size classes corresponded to 57–120 cm CFL (age 1–3) and 121–151 cm CFL (age 4–5). Age was estimated by direct reading on the first ray of the first dorsal fin or by applying age–length curves (Rodríguez-Marín et al. 2007). Most samples (~98%) from the BYB were from the younger age class, while similar proportions of the two age classes were sampled from the MAB (Table 1).

Table 1 Sample collection summary for Atlantic bluefin tuna (*Thunnus thynnus*; ABFT) collected from the Bay of Biscay (BYB) and Mid-Atlantic Bight (MAB)

| Group | Sampling method | <i>n</i> | |
|---------------------------------|----------------------------------|-----------------|-----------------|
| | | Isotope samples | Stomach samples |
| <i>Mid-Atlantic Bight (MAB)</i> | | | |
| Age 1–3 2004 | Troll | 17 | 0 |
| Age 1–3 2005 | Troll | 12 | 10 |
| Age 1–3 2006 | Troll | 11 | 10 |
| Age 4–5 2004 | Troll | 4 | 0 |
| Age 4–5 2006 | Troll | 28 | 22 |
| <i>Bay of Biscay (BYB)</i> | | | |
| Age 2 Summer 2001 | Baitboat | 24 | 21 |
| Age 1–2 Summer 2003 | Baitboat, Troll | 7 | 15 |
| Age 2–4 Summer 2004 | Baitboat | 15 | 18 |
| Age 1–3 Summer 2005 | Baitboat, Rod & reel | 0 | 46 |
| Age 1–4 Summer 2006 | Baitboat, Troll, Mid-water trawl | 0 | 12 |
| Age 1–2 Fall 2000 | Baitboat | 28 | 29 |
| Age 1–3 Fall 2002 | Baitboat | 30 | 13 |
| Age 1–2 Fall 2004 | Baitboat | 15 | 16 |
| Age 2 Fall 2006 | Rod and reel | 0 | 1 |

For stomach samples, information reflects only stomachs that contained natural prey. Isotope samples consist of liver and white muscle

Stomach content analysis (SCA)

Whole stomachs were thawed, weighed (± 0.05 g), and contents were washed over a 1,000 micron sieve. Contents were identified to the lowest possible taxonomic group. Whole prey were weighed (± 0.1 g) and measured (\pm mm). The size and color of the gall bladder and texture of the stomach lining were visually inspected for samples collected from the baitboat fishery to estimate whether stomach contents had been consumed during fishing operations (Talbot and Higgins 1982). For the BYB, the main bait species are horse mackerel (*Trachurus trachurus*), bogue (*Boops boops*), sardines (*Sardina pilchardus*), and anchovies (*Engraulis encrasicolus*) (Rodríguez-Marín et al. 2003). More than 40% of the stomachs collected from this fishery contained only prey identified as bait. Prey identified as bait were eliminated from analyses. Empty stomachs were also excluded, since ABFT may evacuate their guts during capture (Chase 2002).

Stable isotope analysis (SIA)

Prey items and ABFT liver and white muscle samples were thawed, lightly rinsed with deionized water, and dried in glass scintillation vials at 60°C for at least 48 h. Samples were then homogenized using a Mixer/Mill® (SPEX SamplePrep, LLC Metuchen, NJ, U.S.A) with stainless steel vials. Aliquots of homogenized sample (0.6–1.2 mg) were packed into 4 × 6 mm tin cups and analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, % carbon, and % nitrogen using a Costech

ECS4010 elemental analyzer (Costech Analytical Technologies, Inc, Valencia, CA USA) coupled with a DELTA_{plus} XP isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany) at the Colorado Plateau Stable Isotope Laboratory of Northern Arizona University (NAU) and the University of New Hampshire Stable Isotope Laboratory (UNH). All C:N values are reported as uncorrected percent weight calculations ($\frac{\%C}{\%N}$).

All sample $\delta^{13}\text{C}$ values were corrected for lipid content either a priori through chemical extractions or a posteriori using mathematical approaches (see Logan et al. (2008) for details). Carbonates were not removed from crustacean prey samples and therefore may have induced a positive bias on $\delta^{13}\text{C}$ values (Craig 1953). See supplementary material for a more detailed description of isotope sample preparation (S1).

All carbon and nitrogen isotope data are reported in δ notation according to the following equation:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000$$

where X is ^{13}C or ^{15}N and R is the ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ (Peterson and Fry 1987). Standard materials are Vienna Pee Dee belemnite (VPDB) for carbon and atmospheric N_2 (AIR) for nitrogen. Standard deviations of replicate samples analyzed at both labs were $<0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($n = 45$), and within-lab precision was $\sim 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. All $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were normalized on the VPDB and AIR scales with IAEA CH_6 (-10.4‰), CH_7 (-31.8‰), N_1 (0.4‰) and N_2 (20.3‰).

Statistical analysis

Adequacy of stomach content sample sizes was assessed by generating cumulative prey curves (Ferry and Caillet 1996), which show the cumulative number of unique prey items versus number of stomachs sampled. Bootstrapping techniques were used to generate 500 random samples for each sample size. To assess whether a sufficient number of samples had been analyzed to capture prey diversity, the slope of the final four endpoints for each prey curve was compared to a slope of zero using a Student's *t*-test (Bizarro et al. 2007) and Holm-adjusted *P*-values (Holm 1979).

Relationships between ABFT and prey size were explored using quantile regression with standard errors estimated using the xy-pair bootstrap. A total of 1,042 prey items were measured, and regressions were performed for the median (50th percentile) as well as 5th and 95th percentiles to test for patterns in minimum and maximum prey size in relation to ABFT length (CFL).

Mean proportion by weight (MW_i) and mean proportion by number (MN_i) were calculated for each prey group for each stomach sample to generate mean and standard deviations for each prey category. Frequency of occurrence (O_i) was also calculated for each prey group as $\frac{J_i}{P}$, where J_i is the total number of stomachs containing prey *i* and *P* is the total number of stomachs containing natural prey (Chippis and Garvey 2007). Mean percent weight contributions were compared using a Kruskal–Wallis test for crustaceans, cephalopods, and teleost fishes. Nemenyi–Damico–Wolfe–Dunn tests were performed as post hoc analyses when significant differences ($P < 0.05$) were detected.

Comparisons of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C:N were made among seasons, sampling years, and ABFT age classes for liver and white muscle. Homogeneity of variance among groups was first tested using Levene's test. For cases where Levene's test results were non-significant, analysis of variance (ANOVA) and subsequent pairwise *t*-tests were performed with $\alpha = 0.05$ following a Holm test adjustment for multiple comparisons. When significant differences were detected using Levene's test, a one-way analysis of means and subsequent pairwise comparisons using *t*-tests with non-pooled standard deviations were performed. Relationships between ABFT length and tissue C:N were further explored using quantile regression for the MAB dataset. Regressions were performed for the median (50th percentile) as well as 5th and 95th percentiles to test for patterns in minimum and maximum C:N in relation to ABFT length.

Dietary contribution of different prey types was quantified using the package Stable Isotope Analysis in R

(SIAR) (Parnell et al. 2010). Liver isotope data were used for mixing model analyses to reflect diet from local foraging grounds. Isotope discrimination was assumed to be 1.4‰ ($\delta^{13}\text{C}$) and 1.3‰ ($\delta^{15}\text{N}$) based on estimates for other fish species (Sweeting et al. 2007a, b). See supplementary material for a more detailed description of SIAR parameters (S2). All statistical analyses were performed using the program R (R Development Core Team 2008). Values are reported as mean \pm standard deviation (SD) unless otherwise noted.

Results

Stomach contents and prey selection

In cumulative prey curves, the slope of the final four endpoints was significantly different from zero ($P < 0.05$) for all Mid-Atlantic Bight and fall 2002 Bay of Biscay prey curves, but was not following Holm adjustments for the remaining datasets (Fig. 1). Results indicate that sample size was too small to adequately reflect prey diversity for MAB but not for BYB datasets.

Prey length was not significantly correlated with ABFT length for all prey species combined with *P*-values of 0.073, 0.765, and 0.086 for the 95th, 50th, and 5th percentiles, respectively. The largest species were horse mackerel, sardines, and flying squid (*Todarodes sagittatus*) (Fig. 2). Larger (i.e., >100 cm CFL) ABFT fed on myctophids, round herring (*Etrumeus teres*), and swimming crabs. All sizes of ABFT consumed sand lance (*Ammodytes* spp.) in the MAB. In the BYB, ABFT fed mainly on age-0 European anchovy and blue whiting (*Micromesistius pou-tassou*) as well as age-1 horse mackerel (Fig. 2).

Bay of Biscay

Stomach contents In this eastern Atlantic shelf region, dietary weight percentages differed among all three prey groups (fishes, cephalopods, and crustaceans) ($P < 0.0001$). For the summer dataset, prey group rankings were fishes > crustaceans > cephalopods with significant differences among all three groups. In the fall, no cephalopods were present and significantly higher proportions of fishes were observed relative to crustaceans (Table 2).

The four main prey species were horse mackerel, blue whiting, anchovy, and krill (*Meganyctiphanes norvegica*) (Table 2). Prey weight percentages varied among years, with high proportions of horse mackerel in fall 2000 and summer 2001, blue whiting in summer 2003, anchovy in fall 2000 and summer 2005, and krill in summer 2004 (Fig. 3).

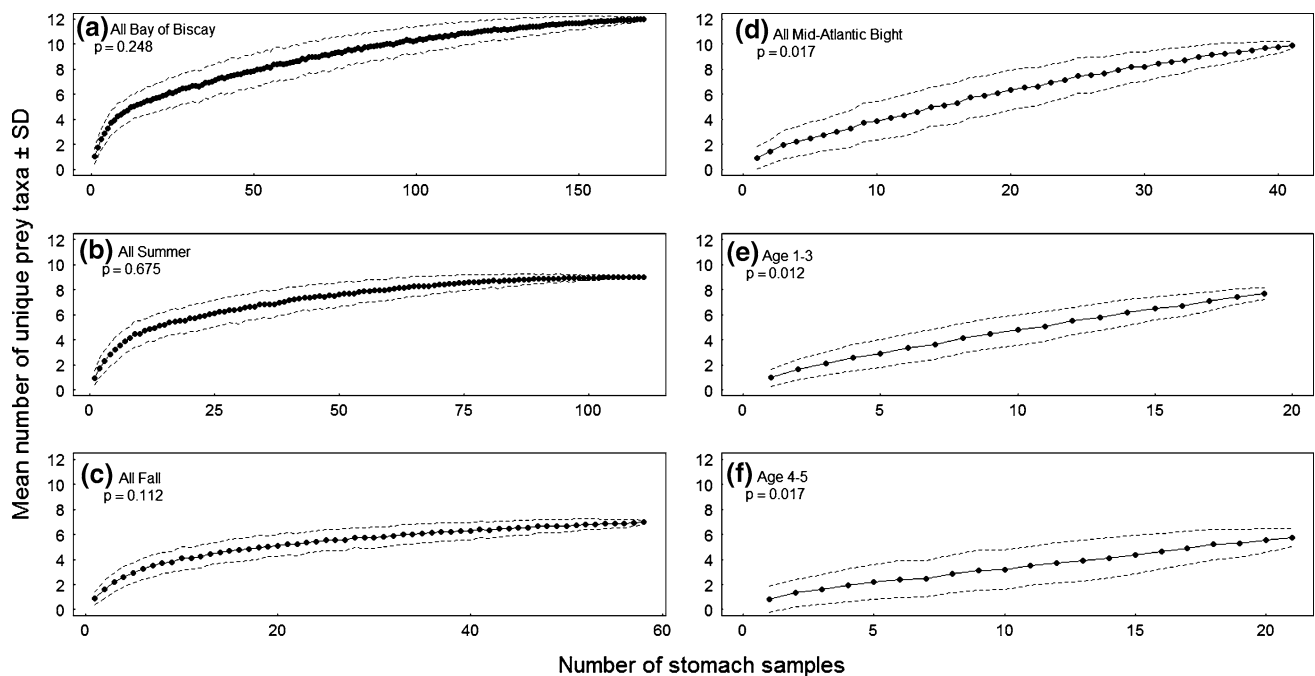


Fig. 1 Cumulative prey curves for Bay of Biscay (BYB) stomach samples based on (a) the entire dataset (b) all summer samples and (c) all fall samples and Mid-Atlantic Bight (MAB) stomach samples based on (d) the entire dataset (e) age 1–3 fish and (f) age 4–5 fish. P -

values < 0.05 correspond to significant differences between the final four data points and a slope of zero and indicate insufficient sample sizes for complete characterization of prey diversity

Stable isotopes Mixing model estimates of dietary contributions were highest for krill prey across both seasons, with anchovies, Atlantic mackerel (*Scorpaenopsis scorpaenoides*), and swimming crabs of secondary importance. Blue whiting, myctophids, horse mackerel, sardines, and omma-strephid squids made up $< 10\%$ of mean dietary proportions (Fig. 4). ABFT liver isotope values were intermediate among prey sources (Fig. 5). ABFT liver $\delta^{15}\text{N}$ values were significantly lower for summer 2004 than all other seasons and years. In 2004, liver C:N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ and white muscle $\delta^{15}\text{N}$ all significantly increased from summer through fall (Table 3).

Mid-Atlantic Bight

Stomach contents Teleosts were the dominant prey group in all three dietary indices, and sand lance were the main taxa for both bluefin size/age classes (Table 4). Teleosts had significantly greater dietary biomass than crustacean or cephalopod prey ($P < 0.0001$), while no significant differences were detected between crustacean and cephalopod prey (Table 4).

Stable isotopes Mixing model estimates of dietary contributions were highest for sand lance and crustaceans (20–40%), intermediate for butterfish (*Peprilus triacanthus*), round herring, and sea horses (*Hippocampus erectus*)

(10–20%), and low for white hake (*Urophycis tenuis*) and squids ($< 5\%$) (Fig. 4). ABFT liver isotope values were intermediate among prey sources (Fig. 5). Liver values varied in C:N and $\delta^{13}\text{C}$, but not $\delta^{15}\text{N}$ (Table 3). Minimum and median liver C:N values increased significantly ($P < 0.05$), but significant differences were not detected among age classes or years (Table 3).

Muscle values varied in C:N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ (Table 3). All muscle C:N value metrics (95th, 50th, and 5th percentiles) significantly increased with ABFT length ($P < 0.05$). C:N values differed between age 1–3 fish in 2005 and age 4–5 fish in 2006, but not among any other age classes, years, or seasons. In 2004, age 1–3 fish had muscle $\delta^{15}\text{N}$ values that differed significantly from all other years and age classes, while for muscle–liver separation, significantly lower values of $\delta^{15}\text{N}$ were measured for age 1–3 ABFT ($0.5 \pm 0.6\text{‰}$) than all other age classes and years ($1.0 \pm 0.3\text{‰}$ to $1.5 \pm 0.4\text{‰}$) (Table 3).

Discussion

Juvenile ABFT in eastern and western North Atlantic foraging grounds mainly consumed zooplanktivorous fishes and crustacean prey, with no major differences in trophic levels between locations. Our results indicate that juvenile ABFT primarily target prey at lower trophic levels

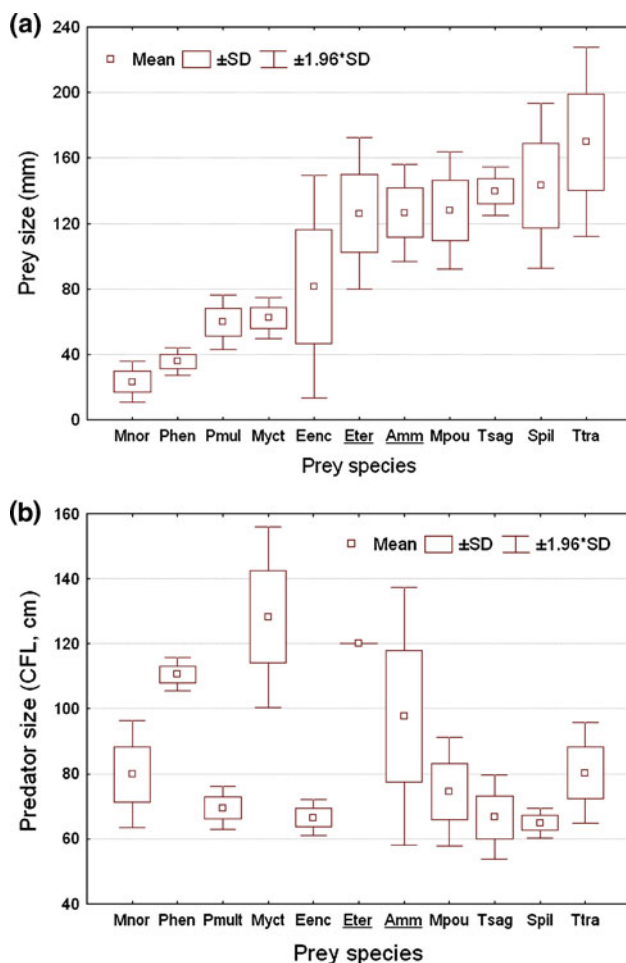


Fig. 2 Box and whisker plots representing Atlantic bluefin tuna (*Thunnus thynnus*; ABFT) sizes versus prey sizes showing (a) the total range of prey sizes and (b) ABFT size classes that contained each prey type. Prey abbreviations: Mnor = *Meganyctiphanes norvegica* (krill), Phen = *Polybius henslowii* (swimming crab), Pmul = *Pasiphaea multidentata* (glass shrimp), Myct = Myctophidae, Eenc = *Engraulis encrasicolus* (European anchovy), Eter = *Etrumeus teres* (round herring), Amm = *Ammodytes* spp. (sand lance), Mpou = *Micromesistius poutassou* (blue whiting), Tsag = *Todarodes sagittatus* (flying squid), Spil = *Sardina pilchardus* (sardine), and Ttra = *Trachurus trachurus* (horse mackerel). Underlined prey species were found in Mid-Atlantic Bight (MAB) ABFT stomachs

compared to adults that mainly feed on adult schooling fishes (Rooker et al. 2007). Stomach contents showed higher teleost prey proportions than results from isotope analyses, but both techniques indicated that cephalopods are minor prey components of juvenile ABFT diet. In comparison, cephalopods made up similarly low proportions (1.9% weight) of stomach content biomass of adult ABFT sampled in the Gulf of Maine (Chase 2002). Isotope data also reflected slightly lower trophic positions than stomach contents. ABFT from the Mid-Atlantic Bight fed at a slightly higher trophic position than individuals sampled in the BYB, because they consumed fewer

crustaceans. Prey size generally did not change across ABFT size classes sampled in this study, as noted previously (Chase 2002). Ram feeding on dense prey aggregations like sand lance or krill could explain why a wide range of ABFT select the same prey sizes (Chase 2002).

The importance of teleosts in ABFT diet varied between analysis techniques, especially for horse mackerel and blue whiting in the BYB. Horse mackerel is the most common bait in local baitboat fisheries (Rodríguez-Marín et al. 2003) and was only observed in stomach samples collected from this fishery, and so, discrepancies between methods are likely due to the inclusion of bait in estimates of natural prey. Blue whiting and horse mackerel were among the largest prey, and higher estimates of dietary biomass for these two species based on stomach contents could be due to slower digestion rates for these species (Hilton et al. 1998).

The importance of crustacean prey in ABFT diet varied between SCA and SIA results in both study areas, although SCA of fish obtained in the MAB was based on small sample sizes that may not adequately reflect prey diversity. Lower crustacean proportions in stomach samples could also be due to differential digestion rates, although sand lance are rapidly digested (Hilton et al. 1998) but still abundant in MAB stomach samples. Stable isotope results showing higher proportions of crustacean prey may also reflect other prey types (e.g., larval fishes: $\delta^{15}\text{N} = 8.1\text{‰}$, (Logan 2009)) with similar isotopic values that were overlooked in SCA samples from the MAB due to small sample sizes.

A potential source of bias in our results is that BYB isotope proportion estimates were based on small prey sample sizes. Similar $\delta^{15}\text{N}$ values for sardines and horse mackerel have been reported, but these values are higher for Atlantic mackerel and anchovies (Bode et al. 2004; Bode et al. 2007). Similar $\delta^{13}\text{C}$ (-19.2‰) but lower $\delta^{15}\text{N}$ (7.6‰) values were reported for swimming crabs (Cartes et al. 2007) relative to present values.

Due to variability in ABFT and prey isotope values, similarity in isotope values among many prey species, and uncertainty in diet-tissue discrimination factors, diet proportion estimates should be considered with some caution. ABFT isotope values were generally intermediate relative to potential prey sources, which creates further uncertainty in diet proportion estimates based on isotope mixing models (Phillips and Gregg 2003). Despite these limitations, isotope mixing models consistently showed a reliance on low trophic level prey.

Bluefin diet and trophic position

ABFT diet in the MAB contained high proportions of sand lance, consistent with previous studies (Eggleston and

Table 2 Mean \pm SD prey composition for Atlantic bluefin tuna (*Thunnus thynnus*; ABFT) collected during summer and fall in the Bay of Biscay (percent weight (%W), percent number (%N), and frequency of occurrence (%O))

| Prey | Summer ($n = 112$) | | | Fall ($n = 59$) | | |
|----------------------------------|----------------------|-----------------|------|-------------------|-----------------|------|
| | %W | %N | %O | %W | %N | %O |
| Phylum Arthropoda | 33.9 \pm 47.1 | 33.9 \pm 46.8 | 37.5 | 18.7 \pm 39.2 | 20.1 \pm 40.1 | 20.3 |
| Class Malacostraca (Crustaceans) | 33.9 \pm 47.1 | 33.9 \pm 46.8 | 37.5 | 18.7 \pm 39.2 | 20.1 \pm 40.1 | 20.3 |
| Unidentifiable Crustaceans | 5.4 \pm 22.6 | 5.4 \pm 22.6 | 5.4 | | | |
| Order Decapoda | 3.4 \pm 17.7 | 2.7 \pm 15.3 | 5.4 | 1.7 \pm 13.0 | 1.7 \pm 13.0 | 1.7 |
| Unidentifiable Decapods | 0.9 \pm 9.5 | 0.9 \pm 9.5 | 0.9 | | | |
| Family Portunidae | | | | | | |
| <i>Polybius henslowii</i> | 1.8 \pm 13.2 | 1.6 \pm 12.2 | 1.8 | | | |
| Family Pasiphaeidae | | | | | | |
| <i>Pasiphaea multidentata</i> | 0.8 \pm 7.6 | 0.2 \pm 1.2 | 2.7 | | | |
| Sub-order Natantia | | | | 1.7 \pm 13.0 | 1.7 \pm 13.0 | 1.7 |
| Order Euphausiacea | 25.2 \pm 43.3 | 25.9 \pm 43.5 | 27.7 | 15.3 \pm 36.2 | 16.7 \pm 37.3 | 16.9 |
| Family Euphausiidae | | | | | | |
| Unidentifiable Euphausiidae | 2.7 \pm 16.2 | 2.7 \pm 16.2 | 2.7 | 6.9 \pm 25.3 | 8.2 \pm 27.2 | 8.5 |
| <i>Meganyctiphanes norvegica</i> | 22.5 \pm 41.6 | 23.2 \pm 41.9 | 25.0 | 8.5 \pm 28.1 | 8.5 \pm 28.1 | 8.5 |
| Order Isopoda | | | | 1.7 \pm 13.0 | 1.7 \pm 13.0 | 1.7 |
| Phylum Chordata | 64.5 \pm 47.7 | 65.1 \pm 47.1 | 67.0 | 81.3 \pm 39.2 | 79.9 \pm 40.1 | 81.4 |
| Unidentifiable Osteichthyes | 12.3 \pm 32.5 | 12.5 \pm 32.6 | 13.4 | 22.2 \pm 40.9 | 22.3 \pm 41.0 | 23.7 |
| Order Perciformes | 17.9 \pm 38.0 | 15.4 \pm 35.2 | 18.8 | | | |
| Family Carangidae | | | | | | |
| <i>Trachurus trachurus</i> | 16.8 \pm 37.3 | 14.4 \pm 34.3 | 17.0 | 27.8 \pm 43.1 | 27.5 \pm 42.9 | 32.2 |
| Family Scombridae | | | | | | |
| <i>Scomber scombrus</i> | 1.1 \pm 9.8 | 1.1 \pm 9.6 | 1.8 | | | |
| Order Myxophiformes | | | | | | |
| Family Myctophidae | 1.7 \pm 13.0 | 1.5 \pm 11.5 | 1.8 | | | |
| Order Gadiformes | | | | | | |
| Family Gadidae | | | | | | |
| <i>Micromesistius poutassou</i> | 18.2 \pm 37.8 | 21.3 \pm 39.6 | 24.1 | 5.1 \pm 22.2 | 5.1 \pm 22.2 | 5.1 |
| Order Clupeiformes | | | | 26.2 \pm 41.1 | 25.1 \pm 40.2 | 32.2 |
| Family Clupeidae | | | | | | |
| <i>Sardina pilchardus</i> | | | | 4.1 \pm 18.0 | 3.1 \pm 15.0 | 5.1 |
| Family Engraulidae | | | | | | |
| <i>Engraulus encrasicolus</i> | 14.4 \pm 34.7 | 14.4 \pm 34.7 | 15.2 | 22.1 \pm 39.4 | 22.0 \pm 39.1 | 27.1 |
| Phylum Mollusca | 0.8 \pm 8.0 | 0.7 \pm 6.3 | 1.8 | | | |
| Class Cephalopoda | 0.8 \pm 8.0 | 0.7 \pm 6.3 | 1.8 | | | |
| Order Teuthoidea | | | | | | |
| Family Ommastrephidae | | | | | | |
| <i>Todarodes sagittatus</i> | 0.8 \pm 8.0 | 0.7 \pm 6.3 | 1.8 | | | |
| Phyophyta | 0.8 \pm 7.6 | 0.3 \pm 3.2 | 1.8 | | | |

Bochenek 1990; Barr 1991). A number of studies have found sand lance abundance to be inversely related on a decadal scale to that of co-occurring herring (*Clupea harengus*) and mackerel (Sherman et al. 1981; Nelson and Ross 1991). Despite large population fluctuations in sand lance in the MAB over recent decades (Nelson and Ross 1991), juvenile ABFT fed on sand lance during both high

(Barr 1991) and low (Eggleston and Bochenek 1990) abundance periods. No major prey group has filled the sand lance niche during periods of lower abundance, and Atlantic mackerel, herring, butterfish, and longfin squid (*Loligo pealeii*), which occupy similar trophic positions to sand lance (Bowman et al. 2000), are secondary prey items for ABFT in this and in previous studies (Eggleston and

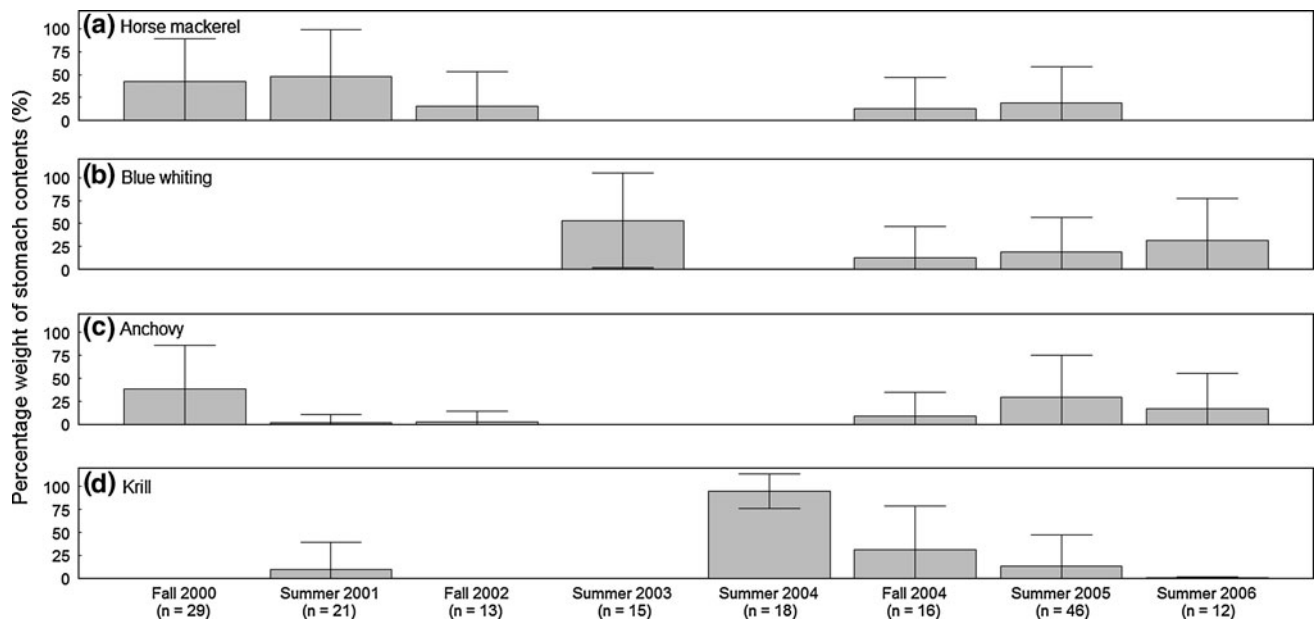


Fig. 3 Mean proportion by weight (MW_i) for each sampling year and season in the Bay of Biscay (BYB) for the four species with highest overall MW_i values: horse mackerel (*Trachurus trachurus*), blue

whiting (*Micromesistius poutassou*), anchovy (*Engraulis encrasicolus*), and krill (*Meganyctiphanes norvegica*)

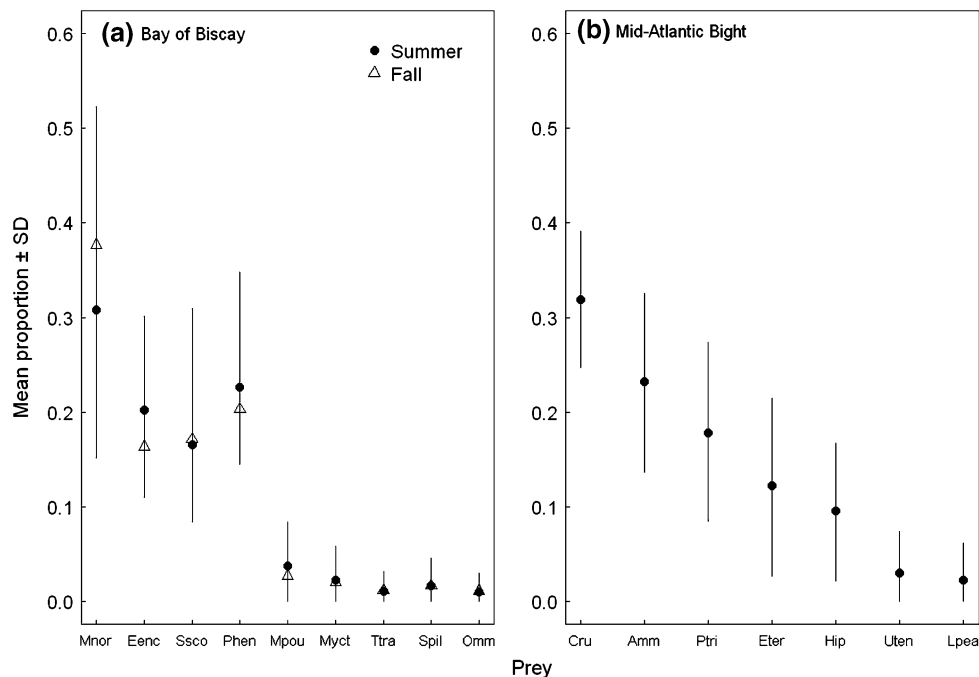


Fig. 4 Stable isotope mixing model dietary proportion estimates for Atlantic bluefin tuna (*Thunnus thynnus*; ABFT) from (a) the Bay of Biscay (BYB) and (b) Mid-Atlantic Bight (MAB). For the Bay of Biscay, estimates were generated separately using ABFT liver isotope data from summer and fall. For the Mid-Atlantic Bight, all liver data were pooled for a single analysis. Proportion estimates are mean \pm SD. (BYB: Mnor = *Meganyctiphanes norvegica* (krill; $n = 4$), Eenc = *Engraulis encrasicolus* (European anchovy; $n = 1$), Ssco = *Scomber scombrus* (Atlantic mackerel; $n = 3$),

Phen = *Polybius henslowii* (swimming crab; $n = 1$), MP = *Micromesistius poutassou* (blue whiting; $n = 2$), Myct = Myctophidae ($n = 1$), Ttra = *Trachurus trachurus* (horse mackerel; $n = 1$), Spil = *Sardina pilchardus* (sardine; $n = 1$); MAB: Cru = Crustacean ($n = 3$), Amm = *Ammodytes* spp. (sand lance; $n = 5$), Ptri = *Peprilus triacanthus* (Atlantic butterfish; $n = 2$), Eter = *Etrumeus teres* (round herring; $n = 3$), Hip = *Hippocampus erectus* (sea horse; $n = 1$), Uten = *Urophycis tenuis* (white hake; $n = 3$), Lpea = *Loligo pealeii* (longfin squid; $n = 2$))

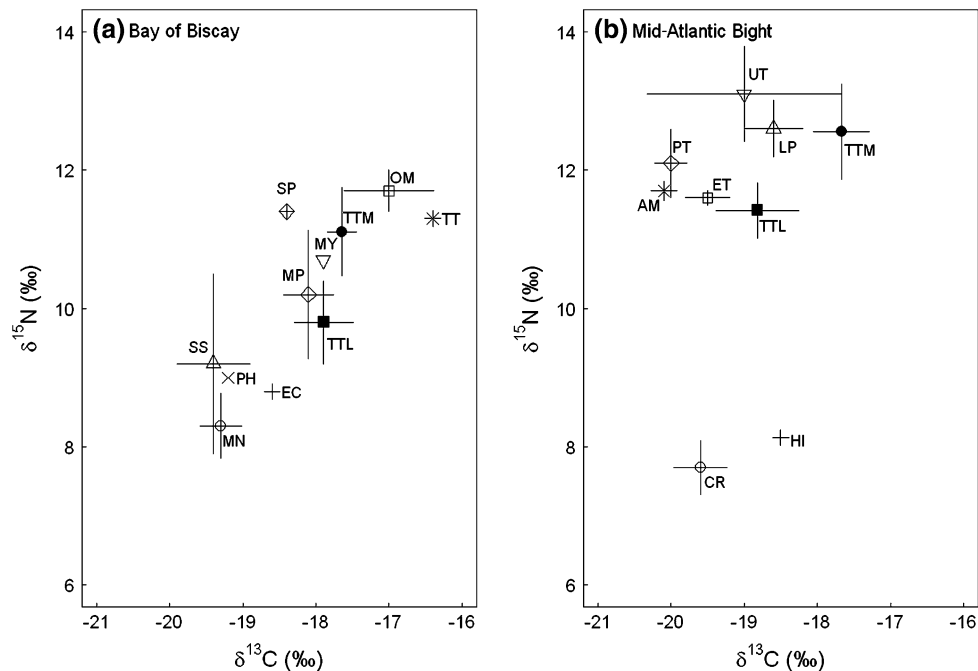


Fig. 5 Mean \pm SD $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from (a) the Bay of Biscay (BYB) and (b) Mid-Atlantic Bight (MAB) of prey and Atlantic bluefin tuna (*Thunnus thynnus*; ABFT) liver and muscle. (BYB: MN = *Meganyctiphanes norvegica* (krill; $n = 4$), SS = *Scomber scombrus* (Atlantic mackerel; $n = 3$), PH = *Polybius henslowii* (swimming crab; $n = 1$), EC = *Engraulis encrasicolus* (European anchovy; $n = 1$), MP = *Micromesistius poutassou* (blue whiting; $n = 2$), SP = *Sardina pilchardus* (sardine; $n = 1$), MY = Myctophidae ($n = 1$), OM = Ommastrephidae ($n = 4$), TT = *Trachurus*

(horse mackerel; $n = 1$), TTL = *Thunnus thynnus* liver ($n = 118$), TTM = *Thunnus thynnus* muscle ($n = 118$); MAB: CR = Crustacean ($n = 3$), HI = *Hippocampus erectus* (sea horse; $n = 1$), AM = *Ammodytes* spp. (sand lance; $n = 5$), PT = *Peprilus triacanthus* (Atlantic butterfish; $n = 2$), ET = *Etrumeus teres* (round herring; $n = 3$), UT = *Urophycis tenuis* (white hake; $n = 3$), LP = *Loligo pealeii* (longfin squid; $n = 2$), TTL = *Thunnus thynnus* liver ($n = 72$), TTM = *Thunnus thynnus* muscle ($n = 72$))

Bochenek 1990; Barr 1991). Both SCA and SIA confirm that age 1–5 years ABFT occupy a common niche along these coastal foraging grounds as sand lance predators.

Anchovy populations in the BYB have recently declined (Ibaibarriaga et al. 2008; ICES 2008), and their low representation in our sample could reflect reduced availability and a consequent dietary change for ABFT. Anchovy recruitment was relatively high for 2000, but then declined for the remaining years of our study (Ibaibarriaga et al. 2008). Observed dietary trends for ABFT in the Bay of Biscay appear to track availability of anchovies and alternate prey such as krill. Anchovies were a major prey in 2000, while krill were absent from stomach contents. In summer 2005, despite low overall stock abundance, age-0 anchovy abundance was among the highest across 2003–2006 in the BYB (Boyra et al. 2008). Anchovies made up nearly half of stomach content biomass in August 2005, when they transition from the larval to juvenile phase (Irigoien et al. 2007). Krill had high densities (Lezama et al. 2008; Irigoien et al. 2009) and were the main diet item in summer 2004, while anchovies were absent. These results suggest that ABFT are true generalists, changing diet to reflect prey community composition.

Anomalous oceanographic conditions were documented in 2004 in the BYB and MAB (Taylor et al. 2005; Fontán et al. 2008). Stable isotope values for fish sampled in summer 2004 were distinct from other seasons and years. While differences were likely due to increased feeding on krill in the BYB, significant differences in muscle $\delta^{15}\text{N}$ and muscle–liver $\delta^{15}\text{N}$ separation for age 1–3 ABFT in the MAB suggest recent dispersal from offshore areas, where N_2 fixation and recycled nitrogen produce low $\delta^{15}\text{N}$ values (Wada and Hattori 1991). In 2004, increased cold, fresh Scotian shelf water entered the eastern Gulf of Maine, which was then advected later in the year onto George’s Bank and into the MAB (Taylor et al. 2005). Differences in oceanographic conditions could have influenced timing of arrivals onto shelf regions. These data suggest that offshore foraging grounds may also be important to juvenile ABFT.

Prey and ABFT condition

Community changes to prey with lower energy content could adversely affect a species with high metabolic demands such as ABFT (Golet et al. 2007). Significant declines in the somatic condition of adult ABFT in the Gulf

Table 3 Mean \pm SD for liver and muscle carbon and nitrogen values from Atlantic bluefin tuna (*Thunnus thynnus*, ABFT) from the Bay of Biscay (BYB) and Mid-Atlantic Bight (MAB). Values with different letter superscripts in a given column for each sampling region are significantly different ($P < 0.05$)

| Age class (Years) | Year | Season | Muscle–Liver separation | | | | Liver | | | | Muscle | | | |
|---------------------------|------|--------|-------------------------|------------------------------|------------------------------|-----|------------------------------|--------------------------------|-----------------------------|---------------------------|------------------------------|--------------------------------|-------------------------------|---------------------------|
| | | | n | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | C:N | n | C:N | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) | n | C:N | $\delta^{13}\text{C}$ (‰) | $\delta^{15}\text{N}$ (‰) |
| Bay of Biscay | | | | | | | | | | | | | | |
| 1–3 | 2001 | Summer | 24 | 0.4 \pm 0.4 ^{b,d} | 1.3 \pm 0.5 ^{b,c} | 24 | 5.2 \pm 1.0 ^b | -18.0 \pm 0.4 ^c | 9.9 \pm 0.5 ^a | 24 | 3.2 \pm 0.2 ^a | -17.6 \pm 0.2 ^{a,b} | 11.1 \pm 0.6 ^{a,b} | |
| 1–3 | 2003 | Summer | 7 | 0.8 \pm 0.2 ^{b,c} | 0.8 \pm 0.6 ^b | 7 | 4.6 \pm 0.6 ^{b,c} | -18.5 \pm 0.2 ^b | 9.9 \pm 0.2 ^a | 7 | 3.1 \pm 0.1 ^a | -17.8 \pm 0.1 ^b | 10.7 \pm 0.6 ^{a,b} | |
| 1–3 | 2004 | Summer | 14 | 0.8 \pm 0.2 ^c | 1.8 \pm 0.5 ^a | 14 | 4.9 \pm 0.5 ^b | -18.3 \pm 0.3 ^b | 8.8 \pm 0.3 ^b | 15 | 3.1 \pm 0.1 ^a | -17.6 \pm 0.2 ^{a,b} | 10.6 \pm 0.6 ^a | |
| 1–3 | 2000 | Fall | 24 | 0.1 \pm 0.3 ^{a,c} | 1.5 \pm 0.4 ^{a,c} | 28 | 6.3 \pm 1.2 ^{a,c} | -17.6 \pm 0.4 ^a | 9.9 \pm 0.3 ^a | 27 | 3.2 \pm 0.1 ^a | -17.6 \pm 0.2 ^a | 11.4 \pm 0.3 ^b | |
| 1–3 | 2002 | Fall | 29 | 0.3 \pm 0.4 ^{a,d} | 1.1 \pm 0.4 ^{b,c} | 30 | 5.6 \pm 1.2 ^{b,c} | -18.0 \pm 0.4 ^c | 9.9 \pm 0.5 ^a | 30 | 3.2 \pm 0.1 ^a | -17.7 \pm 0.2 ^b | 11.0 \pm 0.8 ^{a,b} | |
| 1–3 | 2004 | Fall | 14 | -0.2 \pm 0.4 ^e | 1.3 \pm 0.5 ^{b,c} | 15 | 8.0 \pm 2.2 ^a | -17.9 \pm 0.4 ^a | 10.2 \pm 0.7 ^a | 15 | 3.3 \pm 0.3 ^a | -17.5 \pm 0.2 ^a | 11.5 \pm 0.6 ^b | |
| Mid-Atlantic Bight | | | | | | | | | | | | | | |
| 1–3 | 2004 | Summer | 17 | 1.2 \pm 0.3 ^a | 0.5 \pm 0.6 ^a | 17 | 4.7 \pm 0.8 ^a | -18.9 \pm 0.5 ^b | 11.2 \pm 0.4 ^a | 17 | 3.2 \pm 0.1 ^{a,b} | -17.7 \pm 0.4 ^{a,b} | 11.7 \pm 0.9 ^a | |
| 1–3 | 2005 | Summer | 12 | 1.1 \pm 0.3 ^a | 1.0 \pm 0.3 ^c | 12 | 4.7 \pm 0.6 ^a | -18.8 \pm 0.3 ^{a,b} | 11.6 \pm 0.3 ^a | 12 | 3.1 \pm 0.1 ^b | -17.7 \pm 0.4 ^{a,b} | 12.6 \pm 0.4 ^b | |
| 1–3 | 2006 | Summer | 11 | 1.4 \pm 0.4 ^a | 1.2 \pm 0.3 ^{b,c} | 11 | 5.5 \pm 1.4 ^a | -19.5 \pm 0.5 ^a | 11.4 \pm 0.3 ^a | 11 | 3.3 \pm 0.3 ^{a,b} | -18.0 \pm 0.3 ^a | 12.7 \pm 0.3 ^b | |
| 4–5 | 2004 | Summer | 4 | 1.3 \pm 0.4 ^a | 1.3 \pm 0.6 ^{b,c} | 4 | 4.8 \pm 0.5 ^a | -18.6 \pm 0.3 ^{a,b} | 11.8 \pm 0.2 ^a | 4 | 3.2 \pm 0.1 ^{a,b} | -17.3 \pm 0.2 ^b | 13.1 \pm 0.6 ^b | |
| 4–5 | 2006 | Summer | 28 | 1.1 \pm 0.4 ^a | 1.5 \pm 0.4 ^b | 28 | 5.0 \pm 0.7 ^a | -18.6 \pm 0.6 ^b | 11.4 \pm 0.4 ^a | 28 | 3.4 \pm 0.4 ^a | -17.5 \pm 0.3 ^b | 12.9 \pm 0.2 ^b | |

of Maine could be linked to changes in prey composition or energy content (Golet et al. 2007). Recent modeling projections demonstrate that growth at young ages is linked to age-at-maturity and that growth is also dependent upon food quality and availability (E. Chapman, personal communication).

In the NW Atlantic, lipid content estimates of ABFT prey range from \sim 3 to 7% for sand lance, butterfish, and squid (Lawson et al. 1998; Budge et al. 2002). Sand lance has a relatively high energetic content, which combined with dense schooling behavior (Nizinski 2002) provides an ideal prey for a ram-feeder like ABFT (Rooker et al. 2007).

Available BYB prey items vary widely in quality, with anchovies generally having higher lipid content than krill or blue whiting (Soriguer et al. 1997; Mayzaud et al. 1999). Krill lipid content varies widely depending on season, sex, and reproductive state (Mauchline and Fisher 1969; Mayzaud et al. 1999; Albessard et al. 2001). While further studies are needed to compare the nutritional quality of krill and anchovy prey, differences in their quality could affect ABFT energetics as ABFT appear to feed preferentially on whichever prey group is most abundant.

For age 1–3 ABFT, muscle tissues from both regions had minimal lipid stores (mean C:N \sim 3.2, lipid-free value \sim 3.1 (Logan et al. 2008)), while age 4–5 ABFT from the MAB had slightly higher C:N values (\sim 3.4). ABFT increase in length rather than girth at smaller sizes (<110 cm), then gain greater mass at larger sizes (Mather et al. 1995; Fromentin and Powers 2005), and a corresponding increase in lipid stores was observed for age 4–5 year ABFT in the MAB. No ABFT > 110 cm were analyzed for muscle C:N in the BYB, but summer biomass gain for age 1–3 ABFT in this region is nearly 5–6 times faster than winter growth (Cort 1991), so energy stores should increase during this period of elevated growth. During 2004 when data were collected across the feeding season (BYB), liver C:N significantly increased from summer to fall, suggesting that juveniles might instead store energy reserves in this tissue. In adults, lipid content changes seasonally in muscle tissue (Estrada et al. 2005; Golet et al. 2007), and we may have missed increases in somatic condition because of limited sample size. In a more comprehensive study in the BYB, there was a linear increase in muscle lipid content with size and both inter- and intra-annual variability (Goñi and Arrizabalaga 2010).

Role of ABFT in coastal food webs

Young ABFT seem to occupy a lower trophic position than co-occurring marine mammal and some fish predators such as bluefish (*Pomatomus saltatrix*) in both Atlantic shelf regions (Bowman et al. 2000; Spitz et al. 2006). King mackerel (*Scomberomorus cavalla*), a piscivore (Bowman

Table 4 Mean \pm SD prey composition for Mid-Atlantic Bight (MAB) Atlantic bluefin tuna (*Thunnus thynnus*; ABFT) (percent weight (%W), percent number (%N), and frequency of occurrence (%O))

| Prey | Age 1–3 ($n = 20$) | | | Age 4–5 ($n = 22$) | | |
|----------------------------------|----------------------|-----------------|-------|----------------------|-----------------|-------|
| | %W | %N | %O | %W | %N | %O |
| Phylum Arthropoda | 4.9 \pm 22.1 | 1.3 \pm 5.6 | 5.0 | 0.0 \pm 0.1 | 0.6 \pm 2.7 | 4.5 |
| Class Malacostraca (Crustaceans) | | | | | | |
| Order Decapoda | 4.9 \pm 22.1 | 1.3 \pm 5.6 | 5.0 | 0.0 \pm 0.1 | 0.6 \pm 2.7 | 4.5 |
| Phylum Chordata | 90.9 \pm 26.1 | 67.3 \pm 45.7 | 100.0 | 86.3 \pm 25.1 | 55.9 \pm 48.6 | 100.0 |
| Unidentifiable Osteichthyes | 57.1 \pm 39.5 | 0.0 \pm 0.0 | 90.0 | 46.4 \pm 35.0 | 0.0 \pm 0.0 | 77.3 |
| Order Clupeiformes | | | | | | |
| Family Clupeidae | | | | | | |
| <i>Etrumeus teres</i> | 4.5 \pm 20.0 | 5.0 \pm 22.4 | 5.0 | 3.8 \pm 17.8 | 2.3 \pm 10.7 | 4.5 |
| Order Perciformes | 29.3 \pm 35.6 | 62.1 \pm 47.2 | 70.0 | | | |
| Family Ammodytidae | | | | | | |
| <i>Ammodytes</i> spp. | 26.6 \pm 35.7 | 57.1 \pm 48.2 | 65.0 | 31.4 \pm 36.3 | 50.8 \pm 47.0 | 59.1 |
| Family Stromateidae | | | | | | |
| <i>Peprilus triacanthus</i> | 2.7 \pm 12.2 | 5.0 \pm 22.4 | 5.0 | | | |
| Order Scorpaeniformes | | | | | | |
| Family Scorpaenidae | 0.0 \pm 0.0 | 0.2 \pm 1.0 | 5.0 | 0.0 \pm 0.1 | 0.6 \pm 2.7 | 4.5 |
| Order Gadiformes | | | | | | |
| Family Gadidae | | | | 2.6 \pm 12.2 | 0.8 \pm 3.6 | 4.5 |
| Order Phycidae | | | | | | |
| <i>Urophycis tenuis</i> | | | | 2.6 \pm 12.2 | 0.8 \pm 3.6 | 4.5 |
| Order Syngnathiformes | | | | | | |
| Family Syngnathidae | | | | | | |
| <i>Hippocampus erectus</i> | | | | 2.1 \pm 9.6 | 1.5 \pm 7.1 | 4.5 |
| Parasites | | | | 9.4 \pm 21.1 | 24.2 \pm 42.6 | 27.3 |
| Phylum Platyhelminthes | | | | | | |
| Class Trematoda | | | | | | |
| Order Azygiida | | | | | | |
| Family Hirudinellidae | | | | | | |
| <i>Hirudinella ventricosa</i> | | | | 9.4 \pm 21.1 | 24.2 \pm 42.6 | 27.3 |
| Phylum Mollusca | 1.1 \pm 3.6 | 6.5 \pm 22.5 | 15.0 | 0.3 \pm 1.4 | 1.1 \pm 5.3 | 4.5 |
| Class Cephalopoda | 1.1 \pm 3.6 | 6.5 \pm 22.5 | 15.0 | 0.3 \pm 1.4 | 1.1 \pm 5.3 | 4.5 |
| Order Teuthoidea | 0.8 \pm 3.3 | 1.5 \pm 4.5 | 10.0 | | | |
| Unidentifiable Teuthoidea | 0.0 \pm 0.1 | 0.8 \pm 3.7 | 5.0 | | | |
| Family Loliginidae | 0.7 \pm 3.3 | 0.6 \pm 2.8 | 5.0 | | | |
| Order Octopoda | 0.3 \pm 1.5 | 5.0 \pm 22.4 | 5.0 | 0.3 \pm 1.4 | 1.1 \pm 5.3 | 4.5 |
| Plastic material | | | | 0.0 \pm 0.1 | 0.0 \pm 0.0 | 4.5 |
| Unidentifiable material | 3.0 \pm 13.6 | 0.0 \pm 0.0 | 5.0 | 4.0 \pm 12.6 | 0.0 \pm 0.0 | 18.2 |

et al. 2000) from the MAB, had higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to ABFT (Logan 2009). King mackerel liver samples had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of $-17.9 \pm 0.3\text{‰}$ and $12.5 \pm 0.3\text{‰}$ ($n = 3$), respectively, while our complete ABFT dataset had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of $-18.8 \pm 0.6\text{‰}$ and $11.4 \pm 0.4\text{‰}$. Isotope discrimination values assumed in this study would place king mackerel about one trophic level above ABFT. We attribute these results to higher predation rates on crustaceans and other lower trophic level

prey species by ABFT. In the BYB, 1- to 2-year-old ABFT have low $\delta^{15}\text{N}$ values, corresponding to values of smaller primary consumers (e.g., sardines) (Bode et al. 2007). Adult ABFT can reach a trophic level similar to top pelagic predators such as odontocetes and sharks (Estrada et al. 2003, 2005; Sara and Sara 2007), suggesting that ABFT undergo an ontogenetic dietary shift of several trophic levels. Young ABFT fed on similar prey items to ABFT in NW Atlantic foraging grounds (Estrada et al. 2005), but

lower trophic level prey than ABFT of the same size classes in the Mediterranean Sea (Sanz Brau 1990; Sinopoli et al. 2004; Sara and Sara 2007).

Conclusions

Young ABFT feed mainly on zooplanktivorous fishes and crustaceans in foraging grounds in the eastern and western Atlantic Ocean. Our results generally support past findings that ABFT in the MAB forage mainly on sand lance, but isotope results suggest similar contributions of lower trophic level prey. For the Bay of Biscay, ABFT diet appeared to change in response to prey species abundance, with anchovies and krill as major prey groups when each was abundant. Further studies comparing the quality and abundance of these prey groups would better define potential impacts on ABFT feeding in this region. Long-term monitoring of trophic relationships will be necessary to understand ecosystem changes and top predator population dynamics in relation to climate change and human exploitation.

Acknowledgments We thank R. Doucett and A. Ouimette for assistance with stable isotope analyses. We also thank B. Galuardi for providing help with statistical analyses. We thank C. Speaks for assisting in sample collection and R. Toppin for helping with stomach content analyses for the western Atlantic dataset. S. Bean, M. Peck, and three anonymous reviewers also provided valuable comments to earlier drafts of this manuscript. This study was funded by NOAA grant no. NA04NMF4550391 to M. Lutcavage and partially funded by the Spanish data collection programme within the European Union Fisheries Data Collection Regulation Framework as well as project ATM2005Templados funded by the Basque Government to AZTI Tecnalia.

References

- Albessard E, Mayzaud P, Cuzin-Roudy J (2001) Variation of lipid classes among organs of the northern krill *Meganyctiphanes norvegica*, with respect to reproduction. *Comp Biochem Physiol* 129:373–390
- Barr CG (1991) Food and feeding of northern bluefin tuna (*Thunnus thynnus*) and yellowfin tuna (*Thunnus albacares*): a comparative study of the food and feeding habits of the northern bluefin tuna off the coast of Virginia. Master's Thesis, Virginia Institute of Marine Science, College of William and Mary
- Bizzarro J, Robinson H, Rinewalt C, Ebert D (2007) Comparative feeding ecology of four sympatric skate species off central California, USA. *Environ Biol Fishes* 80:197–220
- Bochenek EA (1989) Virginia's pelagic recreational fishery for tunas and billfishes: biological, socioeconomic, and fishery components for 1983–1985 with comments on the 1986 season. PhD Virginia Institute of Marine Science, College of William and Mary
- Bode A, Alvarez-Ossorio M, Carrera P, Lorenzo J (2004) Reconstruction of trophic pathways between plankton and the North Iberian sardine (*Sardina pilchardus*) using stable isotopes. *Sci Mar* 68:165–178
- Bode A, Alvarez-Ossorio M, Cunha M, Garrido S, Peleteiro J, Porteiro C, Valdes L, Varela M (2007) Stable nitrogen isotope studies of the pelagic food web on the Atlantic shelf of the Iberian Peninsula. *Prog Oceanogr* 74:115–131
- Bowman RE, Stillwell CE, Michaels WL, Grosslein MD (2000) Food of Northwest Atlantic fishes and two common species of squid. NOAA Technical Memorandum NMFS-NE-155, 138 pp
- Boyra G, Cotano U, Martinez U, Peña M, Uriarte A (2008) JUVENA series review of the spatial distribution of anchovy juveniles in the Bay of Biscay. XI international symposium on oceanography of the Bay of Biscay, San Sebastián, Spain, April 2008
- Budge SM, Iverson SJ, Bowen WD, Ackman RG (2002) Among and within-species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank, and southern Gulf of St. Lawrence. *Can J Fish Aquat Sci* 59:886–898
- Cartes J, Huguet C, Parra S, Sanchez F (2007) Trophic relationships in deep-water decapods of Le Danois bank (Cantabrian Sea, NE Atlantic): trends related with depth and seasonal changes in food quality and availability. *Deep Sea Res* 54:1091–1110
- Chase B (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
- Chipps SR, Garvey JE (2007) Assessment of food habits and feeding patterns. In: Guy C, Brown M (eds) Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, pp 473–514
- Cort JL (1991) Age and growth of the bluefin tuna. *Thunnus thynnus* (L.) of the Northeast Atlantic. *Col Vol Sci Pap ICCAT* 35:213–230
- Craig H (1953) The geochemistry of the stable carbon isotopes. *Geochim Cosmochim Acta* 3:53–92
- Eggleston DB, Bochenek EA (1990) Stomach contents and parasite infestation of school bluefin tuna *Thunnus thynnus* collected from the Middle Atlantic Bight, Virginia. *Fish Bull* 88:389–395
- Estrada JA, Rice AN, Lutcavage ME, Skomal GB (2003) Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. *J Mar Biol Assoc U K* 83:1347–1350
- Estrada JA, Lutcavage M, Thorrold SR (2005) Diet and trophic position of Atlantic bluefin tuna (*Thunnus thynnus*) inferred from stable carbon and nitrogen isotope analysis. *Mar Biol* 147:37–45
- Ferry LA, Caillet GM (1996) Sample size and data analysis: are we characterizing and comparing diet properly? In: MacKinlay D, Shearer K (eds) Feeding ecology and nutrition in fish, symposium proceedings, San Francisco State University, pp 71–80
- Fontán A, Valencia V, Borja Á, Goikoetxea N (2008) Oceanometeorological conditions and coupling in the southeastern Bay of Biscay, for the period 2001–2005: a comparison with the past two decades. *J Mar Syst* 72:167–177
- Fromentin JM, Powers JE (2005) Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. *Fish Fish* 6:281–306
- Fry B, Baltz DM, Benfield MC, Fleeger JW, Gace A, Haas HL, Quiñones-Rivera ZJ (2003) Stable isotope indicators of movement and residency for brown shrimp (*Farfantepenaeus aztecus*) in coastal Louisiana marshscapes. *Estuaries* 26:82–97
- Gannes LZ, Martínez del Río C, Koch P (1998) Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Comp Biochem Physiol* 119:725–737
- Golet W, Cooper A, Campbell R, Lutcavage M (2007) Decline in condition of northern bluefin tuna (*Thunnus thynnus*) in the Gulf of Maine. *Fish Bull* 105:390–395
- Goñi N, Arrizabalaga H (2010) Seasonal and interannual variability of fat content of juvenile albacore (*Thunnus alalunga*) and

- bluefin (*Thunnus thynnus*) tuna during their feeding migration to the Bay of Biscay. *Prog Oceanogr* 86:115–123
- Hilton G, Houston D, Furness R (1998) Which components of diet quality affect retention time of digesta in seabirds? *Funct Ecol* 12:929–939
- Hinke J, Kaplan I, Aydin K, Watters G, Olson R, Kitchell J (2004) Visualizing the food-web effects of fishing for tunas in the Pacific Ocean. *Ecol Soc* 9:10
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70
- Ibaibarriaga L, Fernández C, Uriarte A, Roel BA (2008) A two-stage biomass dynamic model for Bay of Biscay anchovy: a Bayesian approach. *ICES J Mar Sci* 65:191–205
- ICCAT (2009) Report of the standing committee on research and statistics (Madrid, Spain, October 5–9, 2009)
- ICES (2008) Report of the working group on the anchovy, ICES Headquarters, 13–16 June 2008, ICES CM2008/ACOM:04
- Irigoien X, Fiksen Ø, Cotano U, Uriarte A, Alvarez P, Arrizabalaga H, Boyra G, Santos M, Sagarminaga Y, Otheguy P, Etxebeeste E, Zarauz L, Artetxe I, Motos L (2007) Could Biscay Bay anchovy recruit through a spatial loophole? *Prog Oceanogr* 74:132–148
- Irigoien X, Fernandes J, Grosjean P, Denis K, Albaina A, Santos M (2009) Spring zooplankton distribution in the Bay of Biscay from 1998 to 2006 in relation with anchovy recruitment. *J Plankton Res* 31:1–17
- Lawson J, Magalhaes A, Miller E (1998) Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Mar Ecol Prog Ser* 164:13–20
- Lezama A, Boyra G, Caballero A, Irigoien X, Sagarminaga Y (2008) Krill distribution in the Bay of Biscay by means of multifrequency acoustic techniques. International symposium on ecosystem approach with fisheries acoustics and complementary technologies (SEAFACETS), Bergen, Norway
- Logan J (2009) Tracking diet and movement of Atlantic bluefin tuna (*Thunnus thynnus*) using carbon and nitrogen stable isotopes. PhD Thesis University of New Hampshire, Durham, NH
- Logan J, Jardine T, Miller T, Bunn S, Cunjak R, Lutcavage M (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J Anim Ecol* 77:838–846
- Mather FJ, Mason JM Jr, Jones AC (1995) Historical document: life history and fisheries of Atlantic bluefin tuna. NOAA Technical Memorandum NMFS-SEFSC-370, Miami, FL, 165 pp
- Matthews FD, Damkaer DM, Knapp LW, Collette BB (1977) Food of western North Atlantic tunas (*Thunnus*) and lancetfishes (*Alepisaurus*). NOAA Technical Report NMFS SSRF-706
- Mauchline J, Fisher LR (1969) The biology of euphausiids. In: Russell FS, Yonge M (eds) *Advances in marine biology*, vol 7. Academic Press, New York
- Mayzaud P, Virtue P, Albessard E (1999) Seasonal variations in the lipid and fatty acid composition of the euphausiid *Meganyctiphanes norvegica* from the Ligurian Sea. *Mar Ecol Prog Ser* 186:199–210
- Nelson GA, Ross MR (1991) Biology and population changes of northern sand lance (*Ammodytes dubius*) from the Gulf of Maine to the Middle Atlantic Bight. *J Northw Atl Fish Sci* 11:11–27
- Nizinski MS (2002) Sand lances. Family ammodytidae. In: Collette BB, Klein-MacPhee G (eds) *Bigelow and Schroeder's fishes of the Gulf of Maine*. Smithsonian Institution Press, Washington and London, pp 496–505
- Ortiz de Zárate V, Cort JL (1986) Stomach contents study of immature bluefin tuna in the Bay of Biscay, ICES-CM H:26, 10 pp
- Paine T (1966) Food web complexity and species diversity. *Am Nat* 100:65–75
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5:e9672
- Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136:261–269
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rodríguez-Marín E, Arrizabalaga H, Ortiz M, Rodríguez-Cabello C, Moreno G, Kell LT (2003) Standardization of bluefin tuna, *Thunnus thynnus*, catch per unit effort in the baitboat fishery of the Bay of Biscay (Eastern Atlantic). *ICES J Mar Sci* 60:1216–1231
- Rodríguez-Marín E, Clear N, Cort JL, Megafonou P, Neilson JD, Neves dos Santos M, Olafsdottir D, Rodríguez-Cabello C, Ruiz M, Valeiras J (2007) Report of the 2006 ICCAT Workshop for bluefin tuna direct ageing. (Instituto Español de Oceanografía, Santander, Spain, 3–7 April 2006). *Col Vol Sci Pap ICCAT* 60, pp 1349–1392
- Rooker J, Bremer J, Block B, Dewar H, De Metrio G, Corriero A, Kraus R, Prince E, Rodríguez-Marín E, Secor D (2007) Life history and stock structure of Atlantic bluefin tuna (*Thunnus thynnus*). *Rev Fish Sci* 15:265–310
- Rosen D, Trites A (2000) Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. *Can J Zool* 78:1243–1250
- Sanz Brau A (1990) Sur la nourriture des jeunes thons rouges *Thunnus thynnus* (L. 1758) des côtes du Golfe de Valence. *Rapports et Communications Internationales de la Mer Méditerranée* 32:274
- Sara G, Sara R (2007) Feeding habits and trophic levels of bluefin tuna *Thunnus thynnus* of different size classes in the Mediterranean Sea. *J Appl Ichthyol* 23:122–127
- Sherman K, Jones C, Sullivan L, Smith W, Berrien P, Ejsymont L (1981) Congruent shifts in sand eel abundance in western and eastern north Atlantic ecosystems. *Nature* 291:486–489
- Sinopoli M, Pipitone C, Campagnuolo S, Campo D, Castriota L, Mostarda E, Andaloro F (2004) Diet of young-of-the-year bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758), in the southern Tyrrhenian (Mediterranean) Sea. *J Appl Ichthyol* 20:310–313
- Soriguer F, Serna S, Valverde E, Hernando J, Martín-Reyes A, Soriguer M, Pareja A, Tinahones F, Esteva I (1997) Lipid, protein, and calorie content of different Atlantic and Mediterranean fish, shellfish, and molluscs commonly eaten in the south of Spain. *Eur J Epidemiol* 13:451–463
- Spitz J, Richard E, Meynier L, Pusineri C, Ridoux V (2006) Dietary plasticity of the oceanic striped dolphin, *Stenella coeruleoalba*, in the neritic waters of the Bay of Biscay. *J Sea Res* 55:309–320
- Sweeting CJ, Barry J, Barnes C, Polunin NVC, Jennings S (2007a) Effects of body size and environment on diet-tissue $\delta^{15}\text{N}$ fractionation in fishes. *J Exp Mar Biol Ecol* 340:1–10
- Sweeting CJ, Barry JT, Polunin NVC, Jennings S (2007b) Effects of body size and environment on diet-tissue $\delta^{13}\text{C}$ fractionation in fishes. *J Exp Mar Biol Ecol* 352:165–176
- Talbot C, Higgins PJ (1982) Observations on the gall bladder of juvenile Atlantic salmon *Salmo salar* L., in relation to feeding. *J Fish Biol* 21:663–669
- Taylor MH, Bascuñán C, Manning JP (2005) Description of the 2004 oceanographic conditions on the northeast continental shelf. US Dep Commer, Northeast Fish Sci Cent Ref Doc. 05-03
- Wada E, Hattori A (1991) Nitrogen in the sea: forms, abundances, and rate processes. CRC Press, Boca Raton, FL