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Diet and consumption rate of Atlantic bluefin tuna (*Thunnus thynnus*) in the Strait of Gibraltar

Joan Miquel Sorell[a], José Luis Varela[a,b,*], Nicolas Goñi[c], David Macías[d], Haritz Arrizabalaga[c], Antonio Medina[a]

[a] *Departamento de Biología, Universidad de Cádiz, Campus de Excelencia Internacional del Mar (CEI·MAR), Av. República Saharaui s/n, 11510 Puerto Real, Cádiz, Spain*
[b] *Biology Department, Acadia University, 33 Westwood Ave., B4P 2R6 Wolfville, Nova Scotia, Canada*
[c] *AZTI-Tecnalia, Herrera Kaia Portualdea z/g, Pasaia 20110, Gipuzkoa, Spain*
[d] *Instituto Español de Oceanografía, Centro Oceanográfico de Málaga, Puerto pesquero s/n, Fuengirola, Málaga, Spain*

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ABSTRACT

The diet of Atlantic bluefin tuna (ABFT), *Thunnus thynnus*, caught in the Strait of Gibraltar area (SoG) from late summer through fall was assessed by stomach content (SCA) and stable isotope (SIA) analyses. Our results show that the SoG provides suitable food resources for sub-adult and adult ABFT. The SCA did not show inter-annual differences, and indicated that crustaceans were the most important prey group (alimentary index, AI = 37.47 and AI = 47.22 for 2012 and 2013, respectively), followed by fishes (AI = 28.71 and AI = 25.62, respectively) and cephalopods (AI = 1.55 and AI = 3.03). Diet compositions inferred from mixing models based on muscle and liver isotopic data showed that squid are an important food resource for the ABFT living in the SoG. Feeding patterns were analysed by the graphical method of Amundsen, which suggested that the ABFT exhibits a varying degree of specialisation on different prey. Thus, while most prey species were unimportant and rare, *Sergia robusta* can be considered as the dominant prey. The trophic niche width, estimated from SCA as the antilogarithm of Shannon's entropy, as well as from stable isotope Bayesian ellipses, indicated that the ABFT sampled in 2012 consumed a more diverse diet than those sampled in 2013. Inter-annual differences in daily meal and daily ration were apparent; whereas the estimated daily food intake was 918.91 g day^{-1} in 2012 and 1924.95 g day^{-1} in 2013, the daily ration showed values of 2.52 ± 1.24% body mass (BM) day^{-1} and 5.84 ± 1.06% BM day^{-1}. Such substantial differences are probably due to differences in water temperatures between the sampling dates of the two years.

1. Introduction

Every spring, Atlantic bluefin tuna (ABFT), *Thunnus thynnus* (L., 1758), cross the Strait of Gibraltar (SoG) from the Atlantic Ocean heading for spawning grounds in the Mediterranean Sea (Rodríguez-Roda, 1964). From mid-July, many of these tuna start a post-reproductive migration back to feeding areas in the North Atlantic Ocean (Abascal et al., 2016; Aranda et al., 2013). Yet, significant commercial catches of ABFT by baitboat (August-March) and handline (June-August) (Cort and Abaunza, 2015; de la Serna et al., 2004) are indicative of extended residency of ABFT in the SoG. This ABFT population may consist of individuals from different sources: i) fish arrived from Mediterranean spawning grounds after completing spawning, ii) permanent residents in the area, and iii) individuals in excess of the fishing quota that are eventually released after weeks of confinement in traps. Besides a mere transit passage for many migratory animals such as tunas, the SoG is also used as an important foraging area by many marine animals (Buencuerpo et al., 1998; Cañadas and Sagarminaga, 2000; Cañadas et al., 2005). The oceanographic features of this region cause upwelling of nutrient-rich waters and an increase in primary production (Cheney and Doblar, 1982; Font et al., 2002; Parrilla and Kinder, 1987; Sarhan, 2000; Tintoré et al., 1991) that can support a diverse trophic web.

Recent assessments (see ICCAT, 2014) indicate that the eastern ABFT stock spawning biomass shows clear signs of recovery. A substantial increase of the ABFT population in a particular area may

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[*] Corresponding author at: Departamento de Biología, Universidad de Cádiz, Campus de Excelencia Internacional del Mar (CEI·MAR), Av. República Saharaui s/n, 11510 Puerto Real, Cádiz, Spain.
E-mail address: joseluis.varela@uca.es (J.L. Varela).

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Table 1
Data summary of the ABFT samples used in stomach content analysis (SCA). FL, straight fork length. Collective data are expressed as mean ± SD.

	2012 (Oct 1–Dec 18)	2013 (Aug 25–Oct 18)
FL (cm)	130.45 ± 24.74	119.92 ± 8.86
Number of stomachs sampled	121	61
Percentage of stomachs containing prey	68.60% (n = 83)	72.13% (n = 44)
Percentage of stomachs containing only bait or empty	31.40% (n = 38)	27.87% (n = 17)
Total prey biomass (g)	13905.16	13922.38
Weight of prey in non-empty stomachs	167.53 ± 282.90	316.42 ± 388.88
Number of prey items per non-empty stomach	2.52 ± 1.80	3.14 ± 2.08

have a significant impact on communities of potential prey and cause modifications in the trophic relationships within the ecosystem (Baum and Worm, 2009; Butler et al., 2010). Therefore, an in-depth knowledge of the ABFT feeding habits and trophic structure of its habitat is essential for the management of the resource and the ecosystem preservation.

Traditionally, ABFT diets have been studied by stomach content analysis (SCA), which gives detailed information on prey that have been ingested hours before capture. Stable isotope analysis (SIA) has become a useful method to complement gut analyses as it provides information on consumed prey at longer time scales (Logan et al., 2006; Peterson and Fry, 1987). Generally, carbon stable isotope ratios ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) increase moderately (about 1‰ per trophic level), and give information about dietary sources (Fry, 2006). On the other hand, nitrogen stable isotope ratios ($^{15}N/^{14}N$, $\delta^{15}N$) increase more sharply (about 3‰ from food source to consumer tissues), and are used as indicators of the consumer's trophic level (Post, 2002). Furthermore, the isotopic composition of prey and predators, along with prey-predator isotopic increments can be used in mixing models to estimate the proportion of each type of prey in predator diets (Parnell et al., 2010). Stable isotopes are also good descriptors of trophic niches, and the values of $\delta^{13}C$ and $\delta^{15}N$ in predator tissues allow us to estimate trophic parameters such as niche width and overlap (Bearhop et al., 2004; Newsome et al., 2007; Parnell et al., 2010; Syväranta et al., 2013). The aim of this study is to determine ABFT diet composition and consumption rates in the SoG and assess inter- and intra-annual variations in the feeding patterns using a combination of SCA and SIA.

2. Material and methods

2.1. Samples

ABFT were caught by baitboat in the SoG near Tarifa, southern Spain (lat. 35°55′−36°95′ N, long. 5°85′−5°27′ W) during evening hours between 1st October and 18th December 2012 (n = 121), and between 25th August and 18th October 2013 (n = 61). The straight fork length (FL) was recorded on board to the nearest cm (Table 1). Stomachs and tissue samples of white muscle and liver were stored at −20 °C until analysis. One to 3 specimens of the most representative prey found in the stomach contents were collected from the SoG area and kept at −20 °C until isotopic analysis.

2.2. Stomach content analysis (SCA)

Once defrosted, the stomach contents were blotted dry and prey items were identified to the lowest possible taxon using specific identification keys (Campana, 2004; Clarke, 1986; Froese and Pauly, 2010; Härkönen, 1986; Tuset et al., 2008). Preys were grouped by taxon and their wet weight was recorded to the nearest 0.01 g. Two species of *Scomber*, Atlantic mackerel (*S. scombrus*) and Atlantic chub mackerel (*S. colias*), sand smelt (*Atherina presbyter*), *Trachurus* spp, two species of *Pagellus*, axillary seabream (*P. acarne*) and common pandora (*P. erythrinus*), and bogue (*Boops boops*) were commonly used as live bait or chum by the fishers; hence, these species were not considered in the analyses. Stomachs containing only chum or baitfish were also excluded from SCA.

2.3. Stable isotope analysis (SIA)

Tissue samples of ABFT liver and white muscle, and whole prey, were thawed and washed with distilled water to remove blood and other impurities. The exoskeleton of *Polybius henslowii* was removed prior to SIA. Following freeze-drying, the samples were ground, and aliquots of ∼1 mg were placed into tin capsules for $\delta^{15}N$ analysis. Before $\delta^{13}C$ analysis, lipids were extracted from the samples with chloroform:methanol (2:1 v/v) as described by Varela et al. (2012, 2013). Stable isotopes were measured in a gas flow system using a Thermo Finnigan Flash EA1112 elemental analyser coupled with Thermo Finnigan Delta Plus isotope ratio mass spectrometer. The results were expressed using the standard δ notation as parts per thousand (‰) (Peterson and Fry, 1987).

2.4. Data analysis

Cumulative prey curves (CPCs) were created *a posteriori* to assess whether the number of individuals analysed (total number and number per year) was sufficient to describe the diet composition through presence-absence analysis (Ferry and Cailliet, 1996). The CPCs were generated by randomly resampling the stomachs 1000 times using the software EstimateS 8.2.0 for Windows (Colwell, 2009). Then, the mean number of unique prey types was plotted against the cumulative number of stomachs sampled. The slope resulting from the linear regression calculated from the four end points of CPC was compared with a line of slope zero using Student's *t*-test (Bizzarro et al., 2007).

To determine the relative importance of different preys in the ABFT diet three indices were applied: frequency of occurrence ($\%O_i$ = number of stomachs containing prey item $i \times 100$/total number of non-empty stomachs), percent composition by weight ($\%W_i$ = weight of prey item $i \times 100$/total weight of all prey items), and alimentary index ($AI_i = [\%O_i \times \%W_i]/\ 100$) (Hyslop, 1980; Lauzanne, 1975). Mean percent weight was calculated as $\%\mathrm{MW_i} = \left(1/\mathrm{P}\right)\sum_{\mathrm{j}=1}^{\mathrm{P}}\left(\mathrm{S_{ij}}/\sum_{\mathrm{i}=1}^{\mathrm{Q}}S_{ij}\right) \times 100$, where P is the number of ABFT with non-empty stomachs, Q the number of prey types and S_i the total weight of prey *i* (Chipps and Garvey, 2007). The niche width was estimated from the antilogarithm of the Shannon-Weaver's index *H* (Hill, 1973), calculated as $H = -\sum_i^n \pi_i \ln(\pi_i)$, where π_i is the proportion in weight of prey *i*.

Feeding strategy, prey importance, and inter- and intra- individual components of the trophic niche were evaluated using the graphical method of Costello (1990) as modified by Amundsen et al. (1996). Prey *i*-specific abundance ($\%P_i$) was plotted against$\%O_i$ with $\%P_i = (\sum_i^n S_i/\Sigma St_i) \times 100$, where S_i is the total weight of prey *i*, and St_i the total content weight of all stomachs in which prey *i* occurs (Hyslop, 1980). As in Varela et al. (in press), prey species that only appeared in one stomach were not accounted for in the analyses.

The food consumption rate was estimated according to the equation proposed by Olson and Mullen (1986): $\hat{r} = \sum_{i=0}^{I} \bar{W}_i/A_i$, where $\hat{r}$ is the feeding rate measured in g h^{-1}, $\bar{W}_i$ is the mean weight of the prey *i*, and A_i is the average time required to evacuate the average proportion of prey *i*. Although stomach content data were not available for the entire 24 h period, earlier reports suggest that

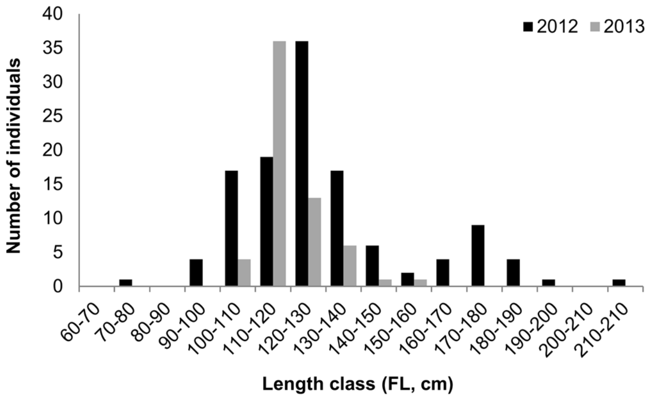

Fig. 1. Length distribution of the sampled ABFT. FL: straight fork length (cm).

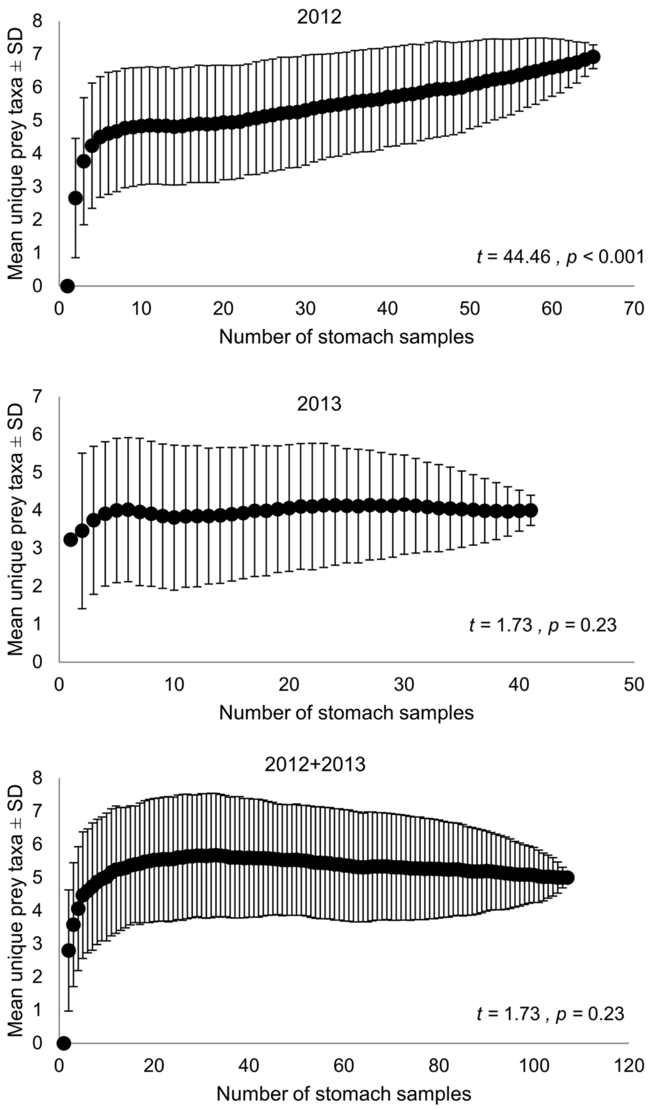

Fig. 2. Cumulative prey curves for stomach samples in 2012, 2013 and both years together.

the ABFT feeds throughout the day (Battaglia et al., 2012; Medina et al., 2015). Therefore, daily meal was estimated by multiplying $\hat{r}$ by 24 h. Daily ration was calculated as daily meal expressed as percentage of body mass. The tuna body mass was estimated from the length according to the equation $BM = 0.00000350801 \times FL^{2.878451}$ (Rodríguez-Marín et al., 2015), where BM is the body mass (g) and FL is the straight fork length (cm).

As there is no available information about evacuation times for ABFT, daily meal and daily ration were calculated from the A_i values determined for particular prey in yellowfin tuna (*Thunnus albacares*) by Olson and Boggs (1986). We believe this approach to be suitable for ABFT, as the yellowfin is a closely related species. Olson and Boggs (1986) assigned values of A_i for squid (4.48), mackerel (*Scomber japonicus*) (5.29), smelt (*Hypomesus pretiosus*) (4.12), and nehu (*Stolephorus purpureus*) (2.24), and the mean for four experimental food species (3.77). Our estimates for each prey were based on the similarity of digestibility by taking into account the size and 'softness' of the prey type (Griffiths et al., 2007; Young et al., 2010). Since empty stomachs probably reflect the natural feeding conditions of the population, they were considered in the analysis (Ménard et al., 2000).

A Bayesian mixing model (SIAR, Parnell et al., 2010) was applied to estimate the contribution of different preys to the ABFT diet, with the prey-tissue discrimination factors previously estimated for the species: $\Delta^{13}C_{muscle}$ (‰) = −0.16 ± 0.64, $\Delta^{15}N_{muscle}$ (‰) = 1.64 ± 0.20, $\Delta^{13}C_{liver}$ (‰) = 0.42 ± 0.34, $\Delta^{15}N_{liver}$ (‰) = 0.68 ± 0.42 (Varela et al., 2011, 2013). The isotopic niche was estimated for each tissue and year by Bayesian standard ellipse corrected areas (SEA_C) using the SIBER package (Jackson et al., 2011) of SIAR (Parnell et al., 2010).

Differences in $\delta^{13}C$ and $\delta^{15}N$ values between tissues and years were analysed by Student's t-test or Mann-Whitney U-test. The strength of the relationship between ABFT FL and isotopic variables was assessed by linear regression analysis. A significance level of $\alpha = 0.05$ was chosen for all statistical tests. Statistical analyses were performed using R (R Core Team, 2015). Collective data are expressed as mean ± SD.

3. Results

3.1. Stomach content analysis (SCA)

The FL of the ABFT used in this study ranged from 77 to 212 cm in 2012 (130.45 ± 24.74 cm) and from 105 to 152 cm in 2013 (119.92 ± 8.86 cm) (Fig. 1). Of the 121 stomachs analysed in 2012, 31.40% were empty or contained only baitfish, and the remaining 68.60% contained 13.9 kg of prey (mean prey weight per non-empty stomach: 167.53 ± 282.90 g). In 2013, 27.87% were empty or contained only bait, and the remaining 72.13% contained 13.9 kg of prey (mean prey weight per non-empty stomach: 316.42 ± 388.88 g). The mean number of different taxa per non-empty stomach was 2.52 ± 1.80 in 2012 and 3.14 ± 2.08 in 2013 (Table 1).

The CPCs for 2013 and the combined data from both years reached the asymptote for the last 4 points ($t = 1.73$, $p = 0.23$). Nevertheless, in 2012 the slope of the last points was significantly different from zero ($t = 44.46$, $p < 0.001$), indicating the need to increase the sample size of this year for a complete characterisation of ABFT diet (Fig. 2). The ABFT diet comprised a broad variety of fish, cephalopod and crustacean species. Additionally, a colony fragment of the tunicate *Pyrosoma atlanticum* was found in one of the tuna stomachs (Table 2). Crustaceans proved to be the predominant prey group in 2012 and 2013 (AI = 37.47 and AI = 47.22, respectively), followed by fishes (AI = 28.71 and AI = 25.62, respectively) and cephalopods (AI = 1.55 and AI = 3.03, respectively). In terms of%W, %O and AI, *Sergia robusta* was the most important prey species in both years, whereas the family Stomiidae was the predominant vertebrate prey. Overall, mesopelagic fishes (stomiids, myctophids, sternoptychids and trichiurids) accounted for the largest amount of fish prey (AI = 16.29 and AI = 21.44 for 2012 and 2013, respectively), whereas epipelagic (clupeids) and bathypelagic (paralepidids and tetragonurids) fishes had minor

Table 2

Results of the stomach content analysis of the ABFT sampled in 2012 and 2013. W, weight of each prey (means are referred to the number of stomachs where the prey appears and not the total number of stomachs analysed); %W, percent weight; %MW, mean percent weight ± SD; %O, percent occurrence; AI, Alimentary index. The trophic niche width is expressed as exp(H), H being the Shannon-Wiener index.

Preys	Mean W ± SD (g)		%W (Total W in g)		%MW		%O (n)		AI	
	2012	2013	2012	2013	2012	2013	2012	2013	2012	2013
Crustaceans	**55.84 ± 137.08**	**110.27 ± 194.18**	**48.59 (6756.13)**	**48.31 (6726.49)**	**69.69 ± 36.10**	**64.98 ± 36.36**	**77.11 (64)**	**97.73 (44)**	**37.47**	**47.22**
Sergia robusta	96.93 ± 133.08	151.29 ± 188.59	27.89 (3877.20)	41.29 (5748.86)	49.56 ± 35.17	58.05 ± 34.95	48.19 (40)	86.36 (38)	13.44	35.66
Acanthephyra pelagica	77.33 ± 172.28	17.67 ± 20.21	14.46 (2010.70)	2.54 (353.43)	19.35 ± 19.48	20.67 ± 35.99	31.33 (26)	45.45 (20)	4.53	1.15
Pasiphaea spp.	28.42 ±39.52	29.38 ± 33.96	2.45 (341.00)	2.95 (411.30)	2.45	4.12 ± 4.01	14.46 (12)	31.82 (14)	0.35	0.94
Unidentified crustaceans	13.29 ± 22.59	2.56 ± 3.45	2.20 (305.64)	0.04 (5.13)	73.09 ± 41.68	100.00 ± 0.00	27.71 (23)	4.55 (2)	0.61	0
Pasiphaea multidentata	30.66 ± 26.78	91.36 ± 119.70	1.54 (214.60)	1.31 (182.72)	12.12 ± 19.35	9.72 ± 8.15	8.43 (7)	4.55 (2)	0.13	0.06
Pasiphaea sivado	2.5	12.53 ± 14.57	0.02 (2.50)	0.18 (25.05)	8.33	2.49 ± 2.78	1.20 (1)	4.55 (2)	0	0.01
Polybius henslowii	4.5		0.03 (4.50)		100.00		1.20 (1)		0	
Hyperiid amphipod	0.1		0.00 (0.10)		3.23		1.20 (1)		0	
Teleost fishes	**49.76 ± 126.25**	**98.95 ±198.82**	**43.32 (6022.87)**	**43.35 (6036.04)**	**58.31 ± 38.24**	**51.26 ± 34.61**	**66.27 (55)**	**59.01 (26)**	**28.71**	**25.62**
Stomiidae	136.47 ± 164.54	184.31 ± 195.24	18.65 (2592.95)	14.56 (2027.42)	37.35 ± 26.63	20.96 ± 15.22	22.89 (19)	25.00 (11)	4.27	3.64
Unidentified mesopelagic fishes	69.39 ± 175.84	159.96 ± 161.20	8.98 (1248.97)	10.34 (1439.63)	42.32 ± 38.52	31.28 ± 26.47	21.69 (18)	20.45 (9)	1.95	2.12
Notoscopelus spp		178.76 ± 168.71		10.27 (1430.07)		23.68 ± 17.74		18.18 (8)		1.87
Sardinella spp	145.31 ± 104.85		8.36 (1162.50)		70.81 ± 35.97		9.64 (8)		0.81	
Myctophidae	93.23 ± 101.80	117.40 ± 99.21	2.01 (279.70)	2.53 (352.20)	37.20 ± 38.39	42.22 ± 41.49	3.61 (3)	6.82 (3)	0.07	0.17
Maurolicus muelleri	13.08 ± 21.68		1.13 (157.00)		45.21 ± 49.31		14.46 (12)		0.16	
Lepidopus caudatus		58.81 ± 17.90		1.69 (235.24)		10.10 ± 4.81		9.09 (4)		0.15
Other unidentified fishes	35.38 ± 63.24	19.81 ± 18.07	2.04 (283.00)	0.57 (79.25)	60.11 ± 44.77	56.36 ± 40.01	9.64 (8)	9.09 (4)	0.2	0.05
Chauliodus sloani	15	282.68	0.11 (15.00)	2.03 (282.68)	1.23	26.36	1.20 (1)	2.27 (1)	0	0.05
Ceratoscopelus maderensis		155.8		1.12 (155.80)		83.36		2.27 (1)		0.03
Lampanyctus spp	25.92 ± 30.49	24.25	0.56 (77.75)	0.17 (24.25)	3.64 ± 2.81	2.13	3.61 (3)	2.27 (1)	0.02	0
Tetragonurus cuvieri	125		0.90 (125.00)		9.87		1.20 (1)		0.01	
Paralepididae	32.00 ± 39.60		0.46 (64.00)		3.39 ± 3.40		2.41 (2)		0	
Arctozenus risso	17	9.5	0.12 (17.00)	0.07 (9.50)	5.44	0.84	1.20 (1)	2.27 (1)	0	0
Cephalopods	**9.25 ± 51.84**	**19.01 ± 53.57**	**8.05 (1119.81)**	**8.33 (1159.85)**	**33.14 ± 36.67**	**24.30 ± 30.56**	**19.28 (16)**	**36.36 (16)**	**1.55**	**3.03**
Histioteuthis spp	30.72 ± 25.58	61.34 ± 54.36	1.99 (276.50)	5.73 (797.48)	13.78 ± 23.40	10.24 ± 7.53	10.84 (9)	29.55 (13)	0.22	1.69
Illex coindetii	47.86 ± 73.17	119.99 ± 182.27	1.72 (239.31)	2.59 (359.97)	40.36 ± 36.72	52.70 ± 49.23	6.02 (5)	6.82 (3)	0.1	0.18
Ommastrephidae	150.33 ± 213.60		3.24 (451.00)		48.20 ± 47.63		3.61 (3)		0.12	
Todaropsis eblanae	141.5		1.02 (141.50)		43.47		1.20 (1)		0.01	
Unidentified cephalopods	4.33 ± 3.69	2.4	0.09 (13.00)	0.02 (2.40)	16.48 ± 22.58	0.66	3.61 (3)	2.27 (1)	0	0
Thaliaceans	**4.76**		**0.03 (4.76)**		**42.29**		**1.20 (1)**		**0**	
Pyrosoma atlanticum	4.76		0.03 (4.76)		42.29		1.20 (1)		0	
			exp (*H*) = 9.50	exp (*H*) = 7.24						

A close examination of otoliths retrieved from unrecognisable remains of fishes in advanced digestion stage allowed the identification of *Sudis hyalina* (Paralepididae), *Stomias boa* (Stomiidae), *Benthosema glaciale*, *Lampanyctus crocodilus* and *Myctophum punctatum* (Myctophidae).

Values of the main prey groups (Crustaceans, Teleost fishes, Cephalopods and Thaliaceans) are shown in bold.

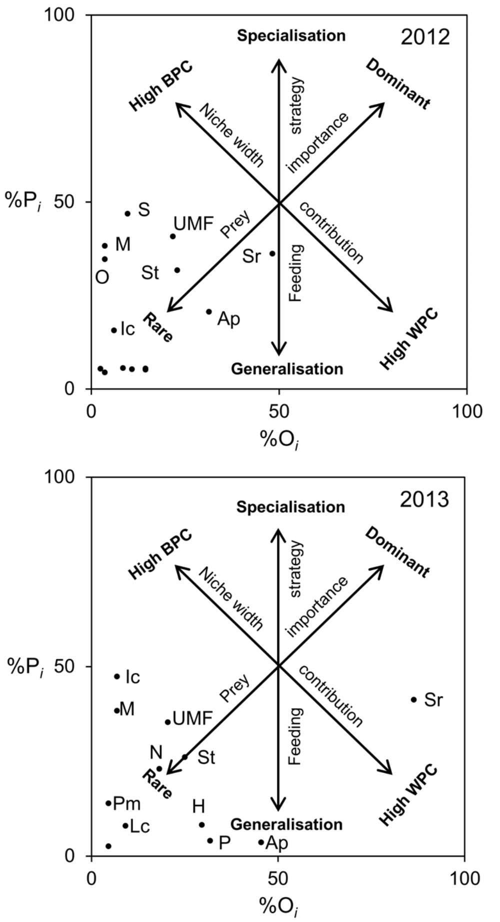

Fig. 3. Plot of prey-specific abundance in weight (%P*i*) against frequency of occurrence of prey species (%O*i*) from ABFT sampled in 2012 and 2013 (based on Costello (1990) and Amundsen et al. (1996)). Ap: *Acantephyra pelagica*; H: *Histioteuthis* sp.; Ic: *Illex coindetii*; Lc: *Lepidopus caudatus*; M: Myctophidae; N, *Notoscopelus* spp.; O: Ommastrephidae; Pm: *Pasiphaea multidentata*; P: *Pasiphaea* spp.; S: *Sardinella* sp.; Sr: *Sergia robusta*; St: Stomiidae; UMF: unidentified mesopelagic fish.

importance in the diet. A close examination of otoliths retrieved from unrecognisable remains of fishes in advanced digestion stage allowed the identification of *Sudis hyalina* (Paralepididae), *Stomias boa* (Stomiidae), *Benthosema glaciale*, *Lampanyctus crocodilus* and *Myctophum punctatum* (Myctophidae). The niche width measured as the antilogarithm of Shannon-Weaver's index showed higher values in 2012 ($\exp(H) = 9.50$) than in 2013 ($\exp(H) = 7.24$).

Amundsen plots show that ABFT in the SoG have a varying degree of specialisation on different prey (Fig. 3). Most prey species showed low occurrence and low prey-specific abundance, suggesting that they are unimportant and rare (lower left quadrant of the graphs). The shrimp *Sergia robusta*, which was consumed by a large number of tuna (%O = 48.19 and %O = 86.36 in 2012 and 2013, respectively), can be considered as the dominant prey.

3.2. Consumption rate

Inter-annual shifts in both daily meal and daily ration were observed. Thus, whereas the estimated daily food intake was 918.91 g day^{-1} in 2012 and 1924.95 g day^{-1} in 2013, the daily ration showed values of 2.52 ± 1.24% body mass (BM) day^{-1} and 5.84 ± 1.06% BM day^{-1}.

Table 3
δ^{15}N and δ^{13}C isotopic values (means ± SD) of ABFT grouped by tissue and year. The right column shows *p*-values resulting from comparisons of means between 2012 and 2013; *p*-values obtained from comparisons between means of isotopic values between muscle and liver are shown in rows beneath the compared data. *t*, Student's *t*-test; *U*, Man-Whitney *U*-test.

	2012 (n = 79)	2013 (n = 52)	*p*-value, test statistic
δ^{15}N			
Muscle	11.09 ± 0.65	11.38 ± 0.41	0.003, *t*
Liver	9.80 ± 0.57	9.76 ± 0.39	0.657, *t*
p-value, test statistic	<0.001, *t*	<0.001, *t*	
δ^{13}C			
Muscle	−17.61 ± 0.37	−17.76 ± 0.24	0.006, *t*
Liver	−17.28 ± 0.48	−17.55 ± 0.50	0.004, *t*
p-value, test statistic	<0.001, *U*	0.003, *U*	

Table 4
Mean ± SD values of δ^{13}C (‰) and δ^{15}N (‰) of major ABFT preys collected in the SoG region in March 2013 and used as input data in SIAR analysis.

Preys	δ^{15}N (‰)	δ^{13}C (‰)
Acanthephyra pelagica (n = 2)	6.09 ± 0.26	−18.83 ± 0.04
Pasiphaea sivado (n = 3)	7.63 ± 0.49	−19.11 ± 0.05
Polybius henslowii (n = 2)	7.23 ± 0.46	−19.13 ± 0.04
Sergia robusta (n = 3)	7.84 ± 0.61	−18.29 ± 1.00
Chauliodus sloani (n = 1)	9.26	−18.72
Maurolicus muelleri (n = 3)	9.21 ± 0.42	−18.91 ± 0.26
Myctophum punctatum (n = 3)	9.18 ± 0.66	−18.28 ± 0.48
Illex coindetii (n = 2)	10.11 ± 0.70	−17.49 ± 0.29
Todaropsis eblanae (n = 3)	10.39 ± 0.57	−17.31 ± 0.22

3.3. Stable isotope analysis

Mean isotopic values of ABFT tissues and preys are shown in Tables 3 and 4. Significant inter-annual isotopic differences were observed in tuna samples (*t*-test, $p < 0.01$) except for liver δ^{15}N (*t*-test, $p = 0.657$). δ^{15}N values from muscle tissue were significantly higher than those from liver (*t*-test, $p < 0.001$), whereas δ^{13}C was higher in liver (Mann-Whitney *U*-test, $p < 0.01$) (Table 3). Among prey, the cephalopods showed the highest values of δ^{13}C and δ^{15}N, whereas the crustaceans had, in general, the lowest isotopic values (Table 4).

Significant (yet poor) relationships were observed between tuna FL and δ^{15}N values ($r^2 < 0.28$, $p < 0.05$), except for liver samples in 2013 ($r^2 = 0.078$; $p = 0.066$) (Fig. 4). In contrast, no significant relationship was found between δ^{13}C and FL ($r^2 < 0.05$, $p > 0.05$), though there was a weak relationship in liver samples from 2013 ($r^2 = 0.09$, $p = 0.044$).

SIAR mixing-models from ABFT muscle and liver samples produced similar outputs. Cephalopods were the most abundant prey group in both 2012 and 2013, the lesser flying squid (*Todaropsis eblanae*) being the most important prey species. The estimated dietary contribution of fishes and crustaceans derived from liver isotopic values was higher than that resulting from muscle tissue data (Table 5). In agreement with the results of trophic niche width estimations from SCA, the niche width estimated from SEA$_c$ was larger in 2012 than it was in 2013 (Table 6).

4. Discussion

4.1. Stomach contents

In contrast to previous studies, the present results of SCA suggest that ABFT feed actively in the SoG. While Rodríguez-Roda (1964) and Varela et al. (2013) found that most stomachs from ABFT caught by traps set in the SoG area were empty, a high percentage of guts analysed in this study (>68%) contained at least one prey item. These contrasting observations may be due to the long time the fish

Table 5
Mixing-model estimates of prey contributions for ABFT muscle and liver. Values are presented as mean proportion estimates with upper and lower 95% confidence intervals.

	Muscle						Liver					
	2012			2013			2012			2013		
Preys	Low 95%	High 95%	mean	Low 95%	High 95%	mean	Low 95%	High 95%	mean	Low 95%	High 95%	mean
Sergia robusta	0.00	20.07	9.26	0.00	10.74	4.87	0.00	26.23	12.03	0.00	28.41	13.30
Acanthephyra pelagica	0.42	14.17	7.57	0.00	6.69	2.92	0.00	14.62	6.19	0.00	16.50	7.64
Pasiphaea sivado	0.00	3.98	1.48	0.00	6.79	2.56	0.00	15.53	6.08	0.00	14.66	5.58
Polybius henslowii	0.00	5.06	1.75	0.00	6.62	2.50	0.00	15.82	6.04	0.00	14.78	5.71
Chauliodus sloani	0.00	3.68	1.29	0.00	9.72	3.75	0.00	20.90	8.30	0.00	14.97	5.75
Maurolicus muelleri	0.00	3.17	1.12	0.00	7.95	3.01	0.00	19.47	7.28	0.00	12.80	4.91
Myctophum punctatum	0.00	7.24	2.63	0.00	16.17	7.15	0.00	25.88	11.42	0.00	24.70	9.93
Illex coindetii	5.26	47.20	25.91	17.64	46.36	32.28	0.76	37.41	20.10	1.41	40.83	21.71
Todaropsis eblanae	29.71	67.50	48.99	28.19	53.94	40.94	4.62	40.88	22.55	6.32	44.76	25.47

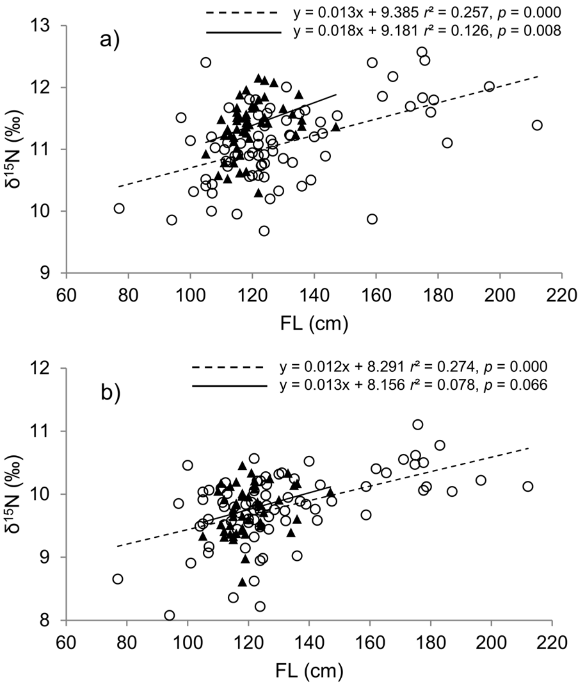

Fig. 4. Relationships between δ^{15}N values from muscle (a) and liver (b) and straight fork length (FL). Open circles, data from 2012; filled triangles, data from 2013. Linear regressions are represented as dashed lines for 2012 and solid lines for 2013.

Table 6
Trophic niche widths of ABFT captured in SoG in 2012 and 2013, as estimated by SIBER analysis from muscle and liver isotopic values. SEA, standard ellipse area; SEA$_c$, corrected standard ellipse area. The right column shows statistical differences in SEA between tissues and years.

Group	SEA	SEAc	Group differences Probability (%)
			1 vs 2 (00.00)
Muscle 2012 (1)	0.75	0.76	1 vs 3 (65.75)
			1 vs 4 (08.83)
Muscle 2013 (2)	0.24	0.24	2 vs 3 (99.99)
			2 vs 4 (98.94)
Liver 2012 (3)	0.82	0.83	3 vs 4 (04.58)
Liver 2013 (4)	0.50	0.51	

spend in the traps before harvesting, which often results in complete digestion of the food (Varela et al., 2013). The percentage of non-empty stomachs was similar to that found by other authors in western Atlantic ABFT foraging grounds (Butler et al., 2010; Chase, 2002; Logan et al., 2015; Pleizier et al., 2012). In addition, Chase (2002) reported a mean weight of prey per non-empty stomach that is consistent with our data. These observations suggest that adult and sub-adult ABFT use waters of the SoG as a feeding ground after the spawning season.

Thus far, studies on trophic biology based on stomach content analysis had revealed that the ABFT feed mainly on fish and squid (Chase, 2002; Karakulak et al., 2009; Logan et al., 2011; Medina et al., 2015). To our knowledge, this is the first study to report crustaceans as the most prominent prey in the diet of *T. thynnus*. The presence of mesopelagic crustaceans (*Sergia*, *Acanthephyra* and *Pasiphaea*) in the gut of ABFT was also observed by Battaglia et al. (2012) in the central Mediterranean Sea. In comparison with fish and squid, these shrimps have a low caloric content (Cartes et al., 2008). Nevertheless, they can occur at high densities in shallow waters in night hours (Sardou et al., 1996; Vestheim and Kaartvedt, 2009), becoming an important food resource for top predators.

Mesopelagic fishes belonging to the families Stomiidae and Myctophidae were found to be abundant in the stomach contents of ABFT caught in the SoG. These teleosts are an important component of food webs, linking zooplankton (their main prey) to top predators (Olivar et al., 2012). Their abundance may be associated with upwelling events (Battaglia et al., 2012; Guglielmo et al., 1995), as those that occur in the SoG (Stanichny et al., 2005). In the Mediterranean Sea, mesopelagic fish represent an important trophic resource not only for ABFT (Battaglia et al., 2012; Karakulak et al., 2009; Medina et al., 2015) but also for other teleosts and dolphins. For instance, Castriota et al. (2007) and Dede et al. (2016) observed that myctophids were the predominant prey in the diet of dolphinfish (*Coryphaena hippurus*) and striped dolphin (*Stenella coeruleoalba*), whereas Consoli et al. (2008) and Goñi et al. (2011) found that *Paralepis* was frequent in the diet of albacore (*Thunnus alalunga*).

The trophic niche breadth estimated from the antilogarithm of Shannon's index indicated that the ABFT sampled in 2012 showed a more diverse diet than those sampled in 2013. Medina et al. (2015) reported lower values of exp (*H*) for age-0 ABFT collected in the western Mediterranean Sea (1.27–2.31), suggesting that juvenile specimens show lower diet diversity than sub-adults and adults. An increase of trophic niche breadth with increasing body size is not unexpected, since larger individuals are able to feed on large and small prey species, whereas smaller ones are usually restricted to small items (Costa, 2009).

4.2. Consumption rate

The present study provides the first information about daily meal and daily ration for ABFT from the eastern stock. The daily food consumption (918.91–1924.95 g day^{-1}) suggests that the ABFT plays an important role structuring the pelagic ecosystem of the SoG. In the western Atlantic, the daily food intake reported for this species (3180 g day^{-1}) was considerably higher (Butler et al., 2010). In comparison with other tuna species, the daily meal estimated here is higher than that calculated for yellowfin tuna in the Arabian Sea (545.65 g day^{-1}) (Varghese and Somvanshi, 2016) and for longtail tuna (*Thunnus tonggol*) in Australian waters (123.27–229.04 g day^{-1}) (Griffiths et al., 2009), whereas similar values (1530.90 g day^{-1}) were reported for sub-adult yellowfin tuna in the Equatorial Atlantic Ocean (Ménard et al., 2000). Furthermore, the daily ration (2.52–5.84% BM day^{-1}) of ABFT in the SoG is fairly higher than those reported for bluefin tunas in the western Atlantic Ocean (2.03% BM day^{-1}) (Butler et al., 2010) and in the southwestern Pacific Ocean (0.73–2.69% BM day^{-1}) (Young et al., 1997). In contrast, Maldeniya (1996) estimated similar values for yellowfin tuna in Sri Lankan waters (2.30–5.50% BM day^{-1}).

The inter-annual differences in both daily meal and daily ration may be due to differences in the water temperature between the two periods of sampling. In 2012, all tuna samples were collected in fall (SST: $19.65 \pm 1.76\,^{\circ}$C), whereas most of the 2013 samples were taken in late summer (SST: $22.28 \pm 0.22\,^{\circ}$C). This is consistent with the observations of Carey et al. (1984) that the stomach temperature of ABFT impounded in St Margaret's Bay (Nova Scotia, Canada) significantly decreased from August to September-October. Warmer average water temperatures in the summer may result in higher visceral temperature, which may accelerate the digestion process (Carey et al., 1984), and in turn enhance the food intake rate.

4.3. Stable isotope analysis

The values of δ^{15}N measured from ABFT muscle samples (11.09 and 11.38‰) were similar to those observed in pre-spawning ABFT captured in the SoG (10.94-11.14‰) (Varela et al., 2013). These values can also be compared to those obtained in marine mammals co-occurring in the area. De Stephanis et al. (2015) reported similar δ^{15}N values for long-finned pilot whales (*Globicephala melas*) (11.38 ± 0.44‰), whereas higher δ^{15}N values were estimated for killer whales (*Orcinus orca*) (12.66 ± 0.33‰). These observations suggest that ABFT and pilot whales are located at a similar trophic level and might compete for the same resources, whereas killer whales apparently occupy higher trophic positions. Recent studies (De Stephanis et al., 2015; Esteban et al., 2014) have shown, in fact, that ABFT are significantly preyed upon by killer whales. Therefore, as suggested for yellowfin tuna (Scott et al., 2012), the ABFT in the SoG behaves as a mesopredator rather than an apex predator.

The diet composition estimated using isotopic mixing models from both muscle and liver tissues suggests that ABFT in the SoG feed mainly on ommastrephid squids (*Illex coindetii* and *Todaropsis eblanae*), which are located at high trophic levels of the food webs. Nevertheless, the mixing model performed from liver SIA data estimated a higher contribution of prey located at lower trophic levels (mesopelagic fishes and crustaceans).

The marked difference regarding *S. robusta* contribution between SIA and SCA may be due to a sampling bias, since tunas were captured at evening hours when sergestids appear in high densities in shallow waters (Sardou et al., 1996; Vestheim and Kaartvedt, 2009). Otherwise, mixing-model dietary estimations results should be taken cautiously, since the large difference in δ^{15}N between muscle and liver tissues (1.28 ± 0.52 and 1.67 ± 0.40 for 2012 and 2013, respectively) may indicate that the studied tuna are recent migrants into the SoG (see Logan et al., 2011). Hence, muscle, which shows a slow turnover rate compared to liver in tunas (Graham, 2008), might not be in equilibrium with local prey species.

Overall, the δ^{15}N values measured in muscle and liver showed a positive (though weak) relationship with body size. In the central Mediterranean Sea, a similar pattern was observed for ABFT over a weight range of 0.7–225 kg (Sarà and Sarà, 2007). Jennings et al. (2002) suggested that larger specimens often show higher δ^{15}N values than smaller individuals because they can feed on larger prey items located at higher trophic levels. In contrast, no relationship between fish size and δ^{15}N was observed for yellowfin tuna in the Pacific and Indian oceans (Ménard et al., 2007; Olson et al., 2010), though these studies focused on a relatively narrow size range.

In agreement with SCA results, the diet diversity measured by the Bayesian standard ellipse corrected areas (SEAc) (Jackson et al., 2011) showed a broader trophic niche in 2012. The difference in SEA$_c$ values between liver and muscle tissues may be explained by a recent diet shift that is not reflected in the isotopic composition of muscle due to its slower turnover rate compared to liver (Medina et al., 2015).

5. Conclusion

Currently, the occurrence of Atlantic bluefin tuna (ABFT) catches all the year round by either commercial or recreational fishers in the Strait of Gibraltar (SoG) is indicative of residency of a significant ABFT population. At least from late summer through fall, adult and sub-adult ABFT appear to use SoG waters as a suitable feeding ground. Stomach content analysis shows that they feed primarily on invertebrates, mainly crustaceans, and, to a lesser extent, on mesopelagic fish. These resident tuna, therefore, behave as mesopredators rather than apex predators, and are likely competitors of other pelagic predators for the same trophic resources in the area.

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