



# Trophic preferences of three pelagic fish inhabiting the Galapagos Marine Reserve: ecological inferences using multiple analyses

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**Abstract** There is a great need to understand how resource interactions alter the functioning of ecosystems, where the selective elimination of pelagic fishes can lead to changes in food web structure. This work analyzes the trophic niches of three species of commercial importance in the Galapagos Marine Reserve, yellowfin tuna, *Thunnus albacares* (TA), skipjack tuna, *Katsuwonus*

*pelamis* (KP), and wahoo, *Acanthocybium solandri* (AS), via multiple analyses. According to the prey-specific index of relative importance, the most important prey for TA was *Dosidicus gigas*, while for AS it was unidentified pelagic fish. Interspecific differences were found between the isotopic signatures of AS and those of TA and KP. The isotope mixing model provides evidence for some predominance of *D. gigas* in the diets of TA and KP, while the fishes *Selar crumenophthalmus* and *Paranthias colonus* contribute to the diet of AS. The stable isotope Bayesian ellipses show a high overlap between TA and KP, suggesting a similar use of resources and feeding areas, while the ellipse of AS does not overlap with that of the other species. Both AS and TA were present around the islands more commonly during the day, with a peak in detections in the morning for AS and a greater presence of TA throughout the afternoon; there were only a few detections of KP in the days immediately after tagging. In summary, the results of this study suggest a pelagic foraging strategy with differential consumption of prey between AS and the other species.

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## Introduction

There is great concern regarding how resource extraction alters the structure and function of marine ecosystems (Hampton et al. 2005; Sibert et al. 2006), given that the

selective elimination of several predators, such as large pelagic fishes, can lead to changes in the structure and abundance of lower trophic levels (Marasco et al. 2007; Chen et al. 2016). This increases the need to generate ecological information regarding the foraging behavior and the displacement patterns of these species to understand how the flow of energy is established in a trophic web subject to changes induced by human exploitation and climate change (Dalglish et al. 2010; Doney et al. 2012).

Trophic studies provide ecological information on the behavior of predators, which facilitates the interpretation of energy interactions that are established within the ecosystem (Hunsicker et al. 2012; Duffy et al. 2015). Polyspecific associations include different species that migrate, interact and forage together for different periods of time (Nikolsky 1963; Au 1991), and one of the main reasons for forming such associations is the search for food (Scott et al. 2012). This type of behavior frequently involves migratory species of commercial importance, such as scombrids, that are distributed in tropical areas (Graham et al. 2007; Olson et al. 2016).

Yellowfin tuna (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*) and wahoo (*Acanthocybium solandri*) are pelagic species of high mobility and rapid growth that belong to the family Scombridae. These species are common in the eastern Pacific Ocean, with their distribution extending from Southern California to Peru (Fischer et al. 1995; Theisen et al. 2008; Alatorre-Ramirez et al. 2017). Both *T. albacares* and *K. pelamis* are epipelagic species that form large aggregations in oceanic areas (Arai et al. 2005; Scott et al. 2012), while *A. solandri* prefers areas near reefs and rocky slopes of oceanic islands (Oxenford et al. 2003; Sepulveda et al. 2011). All species are very active and can travel long distances in a short time, so they require large amounts of energy to meet their metabolic and physiological needs (Korsmeyer and Dewar 2001; Oxenford et al. 2003).

The availability of food resources is often considered to be a determining factor in the abundance and distribution of large pelagic fishes (Nikolsky 1963; Gislason et al. 2010), suggesting that foraging strategy could be a factor that explains the association of these species (Baque-Menoscal et al. 2012; Páez-Rosas et al. 2018). The diets of *T. albacares*, *K. pelamis* and *A. solandri* in several regions of the Pacific Ocean indicate intraspecific differences related to size and catch location (Olson

et al. 2014; Varela et al. 2017), positioning these predators as secondary carnivores that feed mainly on filter-feeding fishes and cephalopods (Oxenford et al. 2003; Alatorre-Ramirez et al. 2017). However, in areas such as the equatorial Pacific, very little is known about their feeding habits and trophic interactions.

Trophic studies in large pelagic fishes have traditionally been based on analyses of stomach contents (Vaudo and Heithaus 2011). This technique has a high level of taxonomic resolution but has a limited scope, since pelagic fishes often have empty stomachs at the time of capture (Hyslop 1980; Rosas-Luis et al. 2016), a characteristic that in tunas has been associated with rapid rates of gut evacuation (Olson and Boggs 1986). Therefore, the detection of prey is highly conditioned to the rates of digestion of these species (Galván-Magaña et al. 2013). A technique that complements traditional methods involves the analysis of stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) in the body tissues. This approach provides information about the food assimilated by a consumer and the type of habitat that it exploits, coastal/oceanic (using  $\delta^{13}\text{C}$ ), and its level and trophic breadth (using  $\delta^{15}\text{N}$ ) (Boecklen et al. 2011; Kim et al. 2012). These isotopic signatures are used as a natural chemical tracer of ecological processes, allowing researchers to identify energy flows and to characterize the primary production sources that sustain the ecosystem inhabited by a predator (Newsome et al. 2007; Martínez del Rio et al. 2009). Acoustic telemetry is another alternative technique for determining foraging strategies in pelagic species, since it allows us to infer the habitat use and displacement patterns of highly mobile species that tend to remain close to oceanic islands (Hearn et al. 2010; Ketchum et al. 2014).

During the last decade, *T. albacares*, *K. pelamis* and *A. solandri* have become resources of commercial importance for the artisanal fishing fleet that operates within the Galapagos Marine Reserve and its surroundings (Castrejon and Charles 2013; Bucaram et al. 2018). However, despite the ecological importance of these species within the trophic dynamics of the region, little is known about their foraging and spatial ecology. In this work, we used a multiple-technique approach to measure diet, trophic plasticity, foraging behavior and habitat use, with the purpose of defining the level of trophic interaction that these scombrids present within the Galapagos Marine Reserve.

## Methods

### Study area

The Galapagos Islands (Fig. 1) are located within an upwelling system due to the confluence of ocean currents and have historically been important for the industrial purse seine tuna fishery, targeting both *T. albacares* and *K. pelamis* (Bucaram et al. 2018). The Galapagos Marine Reserve, created in 1998, excluded industrial fishing from an area of approximately 138,000 km<sup>2</sup> around the island group, but a small-scale fishery of ~400 local fiberglass vessels based on the inhabited islands targets these species for local consumption and export (Hearn 2008; Bucaram et al. 2018).

### Diet analysis

Samples of *T. albacares* ( $n = 238$ ) and *A. solandri* ( $n = 151$ ) were collected simultaneously between January and October 2009; sampling focused on the artisanal hand-line fishery at Santa Cruz Island, which operates within the Galapagos Marine Reserve. The fishes were identified, and the capture location, date, weight, total length (TL) and sex of each specimen were recorded. The stomach contents were also collected and frozen at  $-20\text{ }^{\circ}\text{C}$  for about a month. In the laboratory, we thawed the stomach contents and identified the prey at the finest taxonomic level possible based on keys published in the specialized literature and bibliographic references of the region using cephalopod beaks and crustacean remains (Clarke 1986), axial skeleton, number, position and form of the vertebrae (Allen and Robertson 1994) and otoliths of fishes (Fitch and Brownell Jr 1968; García-Godos 2001).

To determine whether the number of stomachs analyzed was sufficient to accurately represent the diet of these species, a randomized cumulative Shannon diversity curve was made using EstimateS version 8 software. When an asymptotic stabilization of the curve was obtained and a coefficient of variation below 0.05 was achieved, we considered that the minimum number of stomachs required to accurately describe the diet had been reached. The important prey in the diet was determined by the prey-specific index of relative importance (PSIRI) (Brown et al. 2012). This index is expressed as %PSIRI using the following equation:  $\%PSIRI_i = [\%O_i \times (\%PN_i + \%PW_i)]/2$ , where  $\%O_i$  is the frequency of occurrence for prey type  $i$ ,  $\%PN_i$  is the prey-specific

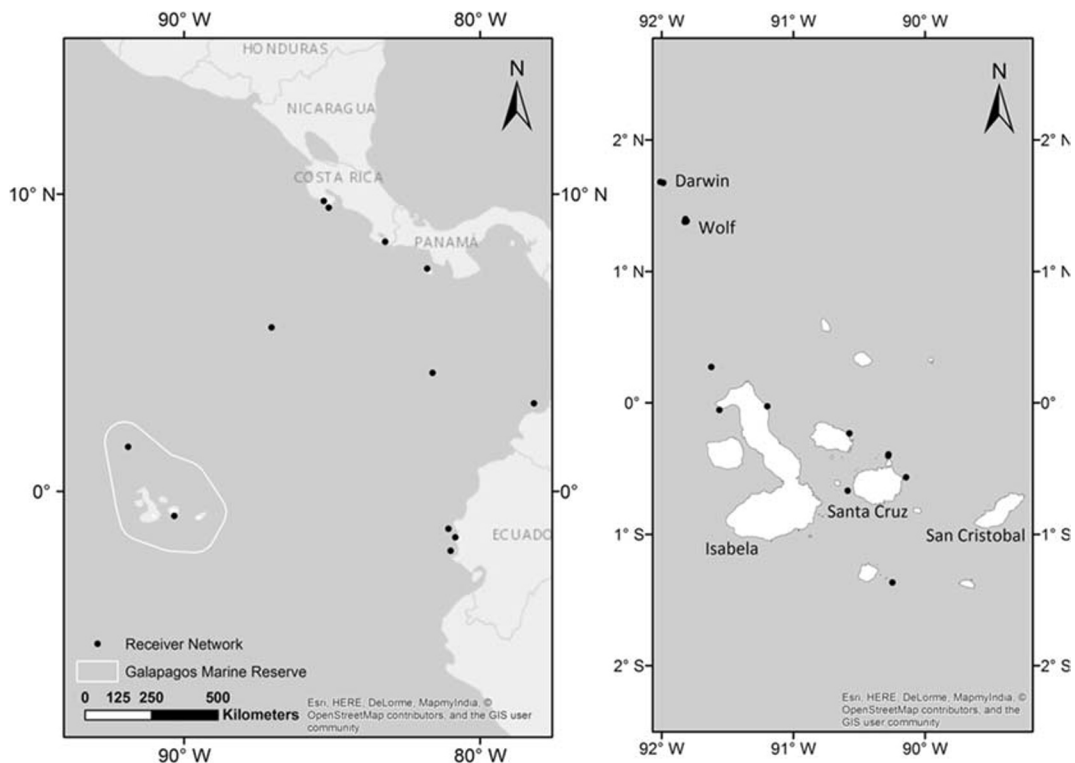
percent by number, and  $\%PW_i$  is the prey-specific percent by weight. This index corrects the mathematical flaws associated with the index of relative importance (IRI) and enables comparisons among studies regardless of the taxonomic level chosen by the researchers (Brown et al. 2012; Nielsen et al. 2018).

We created Amundsen plots to explore foraging strategies (Amundsen et al. 1996). These plots can be used to assess the behavior of predators relative to the abundance of their prey in the diet. In this analysis, prey-specific abundance is plotted against frequency of occurrence, which is defined as the proportion of a prey item ( $i$ ) in relation to all items present in the predators that contain prey  $i$  (Amundsen et al. 1996). When plotted against the frequency of occurrence, prey-specific abundance can be used to evaluate two important aspects of the diet: (1) foraging strategy (specialized vs. general) and (2) prey importance (dominant vs. rare) (Amundsen et al. 1996). To determine interspecific differences in the diet, we used permutation-randomization methods in a Bray-Curtis dissimilarity matrix based on the prey biomass (ANOSIM, PRIMER 6 v. 6.1.6). The global rank dissimilarity was based on the R statistic ( $0 \leq R \leq 1$ ), which is a measure of the dissimilarity between replicates. When R is 1, diet dissimilarity is very high, and when R is 0, diet dissimilarity is very low or the same on average (Clarke and Warwick 2001).

### Stable isotopes

Samples of muscle tissue were taken from *T. albacares* ( $n = 10$ ), *K. pelamis* ( $n = 13$ ) and *A. solandri* ( $n = 14$ ) during January 2014 as part of a research projects focused on monitoring the behavior of large pelagic fishes in the Galapagos Marine Reserve (Galapagos National Park Permits: PC-01-14 and PC-38-16). To reduce the variability when comparing the species, it was decided to sample only adults, estimating their ages based on the species' size at sexual maturity, which occurs in *T. albacares* at 85 cm furcal length (LF) (Schaefer 1998), in *K. pelamis* at 45 cm LF (Batts 1972), and in *A. solandri* at 105 cm LF (Oxenford et al. 2003).

All muscle tissue samples were rinsed with deionized water to eliminate residues that could alter their isotopic signature, and placed in glass vials previously treated for 24 h with a chromic acid mixture prepared from sulfuric acid and potassium dichromate. They were then dried in a desiccator at  $80\text{ }^{\circ}\text{C}$  for 12 h to remove all moisture. A microwave-assisted extraction protocol (MAE) was



**Fig. 1** Map of the Galapagos Islands indicating sample collection sites. The black circle symbols indicate the locations of underwater listening stations in the Galapagos Marine Reserve and other sites in the eastern tropical Pacific. The right map is an inset of the left map

applied (microwave oven model: 1000-W MARS 5x, CEM, Matthews, NC, USA) using 25 ml of a 1:1 chloroform:methanol solution and dried again. This process was applied because lipids are rich in  $^{12}\text{C}$ , which, in sufficiently large quantities, could negatively skew the  $^{13}\text{C}$  isotopic signature (Tieszen et al. 1983; Post et al. 2007). The samples were homogenized with an agate mortar to obtain a very fine powder, of which  $\sim 1$  mg was weighed by means of an analytical microbalance with a precision of 0.001 mg and transferred into a tin capsule for isotopic analysis.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope ratios were determined by a PDZ Europa 20-20 continuous-flow isotope-ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the Stable Isotope Facility of the University of California at Davis (CA, USA). The results, expressed in parts per thousand (‰), were obtained using the following equation:  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = 1000 \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right)$ , where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratios of the sample and the standard, respectively. The standards used were Pee Dee Belemnite (PDB) for  $\delta^{13}\text{C}$  and atmospheric  $\text{N}_2$  for  $\delta^{15}\text{N}$ . Within-run analytical precision was estimated via analysis of two proteinaceous

internal reference materials, which was  $\pm 0.2\text{‰}$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. We also measured the weight percent carbon and nitrogen concentration of each sample and used the C/N ratio as a proxy for lipid content (Logan et al. 2008).

The percentage contributions of various prey to the diet were evaluated via the SIAR method (Stable Isotopes Analysis in R); for this, we used published data of isotopic values of fishes and cephalopods collected in the same region (Ruiz-Cooley et al. 2010; Páez-Rosas et al. 2012) (Table 1), which have previously been identified as important prey items in the diets of these species (Baque-Menoscal et al. 2012; Alatorre-Ramirez et al. 2017; Mendoza-Ávila et al. 2017). This model estimates the probability distribution of the contribution of  $n$  sources (prey) to a mixture and evaluates the uncertainty associated with the isotopic values of the sources and the predator (Parnell et al. 2010). The variability in the percentage contribution of each prey to the diets of the scombrids was determined by the coefficient of variation. In order to represent all the potential trophic spectra of these species, we used isotopic data of crustaceans collected in the northwest

**Table 1** Isotopic signatures of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (mean  $\pm$  SD in ‰) and general information for several prey present in the diet of the scombrids that inhabit the Galapagos Marine Reserve

Prey species	Group	Prey habitat	Collection site in Galapagos Archipelago	n	$\delta^{13}\text{C}$ (per mil)	$\delta^{15}\text{N}$ (per mil)	C/N mass ratio
<i>Selar crumenophthalmus</i> <sup>a</sup>	Pelagic fishes	Epipelagic	Northwest Region	5	$-15.92 \pm 0.28$	$11.92 \pm 0.89$	$3.18 \pm 0.09$
<i>Anchoa spp.</i> <sup>a</sup>	Pelagic fishes	Epipelagic	Northwest Region	4	$-16.60 \pm 0.37$	$10.90 \pm 0.59$	$3.20 \pm 0.03$
<i>Sardinops sagax</i> <sup>a &amp; c</sup>	Pelagic fishes	Epipelagic	Northwest Region	12	$-16.80 \pm 0.75$	$9.74 \pm 0.74$	$3.20 \pm 0.08$
<i>Paranthias colonus</i> <sup>c</sup>	Pelagic fishes	Epipelagic	Northwest Region	12	$-17.05 \pm 0.93$	$11.32 \pm 0.44$	$3.15 \pm 0.02$
<i>Dosidicus gigas</i> <sup>a &amp; b</sup>	Cephalopods	Mesopelagic	Northwest Region	12	$-18.03 \pm 0.30$	$10.13 \pm 1.31$	$2.87 \pm 0.09$
<i>Sthenoteuthis oualaniensis</i> <sup>a</sup>	Cephalopods	Mesopelagic	Northwest Region	3	$-17.71 \pm 0.18$	$10.40 \pm 0.18$	$3.19 \pm 0.04$
<i>Ommastrephes bartramii</i> <sup>a</sup>	Cephalopods	Mesopelagic	Northwest Region	6	$-18.10 \pm 0.10$	$10.10 \pm 0.68$	$3.17 \pm 0.08$
<i>Amphipoda</i> <sup>c</sup>	Crustaceans	Epipelagic	Northwest Region	12	$-19.10 \pm 0.42$	$6.61 \pm 0.62$	$2.83 \pm 0.12$

<sup>a</sup> Data provided by Páez-Rosas et al. (2012)

<sup>b</sup> Data published in Ruiz-Cooley et al. (2010)

<sup>c</sup> Páez-Rosas unpubl. data

region of the archipelago at the end of 2013 (Páez-Rosas, unpublished data). The mixing models require assumptions about the trophic discrimination factor (TDF) between consumers and their sources (Phillips et al. 2014). The isotopic values for the diet items need to be adjusted based on the TDF to accurately assess the contribution of each prey item to the consumer’s diet (Caut et al. 2009). Controlled feeding studies have indicated that TDFs are species- and tissue-specific (Hussey et al. 2010), and TDFs can be based on values reported in the literature (Phillips et al. 2014). Unfortunately, there are few experimental studies examining TDFs for scombrids, so in this work, we assumed a TDF for  $\delta^{15}\text{N}$  of  $2.06 \pm 0.23\text{‰}$  and  $0.33 \pm 0.29\text{‰}$  for  $\delta^{13}\text{C}$ , following Varela et al. (2011), who calculated these values for muscle of tunas.

The Bayesian SIBER (Stable Isotope Bayesian Ellipses in R) package provides a measure of the isotopic resource use area at the population level, and it was used to define the isotopic niche space of these species. Bayesian approach models that use  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values have provided a better understanding of the trophic behavior of marine predators. These models can be adjusted to rule out an imprecise hypothesis, which allows the uncertainty involved in the contribution of the energy sources to be described in probabilistic terms (Jackson et al. 2011). This method is based on the two-dimensional isotopic space of  $\delta^{13}\text{C}/\delta^{15}\text{N}$  and is assessed using Bayesian analysis of standard ellipses, which allows for an unbiased estimate of relative isotopic niche based on fewer samples than those needed in Euclidean approaches (e.g., convex hulls) (Layman et al. 2007).

We used Monte Carlo simulations to correct the bivariate ellipses ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) surrounding the data points in the 95% confidence interval for the distributions of both stable isotopes (Jackson et al. 2011). These corrected standard ellipse areas (SEAc) represent the isotopic niche width and the overlap parameters (Jackson et al. 2011). Furthermore, we calculated the magnitude of the isotopic overlap among the three species based on 100,000 posterior draws of the SEAc parameters.

#### Ultrasonic tag detection and tracking

We used baited rods and reels to catch *T. albacares* ( $n = 5$ ), *K. pelamis* ( $n = 10$ ) and *A. solandri* ( $n = 10$ ) around the islands of Darwin and Wolf in January 2014. The three species were fitted with ultrasonic tags (V16, Vemco Ltd.), which emitted a coded signal at 69 kHz with a random delay of 40–140 s, to avoid successive signal collisions between two tags. The fishes were lifted manually out of the water and measured before surgical implantation of the ultrasonic tag. A small incision was made along the ventral area of the fish, and the tag was inserted into the peritoneal cavity. The incision was closed with a single or two sutures using monofilament. To determine the residency and movements of the tagged fish around and between the islands, we deployed a network of underwater listening stations (VR2W, Vemco Ltd.) at depths of 20–30 m around Darwin (5) and Wolf (8), focusing our coverage on known biological hotspots as previously reported (Hearn et al. 2010). Receiver moorings consisted of a

**Table 2** General diet of *T. albacares* and *A. solandri*. The absolute and percentage values calculated for the index of relative importance (%IRI) and prey-specific index of relative importance (%PSIRI) are given by the following: number (N), percent frequency of occurrence (%FO), percent number (%N), percent prey-specific number (PNI), weight (W), percent weight (%W), percent prey-specific weight (PWi)

Prey	<i>Thunnus albacares</i>											<i>Acanthocybium solandri</i>										
	%FO	N	%N	PNI	W	%W	PWi	%IRI	%PSIRI	%FO	N	%N	PNI	W	%W	PWi	%IRI	%PSIRI				
<b>Cephalopoda</b>																						
<i>Abraliopsis affinis</i>	7.1	69	1.73	26.12	288.7	1.68	23.61	0.49	1.77													
<i>Argonauta</i> spp.	8.88	35	0.88	11.08	419	2.43	22.48	0.6	1.49	1.75	1	0.66	50	25.4	0.25	50	0.04	0.88				
<i>Dosidicus gigas</i>	54.44	1133	28.45	45.16	1685.49	9.79	33.25	42.38	21.34	15.79	14	9.21	77.78	148.6	1.44	77.16	4.37	12.23				
<i>Haliphron atlanticus</i>	4.14	12	0.3	4.01	140.1	0.81	6.7	0.09	0.22													
<i>Histioteuthis heteropsis</i>	2.96	16	0.4	9.42	409.7	2.38	23.81	0.17	0.49													
<i>Mastigoteuthis dentata</i>	5.33	16	0.4	7.38	210.4	1.22	15.66	0.18	0.61													
<i>Octopus rubescens</i>	7.1	82	2.06	21.65	361.5	2.1	15.21	0.6	1.31													
<i>Octopus</i> spp.	2.36	9	0.23	31.85	117	0.68	42.11	0.02	0.44													
<i>Ommastrephes bartramii</i>	31.95	445	11.17	25.65	1020.3	5.92	26.53	11.12	8.34	1.75	1	0.66	25	37.3	0.36	25	0.05	0.44				
<i>Pterygioteuthis giardi</i>	9.47	97	2.44	37.64	270.7	1.57	27.26	0.77	3.07													
<i>Sthenoteuthis oualaniensis</i>	4.14	13	0.33	20.26	869.2	5.05	32.69	0.45	1.1	3.51	3	1.97	62.5	80.9	0.78	62.5	0.25	2.19				
<i>Thysanoteuthis rhombus</i>	2	1.18	0.05	3.56	11.8	0.07	5.66	0	0.05													
Unidentified Cephalopods	8.88	229	5.76	54.72	302.79	1.75	76.22	0.43	1.56													
<b>Crustacea</b>																						
Amphipoda	16.57	202	5.07	41.32	211.49	1.23	39.96	2.12	6.73													
Gonodactylidae	2.37	17	0.43	13.26	11.8	0.07	14.44	0.02	0.33													
Isopoda	3.55	50	1.26	28.38	180.3	1.05	21.82	0.17	0.89	5.26	5	3.29	38.89	107	1.04	25.88	0.59	1.7				
Stomatopoda	7.69	42	1.05	38.87	59.2	0.34	40.09	0.22	3.04													
<i>Neogonodactylus pumilus</i>	1.18	6	0.15	58.33	1.6	0.01	25.45	0	0.5													
Crab megalopa	21.89	636	15.97	41.56	640	3.72	37.78	8.77	8.69	3.51	17	11.18	88.89	166.7	1.61	64.78	1.17	2.7				
Unidentified Crustaceans	2.96	11	0.28	36.7	46	0.27	52.67	0.03	1.32													
<b>Osteichthyes</b>																						
Balistidae	0.59	1	0.03	100	2.2	0.01	100	0	0.59													
Clupeidae	0.59	5	0.13	50	151.8	0.88	87.85	0.01	0.41	1.75	1	0.66	33.33	12.5	0.12	81.7	0.04	1.01				
Exocoetidae										3.51	2	1.32	50	60.5	0.59	68.94	0.17	2.09				
Malacanthidae	1.78	5	0.13	3.65	98.2	0.57	9.29	0.03	0.11													
Myctophidae	7.1	86	2.16	26.1	125.9	0.73	22.73	0.42	1.73													

Table 2 (continued)

Prey	<i>Thunnus albacares</i>										<i>Acanthocybium solandri</i>									
	%FO	N	%N	W	PNI	W	%W	PWi	%IRI	%PSIRI	%FO	N	%N	W	PNI	W	%W	PWi	%IRI	%PSIRI
<i>Anchoa spp.</i>	0.59	3	0.08	33.33	26	0.15	25	0	0.17	1.75	2	1.32	33.33	6	0.06	33.33	0.06	33.33	0.06	0.58
<i>Caranx caballus</i>	2.96	10	0.25	181.8	14.5	1.06	14.97	0.08	0.44	7.02	4	2.63	100	579	5.61	100	1.5	100	1.5	7.02
<i>Chromis atrilobata</i>	1.78	4	0.1	112.6	6.81	0.65	11.71	0.03	0.16	1.75	1	0.66	100	13.2	0.13	100	0.04	100	0.04	1.75
<i>Diplectrum spp.</i>	2.96	8	0.2	274.2	4.77	1.59	14.79	0.11	0.29	3.51	2	1.32	60	38.5	0.37	60	0.15	60	0.15	2.11
<i>Exocoetus monocirrhus</i>	8.88	31	0.78	634.5	14.28	3.68	14.44	0.81	1.27											
<i>Exocoetus volitans</i>	0.59	2	0.05	4.17	25	0.15	4.75	0	0.03											
<i>Hemanthias signifer</i>	0.59	1	0.03	5.56	49	0.28	12.83	0	0.05											
<i>Hemiramphus saltator</i>	0.59	2	0.05	138.4	100	0.8	100	0.01	0.59											
<i>Isacia conceptionis</i>	0.59	2	0.05	15.38	77.2	0.45	29.74	0.01	0.13											
<i>Mycophum nitidulum</i>	1.78	3	0.08	11.1	138.1	0.8	28.69	0.03	0.35											
<i>Opisthonema berlangai</i>	4.73	31	0.78	23.98	461.3	2.68	23.61	0.33	1.13											
<i>Oxyporhamphus micropterus</i>	71	18.93	1.78	23.91	2859.39	16.6	41.69	7.09	6.21											
<i>Paralabrax spp.</i>	1.78	7	0.18	14.83	126	0.73	14.77	0.03	0.26	1.75	1	0.66	20	25.9	0.25	20	0.04	20	0.04	0.35
<i>Prognichthys tringa</i>	22.49	133	3.34	25.81	1826	10.6	28.77	6.38	6.14	8.77	7	4.61	63.33	170.2	1.65	62.3	1.43	63.33	1.43	5.51
<i>Scomber japonicus</i>	0.59	1	0.03	10	2.7	0.02	16.67	0	0.08	3.51	4	2.63	100	1837.8	17.8	100	1.86	100	1.86	3.51
<i>Selar crumenophthalmus</i>	0.59	1	0.03	10	2.7	0.02	16.67	0	0.08	5.26	4	2.63	72.22	29.4	0.28	63.81	0.4	72.22	0.4	3.58
<i>Sphyræna idtiastes</i>	0.59	1	0.03	10	2.7	0.02	16.67	0	0.08	1.75	2	1.32	50	1586.8	15.37	95.98	0.76	50	0.76	1.28
<i>Trachinotus paitensis</i>	0.59	1	0.03	7.14	109	0.63	46.66	0.01	0.16											
<i>Trachurus spp.</i>	1.18	2	0.05	6.04	36.8	0.21	4.85	0.01	0.06	3.51	2	1.32	25	191.9	1.86	37.29	0.29	25	0.29	1.09
<i>Vinciguerra lucretia</i>	3.55	15	0.38	11.75	181	1.05	13.46	0.1	0.45											
Unidentified Fishes	34.91	424	10.65	29.53	1922.69	11.16	30.46	15.5	10.47	35.09	54	35.53	77.86	4166.5	40.36	78.94	69.17	77.86	69.17	27.51
<b>Other items</b>																				
Salpidae	1.75	1	0.66	100	13.2	0.13	100	0.04	1.75											
Unidentified Organic Matter (UOM)	26.32	24	15.79	80.56	1025.1	9.93	76.88	17.58	20.72	26.32	24	15.79	80.56	1025.1	9.93	76.88	17.58	80.56	17.58	20.72

concrete base (25 kg) to which a 3-m rope was attached with a buoy. Receivers were affixed to the rope using heavy-duty cable ties. These receivers were part of a region-wide array (Fig. 1); therefore, if the fish moved to other islands within the GMR or to oceanic islands in the region, they would be detected by similar receivers.

Based on the detection log from the receiver array, we calculated a residency index (RI), expressed as the ratio of the number of days that an individual was detected at the island to the total track length (days elapsed from tagging to last detection). We did not carry out this analysis for individuals whose track length was less than 5 days (selected because there appeared to be a natural break in track lengths at around this point); these animals were considered to have departed the study area, although we recognize that another explanation is that they may have been subject to post-tagging mortality.

To establish whether there was a rhythmic component to the presence of the tagged fish at the islands, we used fast Fourier transformations on the number of

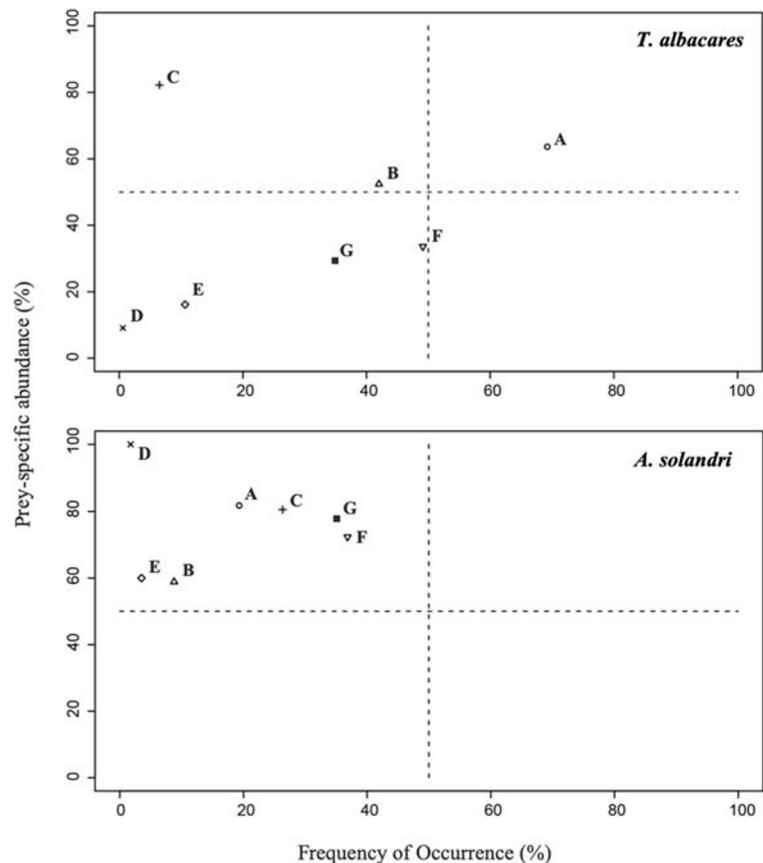
individuals present per hour. We used a circular statistics package (Oriana) to establish whether detections occurred in a uniform manner throughout the day (Rao's spacing test) (Batschelet 1981) or whether they were concentrated around a particular time of day.

## Results

### Diet and foraging strategies

Of the stomachs of *T. albacares* collected, 167 (70.2%) contained food and 71 (29.8%) were empty, while for *A. solandri*, 94 (62.3%) contained food and 57 (37.7%) were empty. The prey diversity accumulation curve reached a CV value  $< 0.05$  at 58 stomachs for *T. albacares* and 41 stomachs for *A. solandri*; thus, we considered that the sample size were adequate ( $n = 238$  and 151, respectively) to represent the diet of both predators. The trophic spectrum of *T. albacares* was very wide, comprising a total of 47 prey, while

**Fig. 2** Amundsen plot showing the numerical prey-specific abundance by frequency of occurrence within the diet of *T. albacares* and *A. solandri*. Prey group abbreviations: (A) Cephalopoda, (B) Crustacea, (C) Unidentified Organic Matter, (D) Other invertebrates, (E) Demersal fishes, (F) Pelagic fishes, (G) Unidentified Fishes





*A. solandri* stomach samples contained a total of 21 prey taxa.

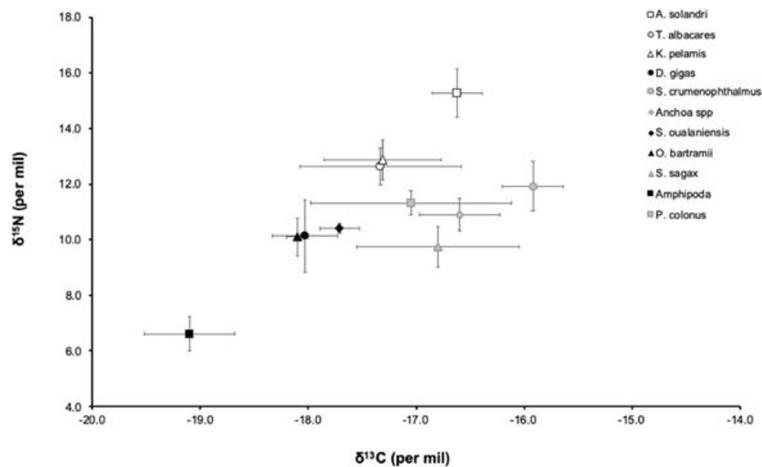
The most important prey for *T. albacares* according to the PSIRI were *Dosidicus gigas* (21.34%), followed by remains of unidentified fishes (10.47%), crab megalopa (8.69%), other squid species such as *Ommastrephes bartramii* (8.34%) and amphipods (6.73%) (Table 2). For this species, invertebrates constituted 63% of the prey items of importance, and the remaining prey items were fishes (Table 2). In contrast, the remains of unidentified fishes (27.51%) were the most important prey item for *A. solandri*, followed by unidentified organic matter (UOM, 20.72%), *D. gigas* (12.23%) and *Caranx caballus* (7.02%) (Table 2). For this predator, fishes made up 57% of the prey items of importance, followed by invertebrates at 20%, and the remaining items were UOM (Table 2). There were significant differences between the diets of both species (R ANOSIM = 0.8,  $p < 0.005$ ).

The Amundsen plot showed that the two predators present different foraging strategies: The diet of *T. albacares* was highly dominated by prey of the Cephalopoda group, while other groups were relatively rare in the diet (Fig. 2). In contrast, *A. solandri* presented a high percentage of prey that were unidentifiable, which resulted in a foraging strategy that was not dominated by a particular group. However, fishes were an important component in the diet of this predator (Fig. 2).

Food sources, niche breadth and isotopic overlap

The mean estimated  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in the muscle of *T. albacares* were  $-17.33 \pm 0.75\text{‰}$  and  $12.63 \pm 0.66\text{‰}$ ; in *K. pelamis*,  $-17.31 \pm 0.54\text{‰}$  and  $12.88 \pm 0.72\text{‰}$ ; and in *A. solandri*,  $-16.62 \pm 0.23\text{‰}$  and  $15.28 \pm 0.86\text{‰}$ , respectively. The C/N ratios of the samples ranged from 2.9 to 3.4; therefore, these were consistent with complete lipid removal and were within the theoretical range established for the assimilation of protein from a predator’s diet (McConnaughey and McRoy 1979; Logan et al. 2008). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were significantly different among species (Kruskal–Wallis test,  $p = 0.001$  and  $p < 0.001$ , respectively), with the signatures of *A. solandri* differing from those of *T. albacares* and *K. pelamis* (multiple comparisons of median ranks,  $p < 0.005$ ). The comparison of  $\delta^{15}\text{N}$  values between species showed that *A. solandri* (mean 15.28‰) were at a higher trophic level than *T. albacares* and *K. pelamis* (mean 12.63 and 12.88‰, respectively) (Fig. 3).

The SIAR provides evidence for some predominance of the Humboldt squid (*D. gigas*) in the diets of *T. albacares* and *K. pelamis*, which presented a mean proportion of 21.1% (ranging from 3.4% to 38.8%) and 29.4% (ranging from 6.7% to 52.1%), respectively, followed by red flying squid (*O. bartramii*) and purpleback squid (*Sthenoteuthis oualaniensis*) as complementary prey in both cases (Fig. 4 and Table 3). In



**Fig. 3** Values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (mean  $\pm$  SD in ‰) in the scombrids that inhabit the Galapagos Marine Reserve, together with isotopic values for different groups of potential prey that make up the trophic web of these species: *S. crumenophthalmus* (gray circle), *Anchoa* spp. (gray diamond), *S. sagax* (gray triangle),

*P. colonus* (gray square), *D. gigas* (black circle), *S. oualaniensis* (black diamond), *O. bartramii* (black triangle) and Amphipoda (black square). For scombrids: *T. albacares* (white circle), *K. pelamis* (white triangle), *A. solandri* (white square)

contrast, fishes including bigeye scad (*Selar crumenophthalmus*) and Pacific creole fish (*Paranthias colonus*) contributed more to the diet of *A. solandri*, with a mean proportion of 23.9% (ranging from 23% to 24.8%) and 15.9% (ranging from 14.8% to 17%), respectively, followed by squid *S. oualiansensis* as complementary prey (Fig. 4).

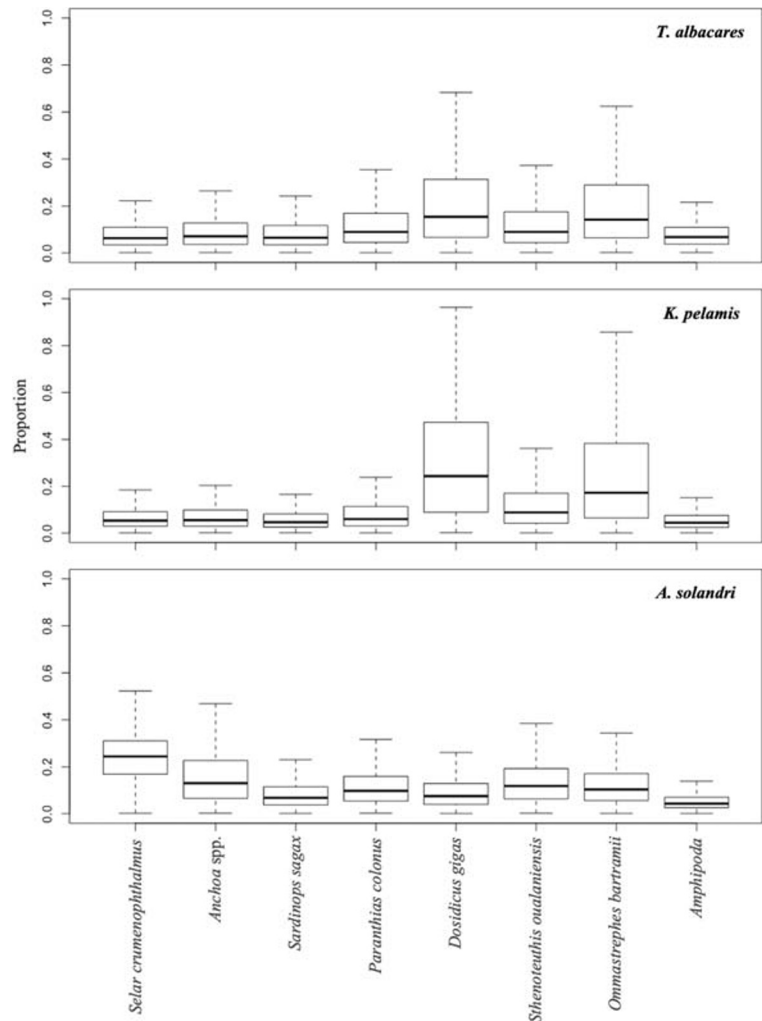
The corrected standard ellipse area (SEAc) showed that *T. albacares* and *K. pelamis* could be exploiting similar habitats, unlike those exploited by *A. solandri* (Fig. 5). These results show that the breadth of the trophic niche of *A. solandri* may be limited to a specific area, as opposed to that of the other species (Table 4). The Bayesian ellipses of *T. albacares* and *K. pelamis* had a high overlap (Fig. 5), showing a similar use of resources and exploitation of the same feeding areas for

both species. In contrast, the ellipse of *A. solandri* did not significantly overlap with that of the other two species (Fig. 5). The overlap area (0.64%) of the Bayesian ellipses from *T. albacares* and *K. pelamis* represented 47.7% of the ellipse surface of *T. albacares* and 66.5% of the ellipse surface of *K. pelamis* (Fig. 5).

#### Site specificity and residence

Of the five *T. albacares* tagged, two were subsequently caught and landed at the main settlement of Santa Cruz Island after only 16 and 23 days, respectively. However, as their RI suggests (Table 5), they remained associated with Wolf Island throughout their entire track record and were also detected on multiple receivers around the

**Fig. 4** Ranges of species proportion to *T. albacares*, *K. pelamis* and *A. solandri* diets produced by the SIAR model using isotope values of prey. The boxes show median values (bold line) and the interquartile range (50% interval), and the dotted line shows the range of some extrema (95% interval)



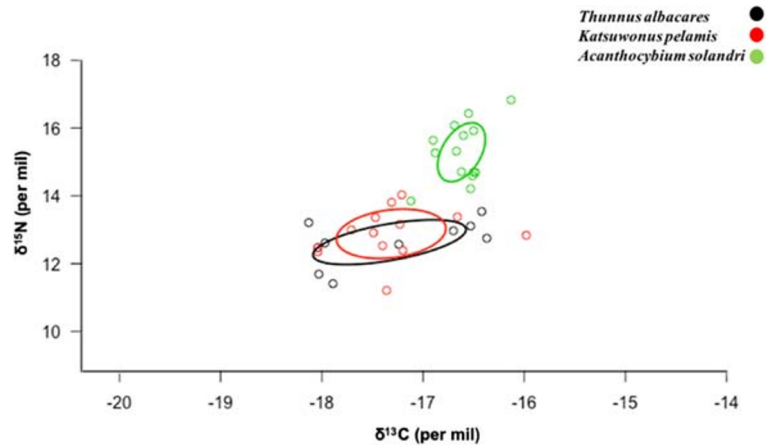
**Table 3** Mean proportion, standard deviation (SD) and convergence diagnostics of prey items on the diet of scombrids that inhabit the Galapagos Marine Reserve. Model fit is assessed by the Gelman diagnostic, where all parameters must be close to 1

Species	Sources	Gelman Diagnostics (Point est.)	Contribution (Mean ± SD)	Contribution in Quantiles		
				25%	50%	75%
<i>Thunnus albacares</i>						
	<i>Selar crumenophtalmus</i>	1	0.08 ± 0.06	0.03	0.06	0.11
	<i>Anchoa spp.</i>	1	0.09 ± 0.08	0.04	0.07	0.13
	<i>Sardinops sagax</i>	1	0.09 ± 0.07	0.04	0.07	0.12
	<i>Paranthias colonus</i>	1	0.12 ± 0.11	0.05	0.09	0.17
	<i>Dosidicus gigas</i>	1	0.21 ± 0.18	0.07	0.15	0.31
	<i>Sthenoteuthis oualaniensis</i>	1	0.13 ± 0.11	0.05	0.09	0.18
	<i>Ommastrephes bartramii</i>	1	0.20 ± 0.17	0.07	0.14	0.29
	<i>Amphipoda</i>	1	0.08 ± 0.05	0.04	0.07	0.11
<i>Katsuwonus pelamis</i>						
	<i>Selar crumenophtalmus</i>	1	0.07 ± 0.05	0.03	0.05	0.09
	<i>Anchoa spp.</i>	1	0.07 ± 0.06	0.03	0.06	0.10
	<i>Sardinops sagax</i>	1	0.06 ± 0.05	0.03	0.05	0.08
	<i>Paranthias colonus</i>	1	0.09 ± 0.09	0.03	0.03	0.11
	<i>Dosidicus gigas</i>	1	0.29 ± 0.23	0.09	0.24	0.47
	<i>Sthenoteuthis oualaniensis</i>	1	0.12 ± 0.11	0.04	0.09	0.17
	<i>Ommastrephes bartramii</i>	1	0.24 ± 0.21	0.06	0.17	0.38
	<i>Amphipoda</i>	1	0.06 ± 0.04	0.02	0.04	0.08
<i>Acanthocybium solandri</i>						
	<i>Selar crumenophtalmus</i>	1	0.24 ± 0.10	0.17	0.24	0.31
	<i>Anchoa spp.</i>	1	0.16 ± 0.12	0.07	0.13	0.23
	<i>Sardinops sagax</i>	1	0.08 ± 0.06	0.04	0.07	0.12
	<i>Paranthias colonus</i>	1	0.12 ± 0.08	0.05	0.10	0.16
	<i>Dosidicus gigas</i>	1	0.09 ± 0.07	0.04	0.08	0.13
	<i>Sthenoteuthis oualaniensis</i>	1	0.14 ± 0.09	0.06	0.12	0.19
	<i>Ommastrephes bartramii</i>	1	0.12 ± 0.08	0.06	0.10	0.17
	<i>Amphipoda</i>	1	0.05 ± 0.04	0.03	0.04	0.07

island, although no inter-island movements were recorded within the Galapagos Marine Reserve. In contrast, of the ten *K. pelamis* tagged at Darwin, only three individuals were detected on our acoustic array (a total of 38 detections) (Table 5). All detections were at a single receiver location on the windward side of the island, where the prevailing current impinges upon the reef. Fish #1 (28 detections) was detected over a 3-day period subsequent to tagging, while fish #2 (six detections) and fish #3 (five detections) were detected only briefly in the 2 days following tagging (Table 5).

The tagged *A. solandri* were tracked for longer (3–26 days) (Table 5). The two individuals at Darwin utilized multiple receivers and provided 559 and 215 detections, respectively, while four other individuals provided 8–251 detections at multiple locations around Wolf Island. No inter-island movements were recorded. Both *A. solandri* and *T. albacares* were present around the islands more commonly during the day, with a peak presence at approximately 08:00 for *A. solandri* and a greater number of detections throughout the afternoon for *T. albacares* (Fig. 6). Spectral density analysis of the

**Fig. 5** Isotopic niche area ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) of *T. albacares*, *K. pelamis* and *A. solandri* in the Galapagos Marine Reserve. The ellipse areas show the degree of trophic niche overlap among the predators



detections showed that both species displayed a clear 24-h periodicity to their presence around the island coasts but that *T. albacares* also displayed a 12-h periodicity (Fig. 6). This finding indicates that *T. albacares* spends more time associated with the reef, while *A. solandri* could travel further offshore at night.

## Discussion

### Diet composition and food sources

The results of this work are consistent with previous studies conducted in other regions of the eastern Pacific Ocean, where the Humboldt squid (*D. gigas*) is one of the main prey items of *T. albacares* (Olson et al. 2014; Alatorre-Ramirez et al. 2017), while small pelagic fishes are an important component of the diet of *A. solandri* (Mendoza-Ávila et al. 2017). The trophic spectrum of *T. albacares* in the Galapagos Marine Reserve proved to be more limited than that observed in other regions of the Pacific Ocean, such as the zones of California and Mexico (Galván-Magaña 1988; Alatorre-Ramirez et al. 2017). The difference is likely related to the distinct

marine diversity among sites and the potential availability of prey in each region (Grove and Lavenberg 1997; Hastings et al. 2010).

*T. albacares* presented an unequal contribution of prey, since despite having a broad trophic spectrum (49 items), only two species of squids (*D. gigas* and *O. bartramii*) accounted for approximately 30% of the prey items of importance in their diet. This coincides with reports by Watanabe (1958) and Alverson (1963), who studied the diet of *T. albacares* throughout the equatorial Pacific, observing a high consumption of medium-sized squids including juvenile Humboldt squid. The importance of squids in the diet of *T. albacares* suggests that they intensify their feeding activities during the night when the squid make their diel vertical migration from the mesopelagic zone to the surface to feed (Nigmatullin et al. 2001; Ruiz-Coolley et al. 2010). This strategy is related to the movement and diving patterns of *T. albacares* in the eastern Pacific (Schaefer and Fuller 2007), where they show loyalty to areas of high prey availability and feed at night in the first 50 m of the water column (Eslava et al. 2003).

Although squids also formed part of the diet of *A. solandri*, this species showed some preference towards small pelagic fishes, such as flying fish (*Prognichthys tringa*) and bigeye scad (*S. crumenophthalmus*). These habits coincide with the diet of *A. solandri* in the western and central Pacific Ocean, where fishes represent the most important group of prey in terms of frequency of occurrence and weight (Iversen and Yoshida 1957; Oyafuso et al. 2016). The trophic spectrum of *A. solandri* suggests a foraging strategy associated with the rocky reefs of the islands, coinciding with reports by Mendoza-Ávila et al. (2017),

**Table 4** Basic standard ellipse area (SEA) and corrected standard ellipse area (SEAc), measured using Stable Isotope Bayesian Ellipses in R, as an estimate of the trophic niche breadth (TNB) of *T. albacares*, *K. pelamis* and *A. solandri*

Species	SEA	SEAc	TNB
<i>Thunnus albacares</i>	1.295	1.457	2.304
<i>Katsuwonus pelamis</i>	1.208	1.318	2.917
<i>Acanthocybium solandri</i>	0.577	0.625	1.355

**Table 5** Tagging data and summary of results from *T. albacares*, *K. pelamis* and *A. solandri* tracked at Darwin and Wolf Islands, in the Galapagos Marine Reserve

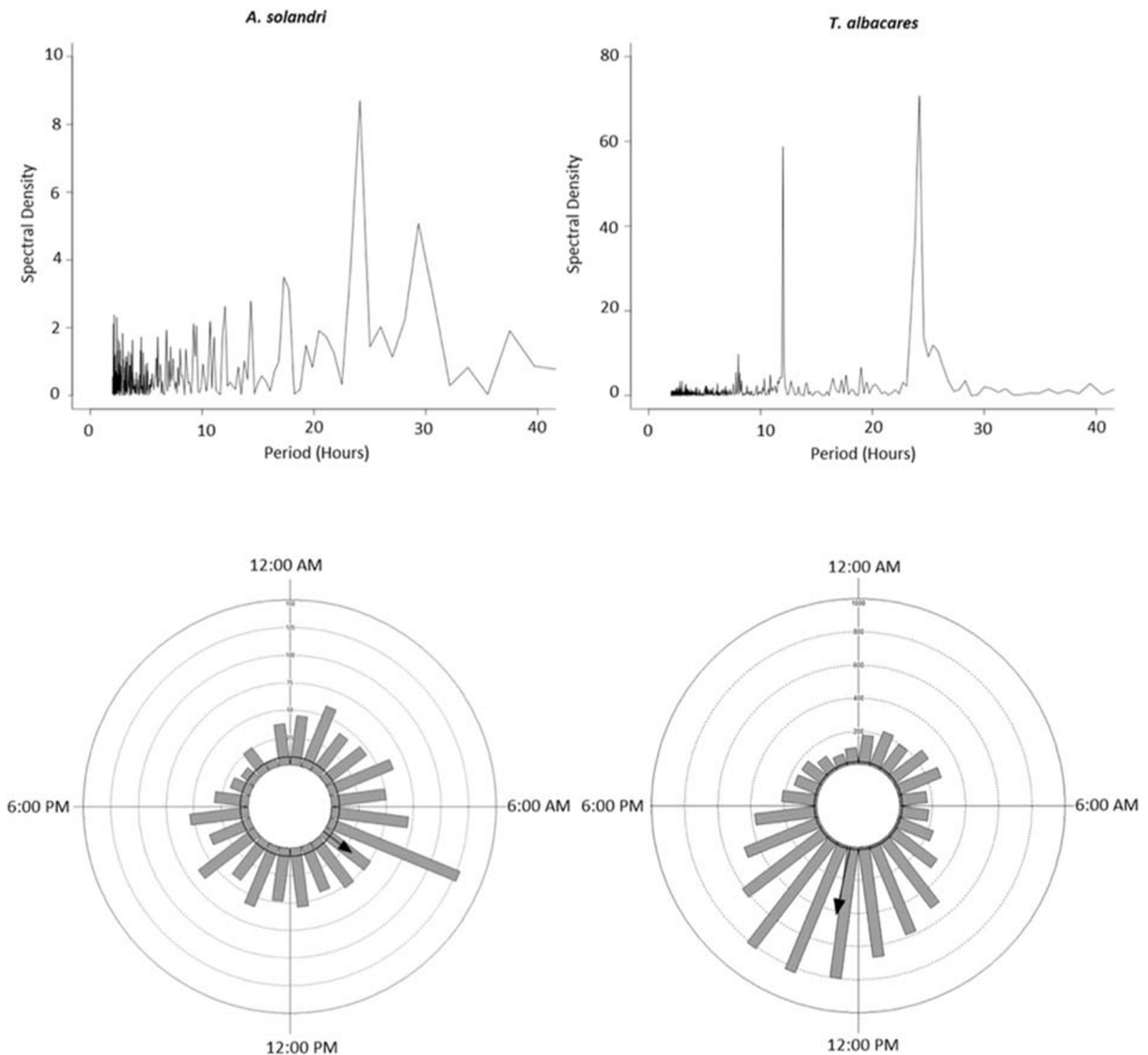
Species	Location	Fork length (cm)	# Detections	Track length (d)	Days detected	Res Index
<i>Thunnus albacares</i>	Wolf	165	869	12	12	1.00
	Wolf	147	5468	261	252	0.97
	Wolf	157	3	1	1	NA
	Wolf	168	1141	47	42	0.89
	Wolf	178	603	25	21	0.84
<i>Acanthocybium solandri</i>	Darwin	102	559	26	25	0.96
	Darwin	114	215	23	15	0.65
	Wolf	99	8	12	1	0.08
	Wolf	123	6	3	2	NA
	Wolf	139	251	4	4	NA
	Wolf	129	106	11	8	0.73
	Wolf	216				
	Wolf	122				
	Darwin	102				
	Darwin	110				
<i>Katsuwonus pelamis</i>	Darwin	48	28	4	3	NA
	Darwin	57	6	2	2	NA
	Darwin	62	4	4	2	NA
	Darwin	51				
	Darwin	56				
	Darwin	59				
	Darwin	57				
	Darwin	65				
	Darwin	48				
	Darwin	54				

who cataloged the populations of *A. solandri* of the eastern Pacific Ocean as generalist predators that focus their feeding on cephalopods and several species of pelagic fishes associated with fish-aggregating devices (FADs). Oxenford et al. (2003) mentioned a preference for occupying areas with aggregations of fishes associated with seamounts. These conditions are in accordance with the movement patterns of *A. solandri*, since this species also has high affinity to the thermocline zone and is usually distributed within the first 20 m of the water column (Bernal et al. 2009; Sepulveda et al. 2011).

The isotopic mixing models confirm the importance of squids and fishes in the diets of *T. albacares* and *A. solandri*, respectively, while for *K. pelamis*, the models suggest a diet based mainly on squids (*D. gigas*, *O. bartramii* and *S. oualaniensis*) and

supplemented to a lesser degree by epipelagic fishes such as the Pacific sardine (*Sardinops sagax*). However, it should be borne in mind that the low isotopic variability among the prey used in the mixing models can limit the resolution of their individual contribution. There are records that found cephalopods to be an important dietary component for the populations of *K. pelamis* in the South Pacific (Nakamura 1965); however, in the North Pacific, this predator focuses on consuming small pelagic fishes and even euphausiids (Alatorre-Ramirez et al. 2017).

Currently, the spatial and temporal dynamics of the main prey that make up the diets of the populations of *T. albacares*, *K. pelamis* and *A. solandri* that live within the Galapagos Marine Reserve are unknown. However, the importance of Humboldt squid in the feeding habits of these species could be associated with the effect of



**Fig. 6** Spectral density analysis for *T. albacares* and *A. solandri*; horizontal bars represent the number of detections in that hour during the recordings. The direction of the arrow shows the mean time, and the length of the concentration

environmental variability in the changes of pelagic food webs of the eastern Pacific Ocean, since there has been a high rate of consumption of this prey by the region's large predators in recent decades (Galván-Magaña et al. 2013; Olson et al. 2014).

#### Foraging strategies and isotopic niche

Several studies have categorized large pelagic fishes as opportunistic species, which means that these species consume the resources available at a given time and place (Alatorre-Ramirez et al. 2017; Mendoza-Ávila

et al. 2017). The trophic spectrum of *T. albacares* indicates a diverse diet; however, it specializes in consuming two to three prey (squids) in greater proportion. The opposite was indicated in *A. solandri*, where a high percentage of its prey were not identifiable, a feature that limited the identification of their diet diversity. However, much of the unidentifiable material was fish remains, which suggests an equitable consumption of prey. These aspects show a differential pattern in the feeding habits of these species, where *T. albacares* was found to be a multispecific predator but with a preference for squids, while *A. solandri* could have a narrower

trophic spectrum with preference for small pelagic fishes.

The isotopic values show that the tunids (*T. albacares* and *K. pelamis*) presented a pelagic strategy, with a consumption of prey of similar trophic levels, while *A. solandri* was found to be more coastal and consumed higher trophic level prey. The foraging strategies of all three species are consistent with those reported in other regions in the eastern Pacific Ocean (Nakamura 1965; Alatorre-Ramirez et al. 2017; Mendoza-Ávila et al. 2017; Varela et al. 2017). The interspecific variation in  $\delta^{13}\text{C}$  values is related to the trophic levels occupied by a predator and the isotopic composition of primary producers, which in turn are the main energy providers for the trophic web (Goericke and Fry 1994; Pancost et al. 1997). In this way, the trophic positions and different levels of primary production create a gradient in the  $\delta^{13}\text{C}$  composition (France 1995; Newsome et al. 2007).

In recent years, it has been shown that large predators limit their trophic niche to three or four specific prey items, changing their level of importance depending on factors such as seasonality and climatic variability (Alatorre-Ramirez et al. 2017). Therefore, species that inhabit regions with limited productivity systems often generate a segregation of resources at both the intra- and interpopulation levels (Matich et al. 2011; Páez-Rosas et al. 2018). These factors are present in the Galapagos Islands, because there are strong fluctuations in marine productivity associated with oceanographic variability and climatic events characteristic of the region, such as ENSO, that significantly affect the ecosystem dynamics in the region (Palacios et al. 2006; Schaeffer et al. 2008).

At the population level, overlap and trophic niche breadth are used to understand the level of interactions within the food web and the role that predators play in the ecosystem (Bolnick et al. 2003; Bearhop et al. 2004). The isotopic niche shows a high overlap between *T. albacares* and *K. pelamis* and suggests that the two species consume similar prey and occupy the same feeding areas (Matich et al. 2011). However, there was no overlap between the isotopic niche of *A. solandri* and the other two predators, revealing a differential consumption of prey during their feeding activities (Jackson et al. 2011). Our results showed that the two tuna species were the most susceptible to competition for resources, which coincides with reports in other areas of the Pacific Ocean (Alverson 1963; Hunsicker et al. 2012).

The trophic breadth for all species was calculated based on the size of the isotopic niche, observing a generalist strategy for *T. albacares* and *K. pelamis*. These results are consistent with what has been reported in other regions of the eastern Pacific Ocean, where they have been cataloged as generalist/opportunistic on the basis of both species consuming prey that form large aggregations but in different proportions depending on their availability in each zone (e.g., pelagic red crab and Humboldt squid), (Hunsicker et al. 2012; Alatorre-Ramirez et al. 2017). The importance of Humboldt squid in the diets of *T. albacares* and *K. pelamis* is consistent with other trophic studies, likely because this prey can easily be found along the continental slope, mainly in upwelling areas (Ehrhardt et al. 1986; Nigmatullin et al. 2001). The small isotopic niche of *A. solandri* suggests exploitation of prey and specific habitats, aspects that may be associated with a preference for feeding near rocky reefs (Oxenford et al. 2003; Sepulveda et al. 2011). This strategy coincides with the results of Oyafuso et al. (2016) and Mendoza-Ávila et al. (2017), who point to epipelagic fishes and several squids as the most representative prey in the diet of *A. solandri* along the eastern Pacific Ocean.

#### Site specificity and residence

Via acoustic telemetry, it was possible to observe that *T. albacares* presents a greater loyalty to study area in comparison with *K. pelamis*, while *A. solandri* registered a certain level of residence for short periods of time. These results are consistent with Schaefer and Fuller (2007) and Sepulveda et al. (2011), who mention that although *T. albacares* and *A. solandri* can perform extensive horizontal movements, both species demonstrate a certain degree of seasonal fidelity to their feeding areas in the tropical Pacific Ocean.

*T. albacares* has different patterns of vertical movements that allow it to remain within the thermocline zone during the night, while throughout the day it frequently dives below the mixed zone (Block et al. 1997; Brill et al. 1999; Schaefer and Fuller 2007). These conditions make it easier for *T. albacares* to develop alternative foraging strategies aimed at capturing prey from deeper areas during the day and thus staying associated longer with island platforms. In contrast, *A. solandri* tends to remain in the upper mixed layer both during the day and at night; however, these animals can perform prolonged horizontal movements at night to

search for prey (Theisen et al. 2008; Sepulveda et al. 2011). This phenomenon would explain the importance of squid in the diets of *T. albacares* and *A. solandri*, since *T. albacares* consumes this prey during the day (performing deep dives) and at night when the squids make their diel migrations to the surface. *A. solandri* limits its vertical movements during the night and can take advantage of the presence of this prey in its range of distribution, using it as complementary prey in its diet.

The movement patterns of *T. albacares* in this study show that three individuals (60%) remained near the sites where they were tagged; however, only one remained in the region for more than 250 days. Movement studies in the central and western Pacific based on conventional marking (plastic labels) indicate some regional loyalty for *T. albacares* within these regions (Itano and Holland 2000; Sibert and Hampton 2003), in agreement with the information presented in this study. In turn, the recapture rate of *A. solandri* (60%) was greater than that reported in other regions (Oxenford et al. 2003; Sepulveda et al. 2011), probably due to a combination of factors, including loyalty to site and the absence of predators. For *K. pelamis*, records were scarce; this is consistent with the low recapture rate reported for this species in the Pacific Ocean (Schaefer and Fuller 2007).

Even though the movement data obtained from these short tracks are consistent with the results from the dietary analysis, it is also possible that the differences displayed between species related to post-tagging mortality rather than foraging strategies. A greater monitoring effort is needed to improve our understanding of the movement patterns, behavior and habitat use of all three of these commercially important species within the Galapagos Marine Reserve.

## Conclusions

By combining stomach content analysis, stable isotope analysis and acoustic telemetry, we described the trophic niches of three scombrids of commercial importance in the Galapagos Marine Reserve. Our findings show the existence of interspecific variation in the foraging strategies of *T. albacares* and *K. pelamis* vs. *A. solandri*, which may be associated with particular energy needs, depending on the availability of resources in its habitat. The trophic spectrum of *T. albacares* and *A. solandri* were found to be narrower than other regions of the

Pacific Ocean, an aspect that could be associated with the availability of prey but may also reflect the limited spatial scale of our sampling. The major diversity of prey in the diet of *T. albacares* could facilitate sharing a foraging strategy with *K. pelamis*, avoiding competitive interactions between these pelagic fishes. It should be noted that the isotopic niche is only a proxy for the trophic niche and that the absence of differences between *T. albacares* and *K. pelamis* does not necessarily mean that their niches are identical. The low number of acoustic records in *K. pelamis* did not allow us to thoroughly study their spatial variations north of the Galapagos Islands. Further studies, therefore, should address this topic to obtain more accurate information on the foraging behavior of this species.

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