

# Feeding habits of thresher sharks *Alopias* sp. in northern Peru: predators of Humboldt squid (*Dosidicus gigas*)

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*The stomach contents of thresher sharks (Alopias spp.; 162–385 cm total length) were collected from five landing points in northern Peru during 2015. A total of 128 thresher sharks were sampled, with 38 individuals identified as Alopias pelagicus and 90 aggregated to the genus level Alopias sp. to prevent any misidentification. The diet comprised 13 and 10 prey taxa for Alopias sp. and A. pelagicus, respectively. Humboldt squid Dosidicus gigas dominated the diet of both groups, with only minor differences in the diet in relation to size classes and location. The diet of Alopias shows a high degree of specialization and the average trophic positions were high for both groups, A. pelagicus (4.4 ± 0.13) and Alopias sp. (4.5 ± 0.14).*

**Keywords:** Alopiidae, diet, jumbo squid, small-scale fisheries

Submitted 11 December 2017; accepted 7 June 2018; first published online 13 July 2018

## INTRODUCTION

Thresher sharks (Family Alopiidae) comprise three highly migratory pelagic species (*Alopias vulpinus*, *A. pelagicus* and *A. superciliosus*), all of which occur in the Pacific Ocean, including Peruvian waters (Smith *et al.*, 2008; Cornejo *et al.*, 2015). Two evolutionarily significant units of *A. pelagicus* have been identified in the Pacific Ocean, with eastern and western Pacific populations (Cardeñosa *et al.*, 2014). Members of this family exhibit low intrinsic reproductive rates, and are susceptible to over-exploitation (Smith *et al.*, 2008; Oldfield *et al.*, 2012; Dulvy *et al.*, 2014). On the west coast of the USA, the population of *A. vulpinus* showed a marked reduction in size and decreases in landings after less than a decade of commercial exploitation during the late 1970s and early 1980s (Holts, 1988; Hanan *et al.*, 1993). In Peru, national landing records suggest that *A. vulpinus* is the fourth most captured shark species, where it is landed mainly in the north of the country (Gonzalez-Pestana *et al.*, 2016). However, it is likely that species misidentification occurred between *A. vulpinus* and *A. pelagicus* (Velez-Zuazo *et al.*, 2015).

Peruvian shark fishery monitoring and management are at a relatively early stage, and no specific management plans have been implemented for the Alopiidae family. Ecosystem-based fisheries management is more holistic than single-species approaches and considers indirect effects on food webs. This

approach requires an ecological understanding of exploited species and their communities. Yet, a lack of ecological data and data on how fishing alters ecosystems function are common limitations that have hampered the implementation of ecosystem-based approaches (Essington & Punt, 2011). Peru has adopted an ecosystem-based approach for management of the Large Marine Ecosystem of the Humboldt Current but this does not include any specific measures related to sharks. Quantitative diet composition estimates provide a basis for understanding a species' prey spectrum and its overall trophic ecology (Bizzarro *et al.*, 2017). Thus, determining the diet composition of thresher sharks is important for developing ecosystem models and management.

The diets of thresher sharks have been studied in the eastern Pacific Ocean (Ecuador, Mexico and California) and Australia (Preti *et al.*, 2001, 2004; Polo-Silva, 2004; Polo-Silva & Grijalba-Bendeck, 2007; Polo-Silva *et al.*, 2009, 2013; Rogers *et al.*, 2012; Galvan *et al.*, 2013; Rosas-Luis *et al.*, 2015), and these studies have shown squids and teleosts to be the main prey. Squid have important roles in marine food webs, both as predators and as prey (Coll *et al.*, 2013). Because of their life history traits (e.g. fast growth) they can have large trophic impacts on food webs (Ehrhardt, 1991; Coll *et al.*, 2013). They are an important component of the eastern Pacific pelagic ecosystem because of their abundance (Olson & Waters, 2003). Thus, their predators might play an important role in squid population dynamics (Coll *et al.*, 2013). As a result, it is important to understand the predator–prey interactions between sharks and squids.

The biology and ecology of thresher sharks in Peruvian waters is poorly understood, with no quantitative information of their diet currently available. This study sought to

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understand the feeding ecology of *Alopias* spp. in northern Peru by analysing stomach contents, including variability by body size, sex, location and season. This study is intended as a baseline for further research on the trophic ecology of thresher sharks in Peru.

## MATERIALS AND METHODS

### Sample collection

Samples were collected at five landing points in northern Peru (Zorritos, Mancora, Las Delicias, San Jose and Salaverry; Figure 1). Stomach contents were collected from small-scale driftnet fishing vessels between February and December 2015. Sharks were sexed and measured to total length (TL), with caudal fin depressed in line with the body to the cm below. Stomachs were extracted and preserved in a 10% formalin solution. Thresher sharks have similar morphological characteristics (Smith *et al.*, 2008); as a result, they can be misidentified. Therefore, a photographic record, when possible, was taken to verify the species. For data analyses, the samples were classified into two groups: individuals that could only be verified at the genus level (*Alopias* sp.) and individuals that could be accurately identified at a species level.

Prey items were analysed in the laboratory and identified to the lowest possible taxon, counted and weighed. Identification guides were used to assist with identification of the teleosts and

cephalopods. For cephalopods, their hard parts (i.e. beaks) were used for species identification (Iverson & Pinkas, 1971; Wolff, 1982; Lu & Ickeringill, 2002; Xavier & Chereil, 2009), in addition, beaks were used to estimate total mass (TM) at ingestion, using regression equations (Lu & Ickeringill, 2002). For teleosts, otoliths and body remains were used for species identification (Chirichigno, 1998; Garcia-Godos, 2001).

### Diet analysis

Diet was quantified using percentages by number (%N), weight (%W) and the frequency of occurrence (%O) (Hyslop, 1980). Two diet indices were calculated: Index of Relative Importance (IRI) (1) and Prey-Specific Index of Relative Importance (PSIRI) (2). The IRI (1) was divided by the total IRI for all items to calculate the Index of Relative Importance on a per cent basis (%IRI; Cortes, 1997).

$$\text{IRI} = \%O \times (\%N + \%W) \quad (1)$$

The Index of Relative Importance (IRI) was modified by the Prey-Specific Index of Relative Importance (PSIRI), which is additive with respect to taxonomic levels. This allows for more reliable comparisons between studies, as PSIRI values are not dependent upon taxonomic level or prey categories (Brown *et al.*, 2012). The %PSIRI was calculated using the equation of Brown *et al.* (2012) (2). We also present the %IRI results to facilitate comparison with other

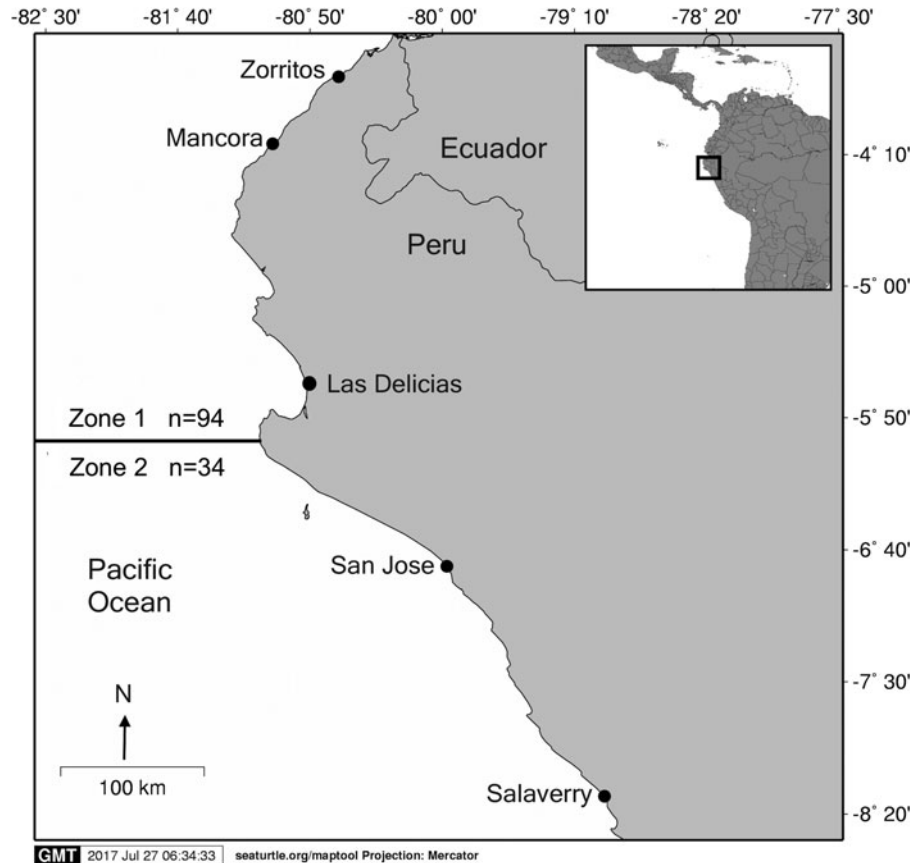


Fig. 1. Landing points where *Alopias* sp. samples were collected. The black line defines the division between zone 1 and zone 2, with the stomach content sample size (n).

studies.

$$\%PSIRI = \frac{\%O \times (\%N + \%W)}{2} \quad (2)$$

## CUMULATIVE PREY CURVES

Cumulative prey curves were constructed to determine if an adequate number of stomachs had been collected to describe the diet (Jimenez-Valverde & Hortal, 2003). The order in which stomachs were analysed was randomized 1000 times to eliminate bias. When a cumulative prey curve reaches an asymptote, the number of stomachs analysed is considered sufficient for describing the diet. According to Soberon & Llorente (1993) a slope value less than 0.1 indicates a good representation of the diet. A more rigorous procedure proposed by Bizzarro *et al.* (2007) establishes that to determine if a cumulative prey curve reaches an asymptote, the slope of the line generated from the endpoints should be compared to a line of zero slope (horizontal asymptote). The endpoints consist of the mean cumulative number of prey taxa generated for the final four stomach samples. Slopes are statistically compared using a Student's *t*-test and slopes that are not significant ( $P > 0.05$ ), indicate that the curve reached an asymptote (Bizzarro *et al.*, 2007).

## TROPHIC NICHE WIDTH

To evaluate the trophic niche width, the Levin standardized ( $B_i'$ ) index was used based on %N values using the following formula (3):

$$B_i = \frac{1}{n-1} \left[ \left( \frac{1}{\sum P_{ij}^2} \right) - 1 \right] \quad (3)$$

$P_{ij}$  is the proportion of the prey  $j$  in the diet of the consumer  $i$  and  $n$  is the number of prey species. Values range from 0 to 1, where values closer to 0 indicate a diet dominated by few prey items (i.e. greater degree of specialization) and values closer to 1 indicate a lesser degree of specialization (Labropoulou & Eleftheriou, 1997).

## TROPHIC POSITION

The relative trophic position (TP) was calculated for each individual based on the %PSIRI values of the prey species present in the stomach content. The equation of Christensen & Pauly (1992) was used (4).

$$TP = 1 + (\sum DC_{ij}) \times (TL_j) \quad (4)$$

$DC_{ij}$  is the composition of the diet in which  $j$  is the proportion of prey items in the diet of the predator  $i$  and  $TL_j$  is the trophic level of the prey items. Trophic positions for prey species were taken from two studies: Espinoza (2014) which presents values for northern Peru and, only when local values were not reported, Cortes (1999) was used (Table suppl. 1).

## DATA ANALYSIS

Diets of the two groups were analysed to determine if differences in the diet exist: at the genus level (*Alopias* spp.) and at the species level (individuals for which species identification had been confirmed through photographic records). Further analysis also depended on four factors: size classes, sex, location and season. Sharks were allocated into two size classes based on the estimated minimum size at maturity: sharks that measured greater than 282 cm TL for females and 267 cm TL for males (Cailliet *et al.*, 1983; Chen *et al.*, 1997; Liu *et al.*, 1999; Polo-Silva & Grijalba-Bendeck, 2007). These values represent the minimum size at maturity for all three thresher shark species (Smith *et al.*, 2008). The division of the study area (zone 1: Zorritos, Mancora and Las Delicias; zone 2: San Jose and Salaverry) was justified based upon biogeographic characteristics of the Tropical East Pacific and Warm Temperate South-eastern Pacific marine provinces where the landing points are located (Spalding *et al.*, 2007) (Figure 1). In addition, the bathymetry along the northern Peruvian margin changes: the continental shelf is narrower in zone 1 (width: 5.5–55.5 km, average: 26 km) in comparison to zone 2 (width: 40.7–129.6 km, average: 96.3 km) (Duperret *et al.*, 1995). The division of the seasons was based upon the seasonality of chlorophyll-*a* concentration and primary production; for which the highest levels occurred during the austral summer and autumn (Pennington *et al.*, 2006). Therefore, data were divided into two seasons: season 1 (June to November) and season 2 (December to May).

Non-metric dimensional scaling (nMDS) ordinations generated from a Bray–Curtis similarity matrix on numeric abundance of prey (%N) was used for two purposes: to determine whether a difference in diet exists between the two groups (at the genus level, *Alopias* spp., and at the species level), and to determine whether body size, sex, location or season exerted the greatest overall influence on the dietary composition of thresher sharks. An overall one-way analysis of similarities (ANOSIM) was used to test whether dietary compositions differed significantly by generating a *R*-statistic and a *P*-value. *R*-statistic values describe the extent of similarity (Clarke, 1993), with values near 1 indicating that the two groups are entirely separate, and values close to 0 indicating that there are no differences between the groups. This was also tested for two different purposes: to determine if there were differences in diet (1) between the two taxonomic groups (*Alopias* spp., and at the species level), and (2) between the factors (e.g. body size). Similarity percentages (SIMPER) were employed to determine the dietary categories that typified particular groups and/or contributed most to the similarities between groups (Clarke, 1993).

## RESULTS

Of the 128 individuals examined, only 19 (14.8%) presented an empty stomach. Specimens of *Alopias* spp. not identified to species level ( $N = 90$ ) measured 162–356 cm TL (mean  $\pm$  SD: 291  $\pm$  38.6), while individuals of *Alopias pelagicus* ( $N = 38$ ) were 206–385 cm TL (mean  $\pm$  SD: 291  $\pm$  31). Length-frequencies varied by factor season, area, sex and maturity stage (Fig. Suppl. 1).

For *Alopias* spp., prey composition comprised 13 prey taxa: three teleosts and 10 cephalopods (including unidentified

cephalopods; Table 1). According to the %PSIRI, the most important prey species were the Humboldt squid (*Dosidicus gigas*) (63.86%), unidentified cephalopods (10.69%), Patagonian squid (*Doriteuthis gahi*) (7.03%) and Peruvian hake (*Merluccius gayi*) (5.01%). The diet of *A. pelagicus* consisted of 10 prey taxa: one teleost and nine cephalopods (including unidentified cephalopods; Table 1). The most important prey species were *D. gigas* (65.3%PSIRI) and sharpnose squid (*Ancistrocheirus lesueurii*) (9.28%). ANOSIM showed no significant differences between the diets of *Alopias* spp. and *A. pelagicus* (Fig. suppl. 2).

According to Soberon & Llorente (1993), the cumulative prey curves showed a trend toward an asymptote with a slope value less than 0.1 (0.03 for *Alopias* spp. and 0.06 for *A. pelagicus*) (Figure 2). However, according to Bizzarro *et al.* (2007), curves for both groups did not reach an asymptote since slopes were significantly different from a zero slope ( $P < 0.05$ ).

The trophic niche widths for *Alopias* spp. ( $Bi = 0.19$ ) and *A. pelagicus* ( $Bi = 0.16$ ) were narrow, with low standardized Levin index values indicating that the diet of *Alopias* shows a high degree of specialization and is dominated by a small number of prey species. The majority of stomachs contained between one (32%) and two (41%) prey species, with *D. gigas* the most common prey species (74% of stomachs that contained a single prey species were of *D. gigas*, and 76% of stomachs that contain two prey taxa also contained *D. gigas*) (Figure 3). Differences between factors were identified: individuals in the season 1, zone 1, size class II and females presented a greater degree of specialization (Table 2). The average trophic positions were high for both *A. pelagicus* ( $4.4 \pm 0.13$ ) and *Alopias* sp. ( $4.5 \pm 0.14$ ). No differences in average trophic positions between factors were identified.

For *Alopias* spp., the average number of prey taxa per stomach content was  $3 \pm 1$  (range: 1–6), and the number of prey items in stomachs ranged from 1–44. For *A. pelagicus*, the average number of prey species per stomach content was  $2 \pm 1$  (range: 1–4), and the number of prey items per stomach ranged from 1–26. The greatest number of prey items was found in a female shark (*Alopias* spp.) that measured 292 cm TL which had 44 pairs of otoliths (equivalent to 44 *M. gayi*).

Since ANOSIM showed no significant differences between the diets of *Alopias* spp. and *A. pelagicus*, all samples were grouped ( $N = 128$ ) for the subsequent analyses. The ANOSIM results showed significant differences in diet between the body size classes (R-statistic = 0.21,  $P < 0.01$ ) and locations (R-statistic = 0.35,  $P < 0.01$ ). The nMDS plot and the overall R-value indicated that there were small, but statistically significant differences in diet according to location and body size (Fig. suppl. 2). Individuals from Zone 1 fed primarily on *D. gigas* (83.60%PSIRI), while individuals from Zone 2 fed on a combination of *D. gigas* (44.01%) and *M. gayi* (23.59%) (Table 3). Both body sizes fed primarily on *D. gigas*; yet size class II presented higher PSIRI values (79.17%) than size class I (59.84%) (Table 3).

## DISCUSSION

This study has shown that thresher sharks are top predators in the waters off northern Peru, with a diet composed mainly of *Dosidicus gigas*. These results complement the findings of other diet studies of *Alopias* spp. in the Eastern Pacific (Ecuador, California and Mexico) that found that cephalopods

(e.g. *D. gigas*) and, to a lesser extent, teleosts (e.g. *M. gayi*) were important prey (Preti *et al.*, 2001, 2004, 2008; Polo-Silva, 2004; Polo-Silva & Grijalba-Bendeck, 2007; Polo-Silva *et al.*, 2009). In contrast, Rosas-Luis *et al.* (2015) found that *A. superciliosus* in Ecuadorian waters fed mainly on teleosts with squids of secondary importance. The present study indicated a higher trophic position (4.4–4.5) in comparison with thresher sharks (i.e. *A. pelagicus*, *A. superciliosus*) sampled off Ecuador (3.7–3.9; Polo-Silva, 2004; Polo-Silva & Grijalba-Bendeck, 2007; Polo-Silva *et al.*, 2009), but a lower value than for thresher sharks (i.e. *A. pelagicus* (4.7), *A. superciliosus* (5.2)) sampled off Mexico (Li *et al.*, 2016). Previous studies of thresher sharks have also found only small differences in the diet according to body size, sex or season (Polo-Silva, 2004; Polo-Silva & Grijalba-Bendeck, 2007; Polo-Silva *et al.*, 2009). Yet, it is important to consider that the assumptions in this study may be different from other studies since data were analysed both to the species level and to the genus level.

According to Soberon & Llorente (1993), the slopes of the cumulative prey curves indicated that overall sample sizes were sufficient to describe the diets of *Alopias* sp. and *A. pelagicus*. Yet, according to Bizzarro *et al.* (2007), sample sizes should be increased to improve the quantitative description of the diet. In addition, previous studies of the diets of *Alopias* have found a greater number of prey (20–27 taxa; Preti *et al.*, 2001, 2004; Polo-Silva, 2004; Polo-Silva & Grijalba-Bendeck, 2007; Polo-Silva *et al.*, 2009). Therefore, the results of this study should be interpreted with caution. Future studies of thresher sharks in northern Peru should increase sample size toward improving their diet description accuracy. Since some species of cephalopods could not be identified to the species level, this represents a knowledge gap that also remains to be resolved.

In the South-eastern Pacific, the diet of *A. pelagicus* has only been studied in Ecuador (Polo-Silva, 2004; Polo-Silva *et al.*, 2009). The authors found that this shark species fed primarily on three species: *D. gigas* (75%IRI), purpleback flying squid (*Sthenoteuthis oualaniensis*) (12%IRI) and Panama lanternfish (*Benthoosema panamense*) (9%IRI). Thus, the diet of *A. pelagicus* in Ecuador is composed of oceanic species. In the present study, *D. gigas* was also the main prey species of *A. pelagicus* (79%IRI) but *S. oualaniensis* and *B. panamense* were absent from the diet of *A. pelagicus* in northern Peru. In the case of *S. oualaniensis*, this may be explained by this species' preference for warmer waters (e.g. Ecuador) than *D. gigas* (Nigmatullin *et al.*, 2001).

In Peru, thresher sharks present similar diets to other shark species. In northern Peru, the smooth hammerhead shark (*Sphyrna zygaena*) has a similar diet to thresher sharks, feeding mainly on two species (i.e. *Doryteuthis gahi* and *D. gigas*) (Gonzalez-Pestana *et al.*, 2017). In Ecuador, blue sharks (*Prionace glauca*) also feed mainly on cephalopods (i.e. *Ancistrocheirus lesueurii*, *Histioteuthis dofleini* and *D. gigas*) (Loor-Andrade *et al.*, 2017). Another ongoing study of the trophic ecology of pelagic elasmobranchs in northern Peru, using stable isotopes, found that *Alopias* spp., *P. glauca* and *S. zygaena* had strong trophic overlaps (Alfaro-Cordova pers. comm.). This suggests that these three commercial shark species are sharing resources, especially *S. zygaena* and *Alopias* spp (Alfaro *et al.*, 2018). Such trophic interactions should be taken into account in any future development of trophic models and ecosystem-based management.

**Table 1.** Prey composition in stomach contents of thresher sharks: *Alopias* sp. (not identified at a species level, N: 90) and *Alopias pelagicus* (N: 38).

Prey category	<i>Alopias</i> spp.							<i>Alopias pelagicus</i>						
	%W	%N	%O	%IRI	(±SD)	%PSIRI	(±SD)	%W	%N	%O	%IRI	(±SD)	%PSIRI	(±SD)
Chordata														
Teleostei														
<i>Engraulis ringens</i>	0.02	2.05	2.44	0.11	(20.43)	0.62	(4.58)	0.05	2.51	2.63	0.03	(0.19)	0.74	(4.56)
Fam. Tetradontidae	0.06	0.51	4.07	0.02	(0.15)	0.3	(1.84)							
<i>Merluccius gayi</i>	2.14	12.83	4.88	4.55	(20.42)	5.01	(21.30)							
Mollusca														
Cephalopoda														
Cephalopods unidentified	0.01	17.66	34.96	8.29	(18.64)	10.69	(20.03)	0	15.06	34.21	5.2	(16.50)	7.88	(18.04)
<i>Ancistrocheirus lesueurii</i>	2.78	2.78	15.45	2.44	(10.80)	4.7	(14.44)	6.44	7.11	28.95	5.84	(16.96)	9.28	(19.68)
<i>Dodiscus gigas</i>	91.06	51.33	73.17	74.52	(36.36)	63.86	(35.42)	84.38	61.09	86.84	79.17	(32.28)	65.3	(32.86)
<i>Doriteuthis gahi</i>	1.11	8.11	14.63	5.80	(21.3)	7.03	(21.84)	0.68	5.02	5.26	3.41	(16.79)	4.93	(21.25)
<i>Gonatus antarcticus</i>	0.89	1.75	9.76	1.34	(9.63)	2.66	(11.19)	1.93	1.67	10.53	0.39	(1.42)	2.29	(7.95)
<i>Histioteuthis hoylei</i>	0.27	1.13	4.88	0.93	(8.71)	1.64	(9.70)	0.88	3.35	7.89	2.75	(15.07)	4.16	(16.23)
<i>Mastigoteuthis dentata</i>	0.02	0.31	2.44	0.92	(9.53)	1.05	(9.55)	0.07	0.42	2.63	0.01	(0.07)	0.25	(1.53)
Octopodea*	0.01	0.82	4.07	1.00	(9.56)	1.16	(9.60)	0	2.09	5.26	2.82	(16.23)	2.9	(16.26)
<i>Octopoteuthis sicula</i>	0.10	0.21	1.63	0.01	(0.12)	0.43	(3.58)							
<i>Ommastrephes bartramii</i>	1.53	0.51	3.25	0.07	(0.58)	0.85	(5.98)	5.58	1.67	7.89	0.39	(1.88)	2.28	(0.08)

SD, standard deviation.

Percentage by number (%N), percentage by weight (%W), percentage by frequency of occurrence (%O), index of relative importance, expressed as a percentage (%IRI), and prey-specific index of relative importance (%PSIRI).

\**Argonauta* sp., *Tremoctopus violaceus*.

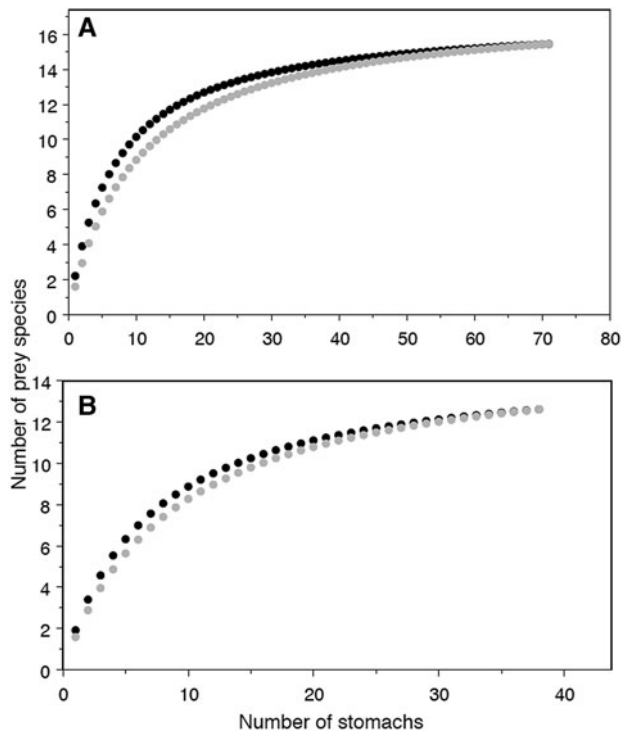


Fig. 2. Randomized cumulative prey curve of *Alopias* sp. (A) and *A. pelagicus* (B) (grey points: observed data; black points: predicted data).

In the eastern Pacific, *D. gigas* is one of the most abundant and largest squids, and Peru reports the highest worldwide fishery landings (Nigmatullin *et al.*, 2001). In Peruvian waters, only two species had previously been reported preying on *D. gigas*: *S. zygaena* and sperm whales (*Physeter macrocephalus*) (Clarke *et al.*, 1976; Gonzalez-Pestana *et al.*, 2017). In this study, results indicate that thresher sharks are also important predators, which could potentially have an impact on the overall population of *D. gigas* in northern Peru; however, more advanced studies are needed to verify this. The potential reduction in predation pressure on squids resulting from fisheries exploitation of their predators (Ward & Myers, 2005; Smith *et al.*, 2007) might cause an increase in cephalopod biomass (Piatkowski *et al.*, 2001;

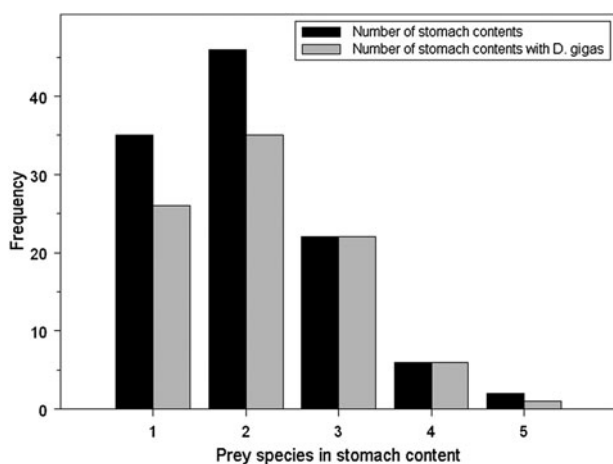


Fig. 3. Number of prey species and number of *Dosidicus gigas* prey in stomach contents of thresher sharks (*Alopias* sp.).

Table 2. Levin's standardized index showing trophic niche width between factors in the diet of thresher sharks (*Alopias* sp.).

Factors	Trophic niche width
Season 1	0.12
Season 2	0.25
Zone 1	0.10
Zone 2	0.20
Female	0.28
Male	0.16
Size class I	0.49
Size class II	0.14

Season 1: June to November. Season 2: December to May. Zone 1: Zorritos, Mancora and Las Delicias. Zone 2: San Jose and Salaverry. Size class I: lower than the benchmark. Size class II: higher than the benchmark. Benchmark was 282 cm TL for females and 267 cm TL for males.

Watters *et al.*, 2008). As with the interplay of the shark species described above, these commercial species of thresher sharks and *D. gigas*, comprising both predator and prey, will require an ecosystem-based approach for both their populations to be managed effectively.

This study presents the first stomach content analyses for thresher sharks in Peru and the southernmost study of its diet in the eastern Pacific. As such, it can serve as a baseline to promote and guide additional, more focused and advanced studies of thresher shark trophic ecology. Future studies should pay close attention to accurately identifying this family to the species level. In addition, since this study consisted mostly of adult-sized animals, future diet studies of thresher shark diets should also include a wider range of body sizes to more adequately assess the life history of thresher shark trophic ecology.

## SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315418000504>.

Table 3. Prey-specific index of relative importance (%PSIRI) of thresher sharks (*Alopias* sp.) according to location (zone 1: Zorritos, Mancora and Las Delicias; zone 2: San Jose and Salaverry) and body size (size class I: lower than the benchmark, size class II: higher than the benchmark; benchmark was 282 cm TL for females and 267 cm TL for males).

Prey category	Location		Body size	
	Zone 1	Zone 2	Size class I	Size class II
<i>Engraulis ringens</i>	0.01	0.02	0.90	0.01
Fam. Tetradontidae	0.01	0.00	0.00	0.01
<i>Merluccius gayi</i>	0.03	23.59	7.23	3.84
Cephalopods unidentified	8.32	8.86	10.70	7.31
<i>Ancistrocheirus lesueuri</i>	2.97	0.00	5.58	1.04
<i>Dosidicus gigas</i>	83.60	44.01	59.84	79.17
<i>Doriteuthis gahi</i>	3.46	6.37	6.74	5.55
<i>Gonatus antarcticus</i>	0.20	7.17	2.13	1.50
<i>Histioteuthis hoylei</i>	1.21	0.08	0.33	1.24
<i>Mastigoteuthis dentata</i>	0.00	4.76	3.27	0.00
Octopoda*	0.08	4.92	3.28	0.14
<i>Octopoteuthis sicula</i>	0.00	0.23	0.00	0.03
<i>Ommastrephes bartramii</i>	0.11	0.00	0.00	0.15

\**Argonauta* sp., *Tremoctopus violase*.

## ACKNOWLEDGEMENTS

We would like to thank Sonia Valle and Aldo Indacochea for supporting this project and facilitating the use of the laboratory of Marine Biology at Universidad Científica del Sur. Also, thanks to José Carlos Xavier, Astrid Jiménez, Sergio Pingo, Silvia Kohatsu, Angie Sánchez and Akemi Arévalo for assistance, collecting, analysing and identifying samples. Bernabé Moreno for facilitating information.

## FINANCIAL SUPPORT

This work was supported by Fondo para la Innovación, la Ciencia y la Tecnología (PIBA-369-2014), The DEFRA Darwin Initiative, UK, and The United States Embassy in Peru.

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