

Short Communication

Isotopic niches of four commercially important pelagic elasmobranch species captured by the small-scale driftnet fishery of northern Peru

Eliana Alfaro-Cordova^{1,2}, Alonso Del Solar¹, Adriana Gonzalez-Pestana^{1,2}
Nicolás Acuña-Perales¹, Javier Coasaca², Francisco Cordova-Zavaleta¹
Joanna Alfaro-Shigueto^{1,2,3} & Jeffrey C. Mangel^{1,3}

¹ProDelphinus, Lima, Perú

²Universidad Científica del Sur, Lima, Perú

³Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall, U.K.

Corresponding Author: Eliana Alfaro-Córdova (eliana@prodelphinus.org)

ABSTRACT. Despite the high landings of elasmobranch in Peru, little is known about some aspects of their basic biology, including their trophic ecology. The present study aims to provide basic information regarding the isotopic niche and trophic interactions of four pelagic elasmobranchs of commercial importance in northern Peru (*Alopias* spp., *Galeorhinus galeus*, *Sphyrna zygaena*, and *Mobula japonica*). One hundred and twenty-four samples were collected from fishing activities between January and December 2015 and processed for stable isotopes analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), using Bayesian statistics to describe their isotopic niche. Differences between species were assessed using PERMANOVA and PERMDISP, allowing testing length, sex, and latitude as covariates. These combined results suggest trophic redundancy among sharks. However, unique areas of no overlap in the SEA_C of all species could evidence a broad niche with a low interaction between these sharks. *M. japonica* had no overlap with any shark species, which indicates a trophic niche that is distinct from other elasmobranch top predators. Increasing sample size and including temporal covariates should help define these isotopic niches better, either by merging or splitting the studied elasmobranchs into more specific groupings. Further complementary studies are required to better understand trophic interactions within the pelagic community ecosystems.

Keywords: mobulids, sharks, community, isotope analysis, trophic ecology, northern Peru.

Elasmobranch populations are in decline worldwide due to fisheries overexploitation (Baum *et al.*, 2003; Dulvy *et al.*, 2008; Fowler, 2014), leading to an international focus on their long-term conservation (Worm *et al.*, 2013; Dulvy *et al.*, 2014). This may have implications that extend beyond simple conservation concerns, given the important ecological roles they have, such as food web regulation (Baum *et al.*, 2009; Borrell *et al.*, 2011).

In Peru, elasmobranch captures occur mainly in small-scale gillnet and longline fisheries, covering not only the fin trade demand but also the consumption of shark and rays flesh at local markets (Alfaro-Shigueto *et al.*, 2010; Alfaro-Cordova *et al.*, 2017). These fisheries have the largest cumulative landings in the Pacific Ocean (Gonzalez-Pestana *et al.*, 2014). Despite these high levels of local consumption, very little is known about the ecological roles of commercial species,

and consequently, the impacts of elasmobranch fisheries on the exploited species, and the wider ecosystem. Usually, feeding ecology has been addressed via the analysis of stomach contents, which gives a snapshot of the last items eaten by the studied consumers at the time of capture. Complementary techniques for the analysis of trophic ecology have been developing over the last decades, aiming to improve both spatial and temporal resolutions, such as the use of stable isotopes.

Stable isotopes are used as natural tracers of trophic structure to obtain complementary information related to the assimilation of prey, as opposed to simple consumption (Fry, 2006; Michener & Lajtha, 2007). Due to fractionation and mixing processes as well as consumer assimilation, excretion and turnover rates, carbon and nitrogen isotopic ratios (expressed by δ , where $\delta^{13}\text{C} = {}^{13}\text{C}/{}^{12}\text{C}$ and $\delta^{15}\text{N} = {}^{15}\text{N}/{}^{14}\text{N}$) can be detec-

table in a predictable manner across marine food webs (Michener & Schell, 1994). Stable isotope analyses of elasmobranchs have provided valuable information about their feeding habitats and trophic positions (Hussey *et al.*, 2012). However, considering the high variability of trophic roles of elasmobranchs among ecosystems and species, further studies are necessary.

The present study provides basic information on trophic interactions of four pelagic elasmobranchs captured by small-scale driftnet fisheries in northern Peru: the pelagic sharks *Alopias* spp., *Sphyrna zygaena* and *Galeorhinus galeus*, and the batoid *Mobula japonica*. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were used to characterize their isotopic niche and estimate their trophic position, in order to further understand their inter-specific connectivity.

Onboard observations were made from January to December 2015 aboard small-scale driftnet fishing vessels targeting pelagic elasmobranchs and operating between $03^{\circ}25' - 09^{\circ}56' \text{S}$ and $83^{\circ}07' - 79^{\circ}18' \text{W}$ (Fig. 1). The total length (TL) and sex of each elasmobranch were recorded. One hundred and twenty-four muscle tissue samples were collected from the base of the dorsal fin for sharks and from the pectoral fin for mobulids (Table 1), and stored embedded in non-ionized salt.

Tissue samples were washed with distilled water and dissected. Lipid and urea were removed using a solution of chloroform: methanol (2:1), followed by a wash with milli-Q water (Logan *et al.*, 2008; Li *et al.*, 2015).

Then, samples were oven-dried at 60°C for 18-24 h. *ca.* 0.5 mg of dry tissue was placed in pre-weighed tin capsules and stored in vacuum-sealed well plates. The isotopic composition of each sample was analyzed at the Laboratorio de Análisis Isotópico (LAI) of Universidad Andrés Bello. The laboratory used a Eurovector elemental analyzer coupled to a Micromass Isoprime isotope ratio mass spectrometer. Stable isotope ratios were presented according to the delta (δ) notation, where the relative variations of stable isotope ratios are expressed in parts-per-thousand from predefined standards (VPDB for carbon and AIR for nitrogen). $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ is calculated by the following equation: $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. Analysis precision was $\pm 0.14\%$ for $\delta^{15}\text{N}$ and $\pm 0.07\%$ for $\delta^{13}\text{C}$.

The isotopic niche width, which can be used as a proxy for ecological niche width, (Newsome *et al.*, 2007) of each elasmobranch species, as well as comparisons among them, were analyzed using Bayesian statistics. All individual values were plotted per species in isotopic space (*i.e.*, $\delta^{15}\text{N}$ vs $\delta^{13}\text{C}$) and

used to calculate their mean core isotopic niche area in terms of their corrected standard ellipse areas (SEA_{C}), which accounts for small samples sizes (Jackson *et al.*, 2011). Thus, SEA_{C} was used to compare the degree of overlap among species. Bayesian estimates of the standard ellipse areas (SEA_{B}) were also calculated to observe the degree of uncertainty around each SEA_{C} . To get a broad understanding of trophic diversity and redundancy among the studied species, community-wide trophic structure metrics were calculated following Layman *et al.* (2007), obtaining values for: i) $\delta^{15}\text{N}$ range (NR), ii) $\delta^{13}\text{C}$ range (CR), iii) total area (TA), iv) mean distance to centroid (CD), v) Mean nearest neighbour distance (MNND), and vi) Standard deviation of MNND (SDNND). Metrics were obtained from the maximum likelihood values of their probability distributions using Bayesian inference, which allows for statistical comparisons between communities (Jackson *et al.*, 2011). The values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were also tested for statistical differences between and within species, through the PERMANOVA and PERMDISP routines (Anderson, 2001, 2006), using total length (TL), sex and latitude as covariates. Isotopic and TL values were \log_{10} -transformed.

The trophic position (TP) of each individual elasmobranch was estimated by applying the Post (2002) equation: $TP_{\text{pred}} = \delta^{15}\text{N}_{\text{pred}} - \delta^{15}\text{N}_{\text{base}}/\text{TEF} + TP_{\text{base}}$, where TP_{pred} is the trophic position of the elasmobranch; $\delta^{15}\text{N}_{\text{pred}}$ is the stable nitrogen signature of the elasmobranch; $\delta^{15}\text{N}_{\text{base}}$ is the stable nitrogen signature of the dietary baseline; TEF is the trophic enrichment factor between an elasmobranch and its prey; and, TP_{base} is the trophic position of the baseline. We used the TEF proposed by Kim *et al.* (2012) for elasmobranchs ($\text{TEF} = 3.7\%$) and copepods ($\text{TP} = 2.5$) sampled in the study area as baseline species (Espinoza, 2014). Considering the presence of intense and shallow oxygen minimum zones south of $\sim 7.5^{\circ}\text{S}$, related to $\delta^{15}\text{N}$ enrichment in the environment (Espinoza, 2014), values of TP were estimated per consumer captured either north or south of latitude 7.5°S , by using $\delta^{15}\text{N}$ values of copepods sampled in both areas (7.6‰ for the north and 9.8‰ for the south) (Espinoza, 2014). All statistical analysis and mathematical calculations were performed using the R language (R Development Core Team, 2016).

Most of the studied species were captured over a wide range of locations (Fig. 1), except *G. galeus*, which showed only coastal interactions with fisheries, between latitudes $5^{\circ}25' \text{S}$ and $7^{\circ}45' \text{S}$, approximately. *S. zygaena*, *Alopias* spp. and *M. japonica* have been shown to be highly migratory species, while *G. galeus* to be a less migratory, coastal benthopelagic species (Couturier *et al.*, 2012; Fowler, 2014). Furthermore,

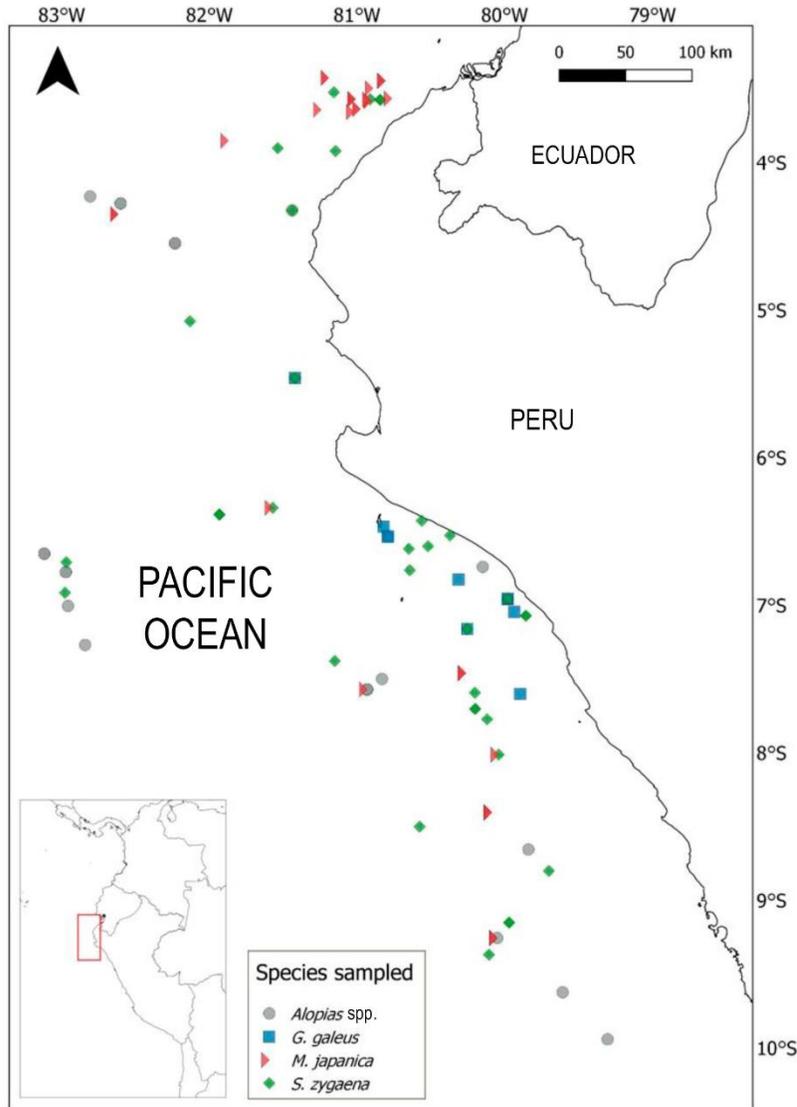


Figure 1. Map showing the locations where elasmobranch samples were collected off northern Peru. The different symbols represent individuals of the four elasmobranch species sampled.

Table 1. Length (L), stable isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and trophic position (TP) for two areas (north and south) of all four species of elasmobranchs analyzed. Values are mean \pm SD. TL: total length; DW: disc width; n: sample size; TP: trophic position based on Kim *et al.* (2012) for the trophic enrichment factor and on Espinoza (2014) for the baseline values.

Species	Common name	Length (cm) (type)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	TPNorth	TPSouth
<i>Alopias</i> spp.	Thresher shark	261.6 \pm 69.5 TL	-15.89 \pm 0.60	14.20 \pm 1.37	28	4.35 \pm 0.37	3.60 \pm 0.36
<i>G. galeus</i>	School shark	116.8 \pm 25.0 TL	-14.74 \pm 0.58	14.99 \pm 1.13	11	4.46 \pm 0.29	4.31 \pm 0.00
<i>S. zygaena</i>	Smooth hammerhead shark	124.07 \pm 58.6 TL	-15.67 \pm 0.52	15.74 \pm 1.88	45	4.81 \pm 0.51	3.89 \pm 0.42
<i>M. japonica</i>	Devil ray	169.7 \pm 42.9 DW	-16.53 \pm 0.62	11.91 \pm 0.67	40	3.65 \pm 0.17	2.88 \pm 0.08

although *M. japonica* individuals were caught down to around latitude 9°15'S, most individuals were caught in northern Peru (~3°30'S), and mainly near the coast.

Alopias spp. and *S. zygaena* had similar SEAC values, and showed relatively large isotopic overlap

(Tables 2-3, Figs. 2-3). The latter exhibited a larger range of $\delta^{15}\text{N}$, which was slightly shifted towards higher values. This suggests that they could be sharing resources, as shown by previous studies on stomach contents analysis in the eastern Pacific (Castañeda &

Table 2. Percentage of isotopic niche overlap among the four study species using their corrected standard ellipse areas (SEAc). Values represent the percentage of consumer *i* being shared with consumer *j*. SEAc: corrected standard ellipse area of consumer *i*; SEAB ML: the maximum likelihood of the standard ellipse area of consumer *i*, using Bayesian inference.

Species _{ij}	<i>Alopias</i> spp.	<i>G. galeus</i>	<i>S. zygaena</i>	<i>M. japonica</i>	SEAc	SEAB ML
<i>Alopias</i> spp.	-	1.43	43.16	0	2.66	2.48
<i>G. galeus</i>	1.84	-	0	0	2.07	1.78
<i>S. zygaena</i>	38.97	0	-	0	2.94	2.83
<i>M. japonica</i>	0	0	0	-	1.33	1.27

Table 3. Statistical significances (*P*-values) of the pairwise comparison of the four study species, using permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) to account for differences between them (***highly significant).

Species _{ij}	<i>Alopias</i> spp.	<i>G. galeus</i>	<i>S. zygaena</i>
<i>Alopias</i> spp.	-		
<i>G. galeus</i>	0.029*	-	
<i>S. zygaena</i>	<0.01***	0.139	-
<i>M. japonica</i>	<0.01***	<0.01***	<0.01***

Sandoval, 2004; Polo-Silva *et al.*, 2013). The ellipses from both sharks were close to *G. galeus* in isotopic space (Fig. 2). Its SEAc was located towards enriched values of $\delta^{13}\text{C}$ and showed only a slight overlap of 1.8% with *Alopias* spp. (Table 2). In terms of convex hulls (total area occupied by each species in isotopic space, see Fig. 2), both *G. galeus* and *Alopias* spp. were almost embedded in *S. zygaena*, which presented the largest ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, 2.74 and 8.25‰, respectively. None of these overlapped with *M. japonica* in terms of SEAc, stretching in total from about -18 to -15‰, with a range of $\delta^{15}\text{N}$ of only around 1‰.

Both PERMANOVA and PERMDISP showed significant differences between species (*P*-value <0.01, $R^2 = 60\%$; and *P*-value <0.01, respectively), while showing no significant differences for TL (*i.e.*, log TL) and sex. However, *S. zygaena* showed that latitudinal variations were significant in explaining its isotopic niche (PERMANOVA, *P*-value <0.01), though only $\delta^{15}\text{N}$ showed a tendency towards enriched values at lower latitudes. Pairwise comparisons between the location of species in isotopic space showed that *M. japonica* was significantly different from all other species (*P*-value <0.01), as well as *Alopias* spp. from *G. galeus* (*P*-value <0.05) and *S. zygaena* (*P*-value <0.01). However, despite not finding any overlap between the SEAc of *S. zygaena* and *G. galeus*, the PERMANOVA did not find any significant differences between the two species. Comparisons between the dispersions (PERMDISP) showed that only *M. japonica*

had significant differences with *Alopias* spp. and *S. zygaena*.

The fact that the convex hull of *G. galeus* fitted inside *S. zygaena*, and that both dispersions were not significantly different (*P*-value = 0.096), may be the reason why PERMANOVA did not detect them as two separate groups. Furthermore, while this tool is robust against heterogeneity of dispersions and unbalanced designs (Anderson, 2006), both the low sample size of *G. galeus* and the high dispersion of *S. zygaena*, result in higher uncertainty. Future designs should aim for more balanced sample sizes, with at least 30 samples per species. This way the covariates may play a bigger role in explaining the isotopic niches with less uncertainty, either by merging or splitting the groups (Table 4).

These results suggest that both *G. galeus* and *M. japonica* have almost unique isotopic niches and resource pools, in contrast with the other studied species. Likewise, high proportions of isotopic areas remain unique for all species, suggesting that they also feed on a variety of other prey items (Shaw *et al.*, 2016), or throughout different areas. However, it is important to consider that these are results from a partial community of consumers, as no teleost predators or mammals were included in the analysis.

Community metrics corroborate other recent studies with similar species and trophic structure (Li *et al.*, 2015; Shaw *et al.*, 2016). The range of values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were ~1.79 and ~3.83, respectively (Fig. 3). Values of mean centroid distance and mean nearest neighbor distance (*i.e.*, CD ~1.35 and MNND ~1.54) indicate similar elasmobranch diet diversity and high trophic redundancy.

Even though this partial community does not comprise a full food chain, the range of $\delta^{15}\text{N}$ (NR ~3.83) reveals at least one trophic level of difference between the secondary consumer *M. japonica* and the top predator *S. zygaena*, which is supported by their difference in the calculated mean trophic position ($\Delta\text{TP}_{\text{North}} \sim 1.16$, $\Delta\text{TP}_{\text{South}} \sim 1.01$, Table 1). The mean TP estimated for *M. japonica* for both north and

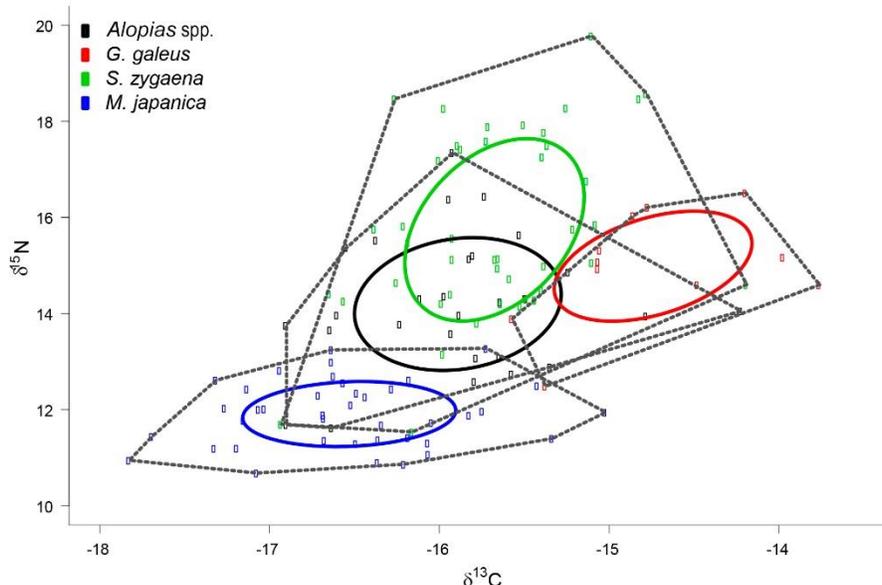


Figure 2. A plot of $\delta^{15}\text{N}$ vs. $\delta^{13}\text{C}$ values of all individuals of the four analyzed elasmobranch species. Colored lines: corrected standard ellipse areas (SEAc), based on a maximum likelihood Bayesian framework, which represent the isotopic niche area of each species. Dashed lines: convex hull or total isotopic area covered by each species.

Table 4. Statistical significances (*P*-values) of the pairwise comparison of the four study species, using permutational multivariate analysis of homogeneity of group dispersions or variances (PERMDISP, Anderson, 2006) to account for differences between them (***)highly significant).

Species _{ij}	<i>Alopias</i> spp.	<i>G. galeus</i>	<i>S. zygaena</i>
<i>Alopias</i> spp.	-		
<i>G. galeus</i>	0.331	-	
<i>S. zygaena</i>	0.213	0.096	-
<i>M. japonica</i>	0.02**	0.605	<0.01***

south (3.65 and 2.88, respectively) were among those published by Sampson *et al.* (2010) in the Gulf of California. These results might suggest a similar diet for *M. japonica* along the Eastern Pacific. The trophic positions of *G. galeus*, *Alopias* spp. and *S. zygaena* found in this study are in the range of values found in other studies of the eastern Pacific (Castañeda & Sandoval, 2004; Galván-Magaña *et al.*, 2013; Li *et al.*, 2016) and of the north-eastern Atlantic for *G. galeus* (Ellis *et al.*, 1996).

Given the combined results of the SIBER routine, the Bayesian community metrics and the PERMANOVA and PERMDISP assessments, there is an indication of a certain degree of niches overlap and trophic redundancy, especially between the three shark species. However, given the migratory nature and the

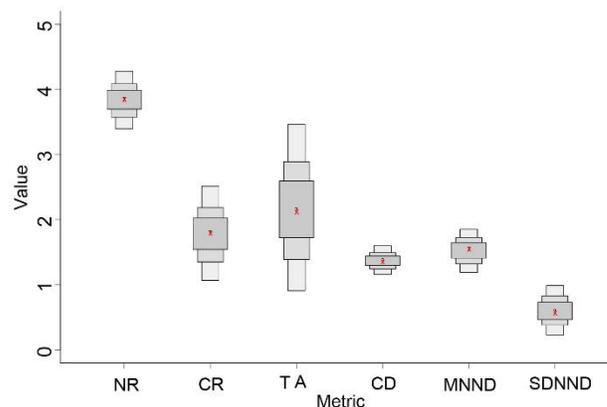


Figure 3. Resultant uncertainty in the six community-wide metrics of trophic structure (Layman *et al.*, 2007) for the five species of consumers, calculated using Bayesian inference. Black dots represent each mode, and grey boxes the credible intervals for 50%, 75%, and 95%, from dark to light, respectively (Jackson *et al.*, 2011). Red crosses show the true population values based on a maximum likelihood estimate. NR: range, CR: $\delta^{13}\text{C}$ range, TA: total area, CD: distance to centroid, MNND: mean nearest neighbour distance and, SDNND: standard deviation of MNND.

slow turnover rates in the muscle tissue of all four species (MacNeil *et al.*, 2005; Logan & Lutcavage, 2010; Malpica-Cruz *et al.*, 2012), it is difficult to address remaining questions on ecological niches and spatial isotopic gradients. This community's isotopic

niches might also be shared with another top- and meso-predators, not included in this study. Increasing the number of species assessed, increasing sample sizes, focusing on all sizes and both sexes, as well as covering larger areas and longer time periods, will shed light on questions dealing with both inter- and intra-specific variations. Furthermore, isotopic niche studies should be compared to each other in terms of SEAC and the uncertainty surrounding such values, based on Bayesian inference and probability distributions.

In order to better understand the relationship between resource use and interactions between different elasmobranch species, further work should focus on analyzing isotope values of principal prey species and tracking individuals toward gathering more precise information on distribution and movement patterns.

ACKNOWLEDGMENTS

We thank the fishermen who participated in this study. We also thank Mariela Pajuelo and Sebastián López, for all the time they dedicated to comment on the methodology and manuscript. This study was funded by FINCyT (Contrato N° 369 PIBA 2014) and the DEFRA Darwin Initiative.

REFERENCES

- Alfaro-Shigueto, J., J.C. Mangel, M. Pajuelo, P.H. Dutton, J. Seminoff & B.J. Godley. 2010. Where small can have a large impact: structure and characterization of small-scale fisheries in Peru. *Fish. Res.*, 106: 8-17.
- Alfaro-Cordova, E., A. Del Solar, J. Alfaro-Shigueto, J.C. Mangel, B. Diaz, O. Carrillo & D. Sarmiento. 2017. Captures of manta and devil rays by small-scale gillnet fisheries in northern Peru. *Fish. Res.*, 195: 28-36.
- Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.*, 26: 32-46.
- Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62: 245- 253.
- Baum, J.K. & B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.*, 78(4): 699-714.
- Baum, J.K., R.A. Myers, D.G. Kehler, B. Worm, S.J. Harley & P.A. Doherty. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, 299: 389-392.
- Borrell, A., A. Aguilar, R.P. Kumarran & L. Cardona. 2011. Trophic ecology of elasmobranchs caught off Gujarat, India, as inferred from stable isotopes. *ICES J. Mar. Sci.*, 68(3): 547-554.
- Castañeda, J. & L. Sandoval. 2004. Hábitos alimentarios de los tiburones martillo *Sphyrna lewini* y *Sphyrna zygaena* en el Pacífico Ecuatoriano. M.Sc. Thesis, Universidad Jorge Tadeo Lozano, Bogota, 138 pp.
- Couturier, L.I.E., A.D. Marshall, F.R.A. Jaime, T. Kashiwagi, S.J. Pierce, K.A. Townsend, S.J. Weeks, M.B. Bennett & A.J. Richardson. 2012. Biology, ecology, and conservation of the Mobulidae. *J. Fish Biol.*, 80: 1075-1119.
- Dulvy, N.K., S.L. Fowler, J. Musick, R.D. Cavanagh, M. Kyne, L.R. Harrison, J.K. Carlson, L.N.K. Davidson, V. Sonja & W.T. White. 2014. Extinction risk and conservation of the world's sharks and rays. *eLife*, 3: 1-35. doi: 10.7554/eLife.00590.
- Dulvy, N.K., J.K. Baum, S. Clarke, L.J.V. Compagno, E. Cortes, A. Domingo, S. Fordham, S. Fowler, M.P. Francis, C. Gibson, J. Martinez, J.A. Musick, S. Soldo, J.D. Stevens & S. Valent. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquat. Conserv.*, 18: 459-482.
- Ellis, J.R., M.G. Pawson & S.E. Shackley. 1996. The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. *J. Fish Biol.*, 76(1): 80-106.
- Espinoza, P. 2014. Trophic dynamics in the northern Humboldt Current System: insights from stable isotopes and stomach contents. Post-doctoral Thesis, Université de Bretagne Occidentale, Plouzané, 159 pp.
- Fowler, S. 2014. The conservation status of migratory sharks. UNEP/CMS Secretariat, Bonn, 30 pp.
- Fry, B. 2006. Stable isotope ecology. Springer, New York, 316 pp.
- Galván-Magaña, F., C. Polo-Silva, S.B. Hernandez-Aguilar, A. Sandoval-Londoño, M.R. Ochoa-Díaz, N. Aguilar-Castro, D. Castañeda-Suárez, A. Cabrera-Chávez-Costa, A. Baigorri-Santacruz, Y.E. Torres-Rojas & L.A. Abitia-Cárdenas. 2013. Shark predation on cephalopods by sharks in the Mexican and Ecuadorian Pacific Ocean. *Deep-Sea Res. II*, 95: 52-62.
- Gonzalez-Pestana, A., C. Kouri & X. Velez-Zuazo. 2014. Shark fisheries in the Southeast Pacific: A 61-year analysis from Peru. *F1000 Res.*, 3: 164.
- Hussey, N.E., M.A. MacNeil, J.A. Olin, B.C. McMeans, M.J. Kinney, D.D. Chapman & A.T. Fisk. 2012. Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. *J. Fish Biol.*, 80: 1449-1484.
- Jackson, A.L., R. Inger, A.C. Parnell & S. Bearhop. 2011. Comparing isotopic niche widths among and within

- communities: SIBER - Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.*, 80: 595-602.
- Kim, S.L., D.R. Casper, F. Galván-Magaña, R. Ochoa-Díaz, S.B. Hernández-Aguilar & P.L. Koch. 2012. Carbon and nitrogen discrimination factors for elasmobranch soft tissues based on a long-term controlled feeding study. *Environ. Biol. Fish.*, 95: 37-52.
- Layman, C.A., D.A. Arrington, C.G. Montaña & D.M. Post. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecol. Soc. Am.*, 88: 42-48.
- Li, Y., Y. Zhang & X. Dai. 2016. Trophic interactions among pelagic sharks and large predatory teleosts in the northeast central Pacific. *J. Exp. Mar. Bio. Ecol.*, 483: 97-103.
- Li, Y., N.E. Hussey, Y. Zhang & X. Dai. 2015. Urea and lipid extraction treatment effects on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in pelagic sharks. *Rapid Commun. Mass Sp.*, 30: 1-8.
- Logan, J.M. & M.E. Lutcavage. 2010. Stable isotope dynamics in elasmobranch fishes. *Hydrobiologia*, 644: 231-244.
- Logan, J.M., T.D. Jardine, T.J. Miller, S.E. Bunn, R.A. Cunjak & M.E. Lutcavage. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modeling methods. *J. Anim. Ecol.*, 77: 838-846.
- MacNeil, M. A., G. B. Skomal & A.T. Fisk. 2005. Stable isotopes from multiple tissues reveal diet switching in sharks. *Mar. Ecol. Progr. Ser.*, 302: 199-206.
- Malpica-Cruz, L., S.H. Herzka, O. Sosa-Nishizaki & J.P. Lazo. 2012. Tissue-specific isotope trophic discrimination factors and turnover rates in a marine elasmobranch: empirical and modelling results. *Can. J. Fish. Aquat. Sci.*, 69: 551-564.
- Michener, R. & K. Lajtha. 2007. Stable isotopes in ecology and environmental science. Blackwell Publishing, Oxford, 526 pp. <http://doi.org/10.1002/9780470691854>.
- Michener, R. & D.M. Schell. 1994. Stable isotope ratios as tracers in marine aquatic food webs. In: K. Lajtha & R. Michener (eds.). *Stable isotopes in ecology and environmental science*. Blackwell Scientific, London, pp. 138-157.
- Newsome, S.D., C. Martinez del Rio, S. Bearhop & D.L. Phillips. 2007. A niche for isotopic ecology. *Front. Ecol. Environ.*, 5: 429-436.
- Polo-Silva, C., S.D. Newsome, F. Galván-Magaña, M. Grijalba-Bendeck & A. Sanjuan-Muñoz. 2013. Trophic shift in the diet of the pelagic thresher shark based on stomach contents and stable isotope analyses. *Mar. Biol. Res.*, 9(10): 958-971.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83: 703-718.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing. [<http://www.R-project.org>]. Reviewed: 10 October 2016.
- Sampson, L., F. Galván-Magaña, R. De Silva-Dávila, S. Aguiniga-García & J.B. O'Sullivan. 2010. Diet and trophic position of the devil rays *Mobula thurstoni* and *Mobula japanica* as inferred from stable isotope analysis. *J. Mar. Biol. Assoc. U.K.*, 90: 969-976.
- Shaw, A.L., B.S. Frazier, J.R. Kucklick & G. Sancho. 2016. Trophic ecology of a predatory community in a shallow-water, high-salinity estuary assessed by stable isotope analysis. *Mar. Coast. Fish.*, 8: 46-61.
- Worm, B., B. Davis, L. Kettener, C.A. Ward-Paige, D. Chapman, M.R. Heithaus, S.T. Kessel & S.H. Gruber. 2013. Global catches, exploitation rates, and rebuilding options for sharks. *Mar. Policy*, 40: 194-204.

Received: 16 December 2016; Accepted: 24 November 2017