

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/346613836>

Diet, trophic interactions and possible ecological role of commercial sharks and batoids in northern Peruvian waters

Article in *Journal of Fish Biology* · December 2020

DOI: 10.1111/jfb.14624

CITATIONS

0

READS

142

14 authors, including:



Adriana Gonzalez Pestana

Pro Delphinus NGO

28 PUBLICATIONS 75 CITATIONS

[SEE PROFILE](#)



Eduardo Segura-Cobena

Universidad Católica de la Santísima Concepción

5 PUBLICATIONS 9 CITATIONS

[SEE PROFILE](#)



Víctor Moscoso

Universidad Científica del Sur

4 PUBLICATIONS 41 CITATIONS

[SEE PROFILE](#)



Joanna Alfaro Shigueto

ProDelphinus

127 PUBLICATIONS 2,508 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Trophic ecology of the most captured sharks and rays in northern Peru [View project](#)



Marine mammal conflict with fisheries [View project](#)

Diet, trophic interactions and possible ecological role of commercial sharks and batoids in northern Peruvian waters

Adriana Gonzalez-Pestana¹, Jeffrey C. Mangel^{1,2}, Eliana Alfaro-Córdova^{1,3}, Nicolas Acuña-Perales^{1,4}, Francisco Córdova-Zavaleta^{1,5}, Eduardo Segura-Cobena^{1,6}, Diego Benites⁷, Maximiliano Espinoza⁷, Javier Coasaca-Céspedes³, Astrid Jiménez^{1,7}, Sergio Pingo^{1,7}, Victor Moscoso³, Joanna Alfaro-Shigueto^{1,3*}, Pepe Espinoza^{3,8}

¹ ProDelphinus. Jose Galvez 780, Lima 18, Peru

² Centre for Ecology and Conservation, School of Biosciences, University of Exeter. Cornwall Campus, Penryn, Cornwall TR10 9EZ, United Kingdom

³ Carrera de Biología Marina, Facultad de Ciencias Veterinarias y Biológicas, Universidad Científica del Sur. Panamericana Sur, Km 19, Lima, Peru

⁴ Universidad Ricardo Palma, Av. Benavides 5440, Surco, Lima, Peru

⁵ Universidad Nacional Agraria La Molina, Av. La Molina. Lima, Perú

⁶ Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Alonso de Ribera 2850, Concepción, Chile.

⁷ Universidad Nacional de Piura Urb. Miraflores s/n, Castilla, Piura Perú⁵

⁸ Instituto del Mar del Perú. Esquina Gamarra con General Valle s/n, Chucuito, Callao, Peru

*corresponding author: Joanna Alfaro-Shigueto, Universidad Científica del Sur, Panamericana Sur, Km 19, Lima, Peru, jalfaros@ucientifica.edu.pe

Funding: Fondo para la Innovación, la Ciencia y la Tecnología (PIBA-369-2014), Rufford Foundation, Whitney Fund for Nature, and Darwin Initiative.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1111/jfb.14624](https://doi.org/10.1111/jfb.14624)

ABSTRACT

The Peruvian sea represents one of the most productive ocean ecosystems and possesses one of the largest elasmobranch fisheries in the Pacific Ocean. Ecosystem-based management of these fisheries will require information on the trophic ecology of elasmobranchs. This study aimed to understand the diet, trophic interactions and the role of nine commercial elasmobranch species in northern Peru through the analysis of stomach contents. A total of 865 non-empty stomachs were analyzed. Off northern Peru, elasmobranchs function as upper-trophic-level species consuming 78 prey items, predominantly teleosts and cephalopods. Two distinctive trophic assemblages were identified: (1) sharks (smooth hammerhead shark *Sphyrna zygaena*, thresher shark *Alopias* spp. and blue shark *Prionace glauca*) that feed mainly on cephalopods in the pelagic ecosystem; and (2) sharks and batoids (Chilean eagle ray *Myliobatis chilensis*, humpback smooth-hound *Mustelus whitneyi*, spotted houndshark *Triakis maculata*, Pacific guitarfish *Pseudobatos planiceps*, copper shark *Carcharhinus brachyurus*, and school shark *Galeorhinus galeus*) that feed mainly on teleosts and invertebrates in the benthonic and pelagic coastal ecosystem. This study reveals for the first time the diet of *T. maculata* and the importance of elasmobranchs as predators of abundant and commercial species (i.e. Jumbo squid *Dosidicus gigas* and Peruvian anchovy *Engraulis ringens*). The results of this study can assist in the design of an ecosystem-based management for the northern Peruvian sea and the conservation of these highly exploited, threatened or poorly understood group of predators in one of the most productive marine ecosystems.

Keywords: diet, ecosystem-based management, elasmobranch, Humboldt, predators, rays, trophic

1. INTRODUCTION

Sharks and batoids are important components of the marine ecosystem as they play important roles as top predators and mesopredators, regulating prey dynamics through direct predation by consumption and also indirectly by modifying prey behavior and physiology (e.g., Bizzarro *et al.*, 2017; Heithaus *et al.*, 2008; Rasher *et al.*, 2017; Sherman *et al.*, 2020; Vaudo & Heithaus *et al.*, 2011). Defining the roles of sharks and batoids and understanding their trophic relationships is essential for understanding ecosystem dynamics (e.g. biological controllers, bioturbation) and predicting anthropogenic (e.g., fishing) or environmental (e.g. climate change or ENSO) impacts in the structure and function of ecosystems (e.g. trophic downgrading, mesopredator release, resource limitation) (Ajemian, 2011; Ainsworth *et al.*, 2011; Bizzarro *et al.*, 2017; Chin *et al.*, 2010; Cisneros *et al.*, 2018; Estes *et al.*, 2011; Heithaus *et al.*, 2008, 2010; Löwemark, 2015; Marshall *et al.*, 2016; Martins *et al.*, 2018; Myers *et al.*, 2007; Ortega-Cisneros *et al.*, 2018; Sherman *et al.*, 2020; Schindler *et al.* 2002; Stevens *et al.*, 2000).

Many elasmobranch populations have declined because of unsustainable catch and bycatch in fisheries (Camhi *et al.*, 2008; Davidson *et al.*, 2016; Ward & Myers, 2005), and as a result they are among the most threatened vertebrate groups (Bräutigam *et al.*, 2015). Peru historically reports the highest accumulated landings for sharks in the Pacific, and for batoids in the eastern Pacific Ocean (Gonzalez-Pestana *et al.*,

2016a,b); yet fisheries management and enforcement is limited (Alfaro-Shigueto *et al.*, 2010; Doherty *et al.*, 2014; Gonzalez-Pestana *et al.*, 2016 a,b; Hilborn & Ovando 2014). Economically and socially, this fishery is important for the country (Alfaro-Shigueto *et al.*, 2010; Christensen *et al.*, 2014; Doherty *et al.*, 2014) and also is globally significant, ranking within the top 20 major shark fishing countries in the last decade (Dulvy *et al.*, 2017; Okes & Sant, 2019).

In Peru, elasmobranchs are an important component for ecosystem-based fishery management (EBFM) since they are commercially and ecologically important with declining populations for many species (Powers & Monk, 2010). One EBFM goal is to ensure that the capture of commercial species does not seriously affect food web structure and its dynamics or functionality; therefore, in developing EBFM, linkages between ecosystem components need to be understood, such as trophic structure, predator–prey relationships, and interactions between fisheries and other top consumers (Arkema *et al.*, 2006; Link, 1999; Livingston *et al.*, 2005; Warzybok *et al.*, 2018). Concerning batoids fisheries, implementation of EBFM is severely hampered by the paucity of data compared to other data rich, commercially important fish stocks (Bizzarro *et al.*, 2017; Hilborn & Ovando, 2014). Furthermore, elasmobranchs research in the southeastern Pacific is lagging compared to most other marine regions (Ducatez, 2019). For example, trophic relationship studies of the Peruvian marine ecosystem do not include elasmobranchs as upper trophic-level species (reviewed in Espinoza, 2014).

Limited information exists on the diets and trophic interactions of elasmobranchs and the roles they play in Peruvian waters. Of the 103 elasmobranch species registered in

Peru, 66 species are sharks (32 interact with fisheries) and 37 species are batoids (23 interact with fisheries) (Cornejo *et al.*, 2015; Gonzalez-Pestana *et al.*, 2016a,b; Last *et al.*, 2016). There is information on diet composition for only eleven of these species (Coasaca-Céspedes *et al.*, 2018; Córdova-Zavaleta *et al.*, 2018; Gonzalez-Pestana *et al.*, 2017, 2018; Samame *et al.*, 1989; Segura-Cobena, 2017; Silva-Garay *et al.*, 2018) and most of these studies only assessed one species. The aim of this study was to understand trophic interactions, identify trophic assemblages and predict the role of nine commercially important elasmobranch species off northern Peru through stomach content analysis, including six of the nine most caught elasmobranch species in Peru.

2. MATERIALS AND METHODS

2.1. Data and sample collection

Nine elasmobranch species were sampled (seven species of sharks and two species of batoids) (Table 1) between January 2015 and August 2016, from four small-scale gillnet fishery landing points located in northern Peru: Zorritos, Mancora, San Jose and Salaverry (Figure 1). Peruvian small-scale fisheries (SSF) are defined as containing vessels with a maximum capacity of 32.6m³ Gross Registered Tonnage, up to 15 meters of length and operate predominantly using manual work (El Peruano, 2001). SSF operate in coastal and offshore locations reaching international waters (FAO, 2010; Mason *et al.*, 2019). SSF is the only fishery that targets elasmobranchs in Peru (Alfaro-Shigueto *et al.*, 2010; Bartholomew *et al.*, 2018; Doherty *et al.*, 2014; Gonzalez-Pestana *et al.*, 2016a, b; Mason *et al.*, 2019). Six species included in this study are among the nine most caught elasmobranch species which represent 80% of the total Peruvian elasmobranch catch (Table 1, Gonzalez-Pestana *et al.*, 2016 a,b).

Within Peruvian SSF, gillnets represent one of the main capture methods for elasmobranchs (Alfaro-Shigueto *et al.*, 2010; Bartholomew *et al.*, 2018; Gonzalez-Pestana *et al.*, 2016a).

Elasmobranchs were identified, sexed and measured (total length [TL] for sharks and guitarfishes and disc width [DW] for eagle rays) (Table 1). Stomachs were extracted and preserved in a 10% formalin solution.

The Peruvian marine ecosystem is subjected to the El Niño Southern Oscillation (ENSO) (Fiedler, 2002). The study period coincided with a moderate El Niño event (average positive anomaly of sea surface temperature = $1.18^{\circ}\text{C} \pm 0.84$) according to El Niño Coastal Index (<http://www.met.igp.gob.pe>).

2.2. Analysis of stomach contents

Stomach contents were analyzed at the Marine Biology Laboratory of the Universidad Científica del Sur in Lima, Peru. Prey items were identified to the lowest possible taxon, counted and weighted. For the identification of teleosts and cephalopods, and their hard parts (i.e. otoliths and beaks), identification guides were used: Chirichigno & Cornejo (1998), García-Godos (2001), Lu & Ickeringill (2002), Xavier & Cherel (2009), and Acuña-Perales *et al.* (2020). Cephalopod beaks were used to reconstruct total mass at ingestion, using regression equations (Lu & Ickeringill, 2002). For the identification of crustaceans and mollusks we used Ramirez *et al.*, (2003) and Moscoso (2013). Unidentified prey items, rare items (e.g. rocks, snails) and parasites (e.g. isopoda) were excluded from subsequent analyses.

Diet was quantified using percent by number (%N), percent by weight (%W), and percent by frequency of occurrence (%F) of prey (Hyslop, 1980). Two indexes were calculated: index of relative importance (IRI) and prey-specific index of relative importance (PSIRI). The index of relative importance (IRI) was calculated as $IRI = \%O (\%N + \%W)$. Then it was divided by the total IRI for all items to get the index of relative importance on a percent basis (%IRI; Cortés, 1997). 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 allowing more reliable comparisons between studies because its values are not dependent upon taxonomic level or prey categories (Brown *et al.*, 2012). First, an index of prey-specific abundance (%P_{Ai}) was calculated: $\%P_{Ai} = \Sigma \%A_{ij} / n_i$, where %A_{ij} is the abundance (by counts [%PN_i] or weights [%PW_i]) of prey category i in stomach sample j and n_i is the number of stomachs containing prey i. Then the %PSIRI was calculated: $[\%FO_i \times (\%PN_i + \%PW_i)] / 2$. We present the results from IRI because these could be used for comparisons with other studies.

2.3. Statistical analysis

For further analysis all prey items were pooled into ten main groups: (1) teleosts, (2) shrimps (Penaeidae), (3) crabs (Brachyura), (4) stomatopods (Stomatopoda), (5) cephalopods (Cephalopoda), (6) gastropods (Gastropoda), (7) bivalves (Bivalvia), (8) annelids (Polychaeta), (9) marine mammals and (10) other crustaceans that could not be identified at a more specific level.

Randomized cumulative prey curves were constructed to examine trophic diversity at taxa level and determine if sample sizes were sufficient to describe the full diet (Ferry & Caillet, 1996). The mean cumulative number of prey taxa present in each sample was then plotted against the randomly pooled number of stomach samples. The presence of an asymptotic relationship indicates that the number of stomachs analyzed is sufficient to represent the diet, and that the increase of the sample beyond the point of curve stabilization would cause little further increase in the measured trophic diversity. A slope value less than 0.1 indicates a good representation of diet (Soberón & Llorente, 1993).

To evaluate trophic niche width we used Levin index (B_i') based on %N values. The index 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).

We calculated the trophic position (TP) based on the %PSIRI values of the prey species presented in the stomach content. We used the following equation: $TP = 1 + (\sum DC_{ij} \times TP_j)$ (Christensen & Pauly 1992) where DC_{ij} is the composition of the diet in which (j) is the proportion of preys in the diet of the predator (i) and TP_j is the trophic position of the preys. The trophic positions of the prey items were taken from Espinoza (2014) which presents values from the Peruvian sea and from Cortés (1999) when local values were not reported.

To identify trophic assemblages of elasmobranch species, we performed the recursive partitioning model (Breiman *et al.*, 1984; Hothorn *et al.*, 2006a) based on the numeric

abundance of prey (%N). A conditional inference tree was generated which identifies distinctive trophic groups of elasmobranchs and the distribution of their prey groupings. This is a non-parametric method that uses a partitioning algorithm to estimate a series of binary decision rules to divide the data into smaller homogeneous subgroups in an optimal way. The p-value is used to determine where splitting is no longer valid. Typically, splitting is accepted at $p < 0.1$ (e.g. Nagy *et al.*, 2010). We applied the prune back procedure to cut the overlarge tree and achieve the best prey composition at each terminal node.

We used the permutational multivariate analysis of variance (PERMANOVA) to determine if a significant difference existed in the overall grouping of the conditional inference tree (Anderson, 2001). If the PERMANOVA pseudo-F was significant ($p < 0.05$), then the permutation analysis of multivariate dispersions (PERMDISP) procedure was applied to confirm the observed differences (Anderson, 2006). Both PERMANOVA and PERMDISP were applied to a Bray-Curtis dissimilarity matrix of numeric abundance of prey (%N) from the diets of nine elasmobranch species. Afterward, the similarity percentage routine (SIMPER) was applied to determine the most typical prey for each grouping level (Clarke, 1993) based on the percentage of contribution of each prey within a group and the dissimilarity between two groups.

The calculations were performed using the R v3.6.2 (R Core Team, 2019) with the packages *rpart* (Therneau *et al.*, 2012), and *party* (Hothorn *et al.*, 2006b) for the classification tree, and *vegan* (Oksanen *et al.*, 2019) for PERMANOVA, PERMDISP and SIMPER tests.

2.4. Ethical Statement

The care and use of experimental animals complied with Ministry of Production (PRODUCE for its acronym in Spanish) animal welfare laws, guidelines and policies as approved by PRODUCE and the TUPA 023.1.

3. RESULTS

We analyzed a total of 865 stomach contents from nine elasmobranch species (Table 1). The cumulative prey curves reached full asymptotic stabilization for all species, except for *Triakis maculata* and *Myliobatis chilensis* (Figure 2). Therefore, for seven elasmobranch species, sufficient stomach contents were examined to adequately and reliably describe their diet. For the other two species, the slopes of their cumulative prey curves (*T. maculata* = 0.03 and *M. chilensis* = 0.01) were slightly higher than the suggested by Soberón & Llorente (1993) which is < 0.01 . Thus, the results for these two species should be interpreted with caution.

We identified 78 prey items at a species or family level: 26 species/families of teleosts, one species of chondrychtyan, 17 species of cephalopods, four species/families of gastropods, three species/families of bivalves, 25 species or families of crustaceans, one family of annelids and one family of marine mammals. Elasmobranch species sampled preyed mainly on teleosts and cephalopods (Figure 3).

Overall, the trophic niche width was narrow with a low Levin index value (< 0.6) (Table 2). The highest value corresponds to *Pseudobatos planiceps* (0.62) - the least specialized - and the lowest value to *Prionace glauca* (0.06) - the most specialized

species. The average trophic position was 4.2 with a range of 4.4 for both *Alopias* spp. and *C. brachyurus*, and 3.8 for *P. planiceps*. The sharks and batoids assessed in this study were predominantly tertiary consumers (TP > 4), except for *P. planiceps* that is a secondary consumer (TP < 4).

Based on the conditional inference tree, we identified two main distinctive trophic assemblages: (1) *Sphyrna zygaena*, *Alopias* spp. and *P. glauca*, and (2) *M. chilensis*, *Mustelus whitneyi*, *P. planiceps*, *T. maculata*, *Carcharhinus brachyurus*, and *Galeorhinus galeus*. PERMANOVA (pseudo-F= 27.64, p = 0.001) and PERMDISP (pseudo-F = 58.86, p = 0.001) showed significant differences between these two trophic assemblages. According to SIMPER, these two trophic assemblages presented an average dissimilarity of 87.6% (Table 3). Accordingly, the prey items which most contributed to dissimilarity between these two groups were cephalopods (54.5%), teleosts (20.6%) and crabs (5.3%) (Table 3).

The first group is composed of sharks that fed mainly on cephalopods and lesser on teleosts (Figure 3) in the pelagic and mostly oceanic region. This group presents higher average similarity percentages (42.8%) compared with the second group (Table 3). Cephalopods were the prey item that most contributed to their diet (95.6%) (Table 3). The most important cephalopod prey species was *Argonauta* spp. (16% of PSIRI) for *P. glauca*, jumbo squid *Dosidicus gigas* (d' Orbigny, 1835) (30% of PSIRI) and Patagonian squid *Doryteuthis gahi* (d' Orbigny, 1835) (31% of PSIRI) for *S. zygaena*, and *D. gigas* (64% of PSIRI) for *Alopias* spp. (Table 4). *P. glauca* was the only species of this group that also fed on crustaceans and marine mammals (Table

4). This group presented on average a higher trophic position of 4.3 ± 0.1 and a lower trophic niche of 0.21 ± 0.15 than the second trophic assemblage.

The second group is composed of sharks and batoids that feed mainly on pelagic and demersal teleosts and on benthonic invertebrates (i.e. mollusks, crustaceans, and annelids) in the coastal region (Figure 3). This group presents an average similarity of 26.2% (Table 3). Teleosts contributed most to the diet of this trophic assemblage (81.2%), followed by crabs (11.1%) (Table 3). *P. planiceps* was the only species that fed on shrimps (14% of PSIRI); while *T. maculata* was the only species that fed on chondrychtyans (i.e. *Urotrygon* sp.) (Table 4). The Peruvian anchovy *Engraulis ringens* (Jenyns, 1842) was an important prey species for *C. brachyurus*, *M. whitneyi* and *M. chilensis*, with PSIRI values of 43, 22, 20%, respectively (Table 4). *G. galeus* was the species that preyed the most on Peruvian hake *Merluccius gayi* (Guichenot, 1848) (10.7% of PSIRI) (Table 4). Of all elasmobranchs, *P. planiceps* was the most important consumer of benthic invertebrates (72% of PSIRI) (Table 4). This group presented on average a lower trophic position of 4.12 ± 0.19 and a higher trophic niche of 0.38 ± 0.20 than the first trophic assemblage.

4. DISCUSSION

4.1. Elasmobranchs: predators of commercial and abundant species

Peru has one of the most productive marine ecosystems in the world (Chavez & Messie, 2009; Pennington *et al.*, 2006) which sustains large populations of elasmobranch prey species. The Peruvian anchovy is a dominant species in the Peruvian marine ecosystem (Salvatecci *et al.*, 2019). Ecologically and economically,

Accepted Article

this species is considered the most important pelagic fish species in the Peruvian marine ecosystem (Espinoza and Bertrand, 2008) and an important prey item for seabirds, teleost fish, marine mammals (reviewed in Pauly *et al.*, 1989; Espinoza, 2014), and in this study we propose elasmobranchs. As a result, the Peruvian anchovy is a key forage prey in the NHC-LME (Checkley *et al.*, 2017). In this study, we highlight its importance in the diets of *C. brachyurus*, *M. whitneyi*, and *M. chilensis*. Recently, off the north and central coast of Peru, the importance of this small pelagic schooling fish in the diet of batoids has been established (i.e. *Myliobatis chilensis*, *Myliobatis peruvianus*, *P. planiceps*, and Diamond stingray *Hypanus dipterurus*, Jordan & Gilbert, 1880) (86, 17, 7, 14 of %PSIRI, respectively) (Segura-Cobena, 2017; Manrique & Mayaute, 2017; Silva-Garay *et al.*, 2018). For *M. whitneyi*, Samame *et al.* (1989) established that off northern Peru this shark is an important predator of Peruvian anchovy. For *C. brachyurus*, studies in South Africa and Argentina have established that this species mainly feeds on small pelagic schooling fish, such as anchovy (Cliff & Dudley, 1992; Lucifora *et al.*, 2009; Smale, 1991). In Peru, for the first time, the importance of *C. brachyurus* as an important predator of Peruvian anchovy is demonstrated. The Peruvian anchovy might also be an important prey for *S. zygaena*.

In the NHC-LME, the abundance and distribution of the Peruvian anchovy is affected by ENSO (Fiedler, 2002; Chavez *et al.*, 2003). During warmer El Niño events this pelagic fish concentrates closer to the coast (reviewed in Bertrand *et al.*, 2004) where it finds small-scale temporal and spatial local refuges with conditions allowing their survival (Bakun & Broad 2003; Bertrand *et al.*, 2004). Therefore, El Niño events influences the availability of the Peruvian anchovy for coastal elasmobranchs predators. Castañeda (1994) found a high consumption of Peruvian anchovy during

an El Niño event (1991-1992) in northern Peru by *M. chilensis*; while in the years before and after this El Niño event its main prey was crustaceans. For *S. zygaena*, in northern Peru, Castañeda (2001) reported that their diet was dominated by anchovy during cold La Niña events and in this study this shark species had a low consumption of anchovy during a warm period. Future studies, could help further clarify the diets of these elasmobranch predators under different ENSO conditions.

Cephalopods were an important prey group for the first trophic assemblage group. Squids have important ecological roles, both as prey and predators, functioning as elements for energy transfer within the marine food web (Coll *et al.*, 2013; Staudinger *et al.*, 2013). In this study, the jumbo squid was one of the most important prey for pelagic sharks, especially for *S. zygaena* and *Alopias* spp. This is the most abundant nektonic squid in the ocean and has an important ecological role in pelagic ecosystems in the eastern Pacific (Nigmatullin *et al.*, 2001; Rosas-Luis *et al.*, 2008). It represents an abundant feeding resource for high-trophic-level predators such as fish, marine mammals, seabirds (Gálvan-Magaña *et al.*, 2013; Nigmatullin *et al.*, 2001) and sharks. In the southeastern Pacific waters of Chile and Ecuador, pelagic sharks and billfishes have been identified as important predators of jumbo squid (Gálvan-Magaña *et al.*, 2013; Ibáñez *et al.*, 2004; López *et al.*, 2010; Llor-Andrade *et al.*, 2017; Polo-Silva *et al.*, 2004; Rosas-Luis *et al.*, 2015,). In the Peruvian marine ecosystem, many studies have highlighted the importance of jumbo squid as a predator (e.g., Alegre *et al.*, 2014), but the sperm whale *Physeter microcephalus* L. (Clarke *et al.*, 1998), and, more recently, *S. zygaena* and *Alopias* spp. (Gonzalez-Pestana *et al.*, 2017, 2018) have been identified as important predators of jumbo squid. This study thus highlights the importance of pelagic sharks as predators of jumbo squid in an area that presents

one of its highest global concentrations (Anderson & Rodhouse, 2001; Nigmatullin *et al.*, 2001). Further studies should identify other predators of jumbo squid (e.g. billfishes, dolphinfish *Coryphaena hippurus* L.) in the Peruvian marine ecosystem, as shown in other regions in the Eastern Pacific (e.g., Tripp-Valdez *et al.*, 2015), in order to improve our understanding of higher-trophic relationships.

Studies have shown that as predators diminish worldwide, cephalopod biomass increases (Caddy & Rodhouse, 1998; Piatkowski *et al.*, 2001). Short-lived, fast-growing cephalopods might flourish with diminishing shark populations, triggering unknown cascading effects in pelagic ecosystems. The potential reduction in predation pressure on squids resulting from fisheries exploitation of their predators (Ward & Myers, 2005) might cause an increase in cephalopod biomass (Piatkowski *et al.*, 2001; Watters *et al.*, 2008, Bornatowski *et al.*, 2018). In northern Peru, the trophic assemblage of pelagic sharks is heavily exploited and include the shark species with the highest fishery landings in the country. It is possible, therefore, that a similar mechanism (e.g. predatory-release effect) could have been occurring here as well, although this will need to be elucidated through future studies.

The behavior and distribution patterns, as well as the levels of biomass of the jumbo squid can be modified during intense El Niño or La Niña events in the NHC-LME (Csirke *et al.*, 2018). In northern Peru, the distribution of the smooth hammerhead sharks varies according to ENSO conditions in which chlorophyll-a, as a proxy of prey availability, is an important predictor of species distribution (Gonzalez-Pestana, 2018). In this study period, pelagic sharks (especially *S. zygaena* and *Alopias* spp.) may have benefitted from ENSO moderate thermal conditions (-2 to +1.5), since jumbo squid are

more abundant under these conditions (Rosa *et al.*, 2013). These trophic interactions need to be assessed further under different ENSO scenarios.

4.2. Impact of fisheries in the conservation of elasmobranchs from an EBFM approach

In this study, many elasmobranch species preyed on commercial species (*i.e.*, Peruvian anchovy and jumbo squid). The Peruvian anchovy is the most heavily exploited fish in world history (FAO, 2020) mainly by Peru; while, the jumbo squid is the most caught squid in the world, of which Peru reports the second highest fishery landings (FAO, 2018, 2020). Fishing can impact the structure and function of marine ecosystems (Smith *et al.* 2011). For example, this fishery extraction could result in scarcity of their prey that could lead to unsatisfied energetic requirements of predators, thus impacting predator populations (Kaplan *et al.*, 2013; Warzybok *et al.*, 2018). Several studies have determined that the fishing of forage fish, such as anchovies, can have a negative effect on their predators, even under relatively low levels of depletion (Kaplan *et al.*, 2013; Smith *et al.* 2011).

Management measures should account for predator foraging needs in setting quotas for prey species (Corkeron 2006; Ruckelshaus *et al.*, 2008). Such approaches have been proposed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR 2006; Ruckelshaus *et al.*, 2008) and the International Council for the Exploration of the Seas (ICES, 2008) to retain prey allotments for predators. Hence, an EBFM approach in the NHC-LME must involve an explicit allocation of fishery quota for predator needs (Pikitch *et al.*, 2004; Link *et al.*, 2002). The Peruvian anchovy is considered a key low trophic level species by the Marine Stewardship

Council (MSC) Fishery Standard based on Smith *et al.*, (2011). The MSC Standard recommends that, in the case of these species, fisheries management should set higher biomass targets to account for forage needs of other predators in the ecosystem. This will enhance the sustainability of their predators particularly when their prey species constitute a high proportion of the biomass in the ecosystem or are highly connected in the food web (Smith *et al.* 2011; Zabel *et al.*, 2003).

In the NHC-LME, several studies have raised concerns and predicted the impacts of the Peruvian anchovy fishery on their predators, such as, seabirds and marine mammals (e.g., Jahncke *et al.*, 2004; Murphy, 1925; Tam *et al.*, 2010). Yet, the effects that this fishery has on elasmobranchs is unknown. The impact of the jumbo squid fishery on their predators is even more obscure, since this species has traditionally been classified only as a predator (e.g., Alegre *et al.*, 2014). This is especially worrisome for *S. zygaena*, *Alopias* spp., and *Mustelus whitneyi*, which are threatened shark species, that mainly prey on these two commercial species. Both species, Peruvian anchovy and jumbo squid, currently have fishing ordinance regulations (DS-005-2017-PRODUCE, DS-014-2011-PRODUCE) that include a fishing quota. In their calculations, they include the predation rate of sea birds and marine mammals (*i.e.*, sea lions). This fishery management could be improved by incorporating the predation rate of sharks and rays when estimating the fishery quota. Elasmobranch species have been largely ignored in the design and implementation of EBFM in the NHC-LME. Future research should model elasmobranch prey requirements to predict the quantities of anchovy and jumbo squid needed to maintain and recover these populations in the NHC-LME (e.g. Williams *et al.* 2011). These will be valuable information for the design of an EBFM approach in the NHC-LME.

4.3. Coastal elasmobranchs: habitat links and bioturbators

The second trophic assemblage group is composed of sharks and batoids that feed on teleosts and invertebrates in the coastal zone. Some of these species move between benthic and pelagic ecosystems to feed, such is the case for *M. chilensis* and *M. whitneyi*, endemic and abundant species off Peru and Chile that prey mainly on pelagic (i.e. Peruvian anchovy) and benthic (i.e. crabs and gastropods) species (Figure 3). The diets of both species are unique compare with their closest relatives, since an important component of their diets are pelagic species. Most smooth-hounds sharks (genus *Mustelus*) and eagle rays (family Myliobatidae) feed on benthonic and demersal species (Bizzarro *et al.*, 2017; Gray *et al.*, 1997; Jacobsen & Bennett, 2013; Navia *et al.*, 2006; Ponte *et al.*, 2016;). Eagle rays possess flattened, well developed tooth plates used for crushing hard-shell prey-item; similarly, smooth-hound sharks possess crushing-type dentition (Motta, 2004). This dentition is suitable for hard benthic prey (e.g., crustaceans) (Motta, 2004). However, the Triakidae family has been classified as pelagic based on its body form (Sternes & Shimada, 2020) and the swimming behaviour of eagle rays is a pectoral oscillatory locomotion which is found in species that live mostly in the water column in pelagic habitats (Rosenberger, 2001). We therefore conclude that these species prey on the benthic-demersal and pelagic ecosystem.

The ecological function of *M. chilensis* and *M. whitneyi* is related to their active movements between pelagic and benthic habitats (Lundberg & Moberg, 2003; Meyer & Schultz, 1985; Polis *et al.*, 1997; Sheaves, 2009). Studies of the movement patterns of Myliobatid rays have shown that cownose *Rhinoptera bonasus* (Mitchill, 1815) and

Accepted Article

spotted eagle rays *Aetobatus narinari* (Euphrasen, 1790) exhibit connectivity among several habitat types, including benthic habitats (Ajemian & Powers, 2014). Similarly, *M. chilensis* and *M. whitneyi* might play an important role transferring resources as mobile links between the benthonic and pelagic habitats, through predation, excretion and defecation (Schindler *et al.*, 1996; Vanni, 1996). For example, Vander Zanden & Vadeboncoeur (2002) has shown that fish linked pelagic and benthic food chains through cross-habitat foraging. This understanding represents a shift towards a more integrated, whole-ecosystem perspective (Vander Zanden & Vadeboncoeur, 2002). Future studies should determine if these predators connect ecosystems at short time scales (e.g., Cartamil *et al.*, 2003; Silliman & Gruber, 1999) or over long time periods through ontogenetic or long-range migrations (Ebert & Cowley, 2003).

In this study, elasmobranchs fed on benthic invertebrates: *P. planiceps* (72% of PSIRI), *M. chilensis* (52% of PSIRI), *M. whitneyi* (51% of PSIRI) and *T. maculata* (21% of PSIRI). Most of these invertebrates inhabit soft bottoms (i.e. sandy and muddy areas) (Carbajal-Enzian *et al.*, 2018; Moscoso, 2013). Batoids and houndsharks are among the most powerful excavators, using a variety of behaviours (e.g. jetting water and beating pectoral fins) to access prey resources (Myrick & Flessa, 1996; O'Shea *et al.*, 2012; Takeuchi & Tamaki, 2014). This process, known as bioturbation, can have a significant impact on the physical and biological habitat properties of the benthic ecosystem (Löwemark, 2015; O'Shea *et al.*, 2012), such as the density and distribution of benthic fauna (Dabruzzi *et al.*, 2013). For example, the lesser guitarfish *Acroteriobatus annulatus* (Müller & Henle, 1841) has been shown to consume up to 77% of the annual benthic invertebrate production of a lagoon in South Africa (Harris *et al.*, 1988).

Bioturbation can facilitate the penetration of oxygen into sediments (Gilbert *et al.*, 1995), affecting the nitrogen cycle (Kogure & Wada, 2005). Also, this process benefits other species by making accessible prey items that are excavated during foraging activities. For example, bioturbation of the southern stingray *Hypanus americanus* (Hildebrand & Schroeder, 1928) allowed bar jacks *Caranx ruber* (Bloch, 1793) to access resources that were otherwise unavailable (Kiszka *et al.*, 2015). Additional research could help further elucidate the specific contribution of batoids and houndsharks as bioturbators of the benthic ecosystem off northern Peru.

4.4. Conclusions and further steps

This study reveals for the first time the diet of *T. maculata*, and the diet of *C. brachyurus* and *G. galeus* in Peru. Elasmobranchs off northern Peru play a crucial role in the marine ecosystem as upper-trophic-level species, especially as predators of cephalopods and teleosts, channeling energy between lower and upper trophic positions. The trophic position of elasmobranchs (3.8 - 4.4) is similar to sea lions (4.8) and sea birds (4.5), whose diets has been extensively studied in the Peruvian marine ecosystem and are widely included in food web diagrams (reviewed in Espinoza, 2014). In the Peruvian marine ecosystem, elasmobranchs are rarely included in ecological models (e.g. Tam *et al.*, 2008; Taylor *et al.*, 2008) and those models that include them do so under a broad category (e.g. Guénette *et al.*, 2008). In this study, this diverse group of elasmobranchs occupies two distinct trophic assemblages with differential roles in the marine ecosystem. Trophic assemblages are used in ecological modelling to reduce complexity, since their designation assumes that all species within a group have similar ecological characteristics (Bizzarro *et al.*, 2017). Therefore, these

results can be useful for managers in designing ecosystem-based conservation and management actions in one of the most productive ocean ecosystems.

Acknowledgements. The authors thank the following institutions who funded this study: Fondo para la Innovación, la Ciencia y la Tecnología (PIBA-369-2014), Rufford Foundation, Whitney Fund for Nature, and Darwin Initiative. They thank Universidad Científica del Sur for facilitating the laboratories to examine the samples, specially to Aldo Indacochea. Special thanks to the fishers from San Jose, Mancora, Salaverry, and Zorritos that contributed with the sample collection. Also, thanks to José Carlos Xavier for helping us in identifying the squid's beaks.

Contributions

A. Gonzalez-Pestana led on research design, data collection and analysis, and manuscript preparation, N. Acuña-Perales, F. Córdova-Zavaleta, J. E. Segura-Cobena, D. Benites, M. Espinoza, J. Coasaca-Céspedes, A. Jiménez, S. Pingo, V. Moscoso assisted with data collection and analysis, E. Alfaro-Córdova assisted with research design, J. Mangel, J. Alfaro-Shigueto and Pepe Espinoza assisted with research design and manuscript preparation.

References

- Acuña-Perales, N., Córdova-Zavaleta, F., Arrese-Dávila, V., Torrejón-Zegarra, R. Rodríguez-Salazar, J., González-Pestana, A., Alfaro-Shigueto, & J., Mangel, J. C. 2020. Guía de identificación de picos de algunas especies de cefalópodos obtenidos en el Mar Peruano. Lima, Perú: ProDelphinus.
- Ainsworth, C. H., Samhuri, J. F., Busch, D. S., Cheung, W. W. L., Dunne, J., & Okey, T. A. (2011). Potential impacts of climate change on Northeast Pacific marine foodwebs and fisheries. *ICES Journal of Marine Science*, **68**, 1217–1229.
- Ajemian, M. J. (2011). *Foraging ecology of large benthic mesopredators: effects of Myliobatid Rays on shellfish resources*. (Doctoral thesis, University of South Alabama, United States of America). Retrieved from:
https://www.academia.edu/1824422/THE_UNIVERSITY_OF_SOUTH_ALABAMA_COLLEGE_OF_ARTS_AND_SCIENCES_FORAGING_ECOLOGY_OF_LARGE_BENTHIC_MESOPREDATORS
- Ajemian, M. J., & Powers, S. P. (2014). Towed-float satellite telemetry tracks large-scale movement and habitat connectivity of myliobatid stingrays. *Environmental Biology of Fishes*, **97**, 1067–1081.
- Alfaro-Shigueto, J., Mangel, J. C., Pajuelo, M., Dutton, P. H., Seminoff, J. A., & Godley, B. J. (2010). Where small can have a large impact: structure and characterization of small scale fisheries in Peru. *Fisheries Resheries*, **106** (1), 8–17.

Alegre, A., Ménard, F., Tafur, R., Espinoza, P., Argüelles, J., Maehara, V., Simier, M., & Bertrand, A. (2014). Comprehensive model of Jumbo squid *Dosidicus gigas* trophic ecology in the northern Humboldt Current system. *PLoS ONE* **9**(1), e85919.

Anderson, C. I. H., & Rodhouse, P. G. (2001). Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environments. *Fisheries Research*, **54**, 133–143.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Australian Ecology*, **26**, 32–46.

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, **62**, 245–253.

Arkema, K. K., Abramson, S. C., & Dewsbury, B. M. (2006). Marine ecosystem-based management: from characterization to implementation. *Frontiers in Ecology and the Environment*, **4**(10), 525–532.

Bakun, A., & Broad, K. (2003). Environmental ‘loopholes’ and fish population dynamics: comparative pattern recognition with focus on El Nino effects in the Pacific. *Fisheries Oceanography* **12**, 458–473.

Bartholomew, D. C., Mangel, J. C., Alfaro-Shigueto, J., Pingo, S., Jimenez, A., & Godley, B. J. (2018). Remote electronic monitoring as a potential alternative to on-board observers in small-scale fisheries. *Biological conservation*, **219**, 35-45.

Bizzarro, J. J., Carlisle, A. B., Smith, W. D., & Cortés, E. (2017). Diet composition and trophic ecology of Northeast Pacific Ocean sharks. *Advances in Marine Biology*, **77**, 111–148.

Bertrand, A., Segura, M., Gutiérrez, M. & Vasquez L. (2004). From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. *Fish and fisheries* **5**, 296-316.

Bornatowski, H., Angelini, R., Coll, M., Barreto, R.R., & Amorim, A.F. (2018). Ecological role and historical trends of large pelagic predators in a subtropical marine ecosystem of the South Atlantic. *Reviews in Fish Biology Fisheries*, **28**(1), 241–259.

Bräutigam, A., Callow, M., Campbell, I. R., Camhi, M. D., Cornish, A. S., Dulvy, N. K., Fordham, S. V., Fowler, S. L., Hood, A. R., McClennen, C., Reuter, E. L., Sant, G., Simpfendorfer, C.A. & Welch, D. J. (2015). Global Priorities for Conserving Sharks and Rays: A 2015–2025 Strategy.

Breiman, L., Friedman, J., Olshen, R., & Stone, C. (1984). *Classification and Regression Trees*. California: Wadsworth & Brooks/Cole Advanced Books & Software

Brown, C., Bizzarro, J. J., Cailliet, G. M., & Ebert, D. A. (2012). Breaking with tradition: redefining measures for diet description with a case study of the Aleutian skate *Bathyraja aleutica* (Gilbert 1896). *Environmental Biology of Fish*, **95**, 3–20.

Camhi, M. D., Lauck, E., Pikitch, E. K., et al. (2008). A global overview of commercial fisheries for open ocean sharks. In M. D. Camhi, E. K. Pikitch, & E. A. Babcock (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Oxford: Blackwell Publishing.

Cartamil, D. P., Vaudo, J. J., Lowe, C. G., Wetherbee, B. M., & Holland, K. N. (2003). Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. *Marine Biology* **142**, 841–847.

Carbajal-Enzian P., Santamaría J., y Danny Baldárrago. (2018). Guía ilustrada para el reconocimiento de poliplacóforos, gasterópodos y cefalópodos con valor comercial en el Perú. Lima: Instituto del Mar del Perú.

Castañeda, J. (1994). La pesquería artesanal y biología pesquera de especies de importancia económica en la caleta San Jose desde Feb. 1991 a Set. 1992. Bachelor Thesis, Universidad Nacional Mayor de San Marcos, Peru.

Castañeda, J. (2001). Biología y pesquería del “tiburón martillo” (*Sphyrna zygaena*) en Lambayeque, 1991–2000. *IMARPE Informe Progresivo*, **139**, 17–32.

[CCAMLR] Commission for the Conservation of Antarctic Marine Living Resources. (2006). Report of the Workshop on Management Procedures, Walvis Bay, Namibia, 17–21 July 2006. WG-EMM-06/40.

Chavez. 2006. Primary production in the eastern tropical Pacific: a review. *Progress in Oceanography*, **69**, 285-317.

Chavez, F., & Messie, M. (2009). A comparative analysis of eastern boundary upwelling ecosystems. *Progress in Oceanography*, **83**, 80– 96.

Checkley, D., Patricia Ayon, Tim Baumgartner, Miguel Bernal, J. Coetzee, Robert Emmett, Renato Guevara et al. (2009). *Habitats of small pelagic fish. In Climate Change and Small Pelagic Fish*. Cambridge: Cambridge University Press.

Checkley Jr, D. M., Asch, R. G., & Rykaczewski, R. R. (2017). Climate, anchovy, and sardine. *Annual Review of Marine Science*, **9**, 469-493.

Chin, A., Kyne, P. M., Walker, T. I., & McAuley, R. B. (2010). An integrated risk assessment for climate change: analysing the vulnerability of sharks and rays on Australia's Great Barrier Reef. *Global Change Biology*, **16**: 1936–1953.

Chirichigno, N., & Cornejo, R. (1998). Clave para identificar los peces marinos del Perú. IMARPE, Lima, Perú.

Christensen, V., & Pauly, D. (1992). ECOPATH II – software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*, **61**, 169–185.

Christensen V., De la Puente S., Sueiro J. C., Steenbeek J., & Majluf, P. (2014). Valuing seafood: The Peruvian fisheries sector. *Marine Policy*, **44**, 302–311.

Clarke, K. R. (1993). Non-parametric multivariate analysis of change in community structure. *Australian Journal of Ecology*, **18**, 117–143.

Clarke, R., Paliza, O., & Aguayo, A. (1998). Sperm whales of the southeast pacific. Part IV: fatness, food and feeding. In: G. Pilleri (Ed.), *Investigations on Cetacea*. Vol XXI.

Cliff, G., & Dudley, S. F. J. (1992). Sharks caught in the protective gill nets off Natal, South Africa. 6. The copper shark *Carcharhinus brachyurus* (Günther). *South African Journal of Marine Science*, **12**(1), 663–674.

Coasaca-Céspedes, J. J., Segura-Cobeña, E., Montero-Taboada, R., Gonzalez-Pestana, A., Alfaro-Córdova, E., Alfaro-Shigueto, J., & Mangel, J. C. (2018). Preliminary analysis of the feeding habits of batoids from the genera *Mobula*

and *Myliobatis* in Northern Peru. *Revista de Biología Marina y Oceanografía*, **53**(3), 367-374.

Corkeron, P. (2006). Opposing views of the “Ecosystem Approach” to fisheries management. *Conservation Biology* **20**, 617–619.

Coll, M., Navarro, J., & Palomera, I. (2013). Ecological role, fishing impact, and management options for the recovery of a Mediterranean endemic skate by means of food web models. *Biology Conservation*, **157**, 108–120.

Córdova-Zavaleta, F., Mendo, J., Briones-Hernandez, S. A., Acuña-Perales, N., González-Pestana, A., Alfaro-Shigueto, J., & Mangel, J. C. (2018). Food habits of the blue shark, *Prionace glauca*, in waters off northern Peru. *Fishery Bulletin*, **116**, 310–322.

Cornejo, R., Velez-Zuazo, X., Gonzalez-Pestana, A., Kouri, C., & Mucientes, G. (2015). An updated checklist of Chondrichthyes from southeast Pacific off Peru. *Checklist*, **11**, 6.

Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fish Aquatic Science*, **54**, 54: 726-738.

Cortés, E. (1999). Standardized diet compositions and Trophic positions of sharks. *ICES Journal of Marine Science*, **57**, 56: 707–717.

Csirke, J., Argüelles Torres, J., Alegre Norza Sior, A. R. P., Ayón Dejo, P., Bouchon Corrales, M., Castillo Mendoza, G., ... & Mariátegui Rosales, L. (2018). Biología, estructura poblacional y pesquería de pota o calamar gigante (*Dosidicus gigas*) en el Perú. Instituto del Mar del Perú.

Dabruzzi, T. F., Bennett, W. A., Rummer, J. L., & Fangué, N. A. (2013). Juvenile ribbontail stingray, *Taeniura lymma* (Forsskal, 1775) (Chondrichthyes, Dasyatidae), demonstrate a unique suite of physiological adaptations to survive hyper thermic nursery conditions. *Hydrobiologia*, **701**, 37–49.

Davidson, L. N. K., Krawchuk, M. A., & Dulvy, N. K. (2016). Why have global shark and ray landings declined: improved management or overfishing? *Fish and Fisheries*, **17**(2), 438-458.

DeVries, T. J., & Pearcy, W. G. (1982). Fish debris in sediments of the upwelling zone off central Peru: a late Quaternary record. *Deep Sea Research*, **28**, 87-109.

Doherty, P. D., Alfaro-shigueto, J., Hodgson, D. J., Mangel, J. C., Witt, M. J., & Godley, B. J. (2014). Big catch, little sharks: Insight into Peruvian small-scale longline fisheries. *Ecology and Evolution*, 1–9.

Ducatez, S. (2019). Which sharks attract research ? Analyses of the distribution of research effort in sharks reveal significant non-random knowledge biases. *Reviews in Fish Biology Fisheries*, **29**(2), 355–367.

Dulvy, N. K., Davidson, L. N. K., Kyne, P. M., Simpfendorfer, C. A., Harrison, L. R., Carlson, J. K., & Fordham, S. V. (2016). Ghosts of the coast: Global extinction risk and conservation of sawfishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **26**(1), 134–153.

Dulvy, N. K., Simpfendorfer, C. A., Davidson, L. N. K., Fordham, S. V., Brautigam, A., Sant, G., & Welch, D. J. (2017). Challenges and Priorities in Shark and Ray Conservation. *Current Biology*, **27**, 565–572.

Ebert, D. A., & Cowley, P. D. (2003). Diet, feeding behaviour and habitat utilisation of the blue stingray *Dasyatis chrysonata* (Smith, 1828) in South African waters. *Marine Freshwater Research*, **54**, 957–965.

El Peruano (2001). Ministerio de la Producción. Ley General de Pesca. Reglamento de la ley general de pesca. Decreto Supremo 012-001-PE, pp. 199905–199921.

Espinoza, P., & Bertrand, A. (2008). Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current system. *Progress in Oceanography*, **79**(2–4), 215–227.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... & Marquis, R. J. (2011). Trophic downgrading of planet Earth. *Science*, **333**(6040), 301–306.

Espinoza, P. (2014). *Trophic dynamics in the northern Humboldt Current system: insights from stable isotopes and stomach content analyses*. (Doctoral thesis, Université de Bretagne Occidentale, Brest, France).

Retrieved from <http://biblioimarpe.imarpe.gob.pe/handle/123456789/2335>

FAO. (2010). National fisheries sector overview: Peru.

FAO. (2018). The State of World Fisheries and Aquaculture 2018 - Meeting the sustainable development goals. Rome.

Ferry, L. A., & Cailliet, G. M. (1996). Sample size sufficiency and data analysis: are we characterizing and comparing diet properly? In D. MacKinlay, K. Shearer (Eds.), *Feeding ecology and nutrition in fish: proceedings of the symposium on the feeding ecology and nutrition in fish*. International Congress on the Biology of Fishes, San Francisco, CA.

Fiedler, P.C. (2002). Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. *Marine Ecology Progress Series*, **244**: 265-283.

García-Godos, I. (2001). Patrones Morfológicos del otolito Sagitta de algunos peces óseos del mar peruano. *Boletín del Instituto del Mar del Perú*, **20**, 1–2.

Gilbert, F., Bonin, P., & Stora, G. (1995). Effect of bioturbation on denitrification in marine sediment from the West Mediterranean littoral. *Hydrobiologia*, **304**, 49–58.

Gonzalez-Pestana, A., Kouri, J.C., & Velez-Zuazo, X. (2016a). Shark fisheries in the Southeast Pacific: A 61-year analysis from Peru. *F1000 Research*, **3**, 164.

Gonzalez-Pestana, A., Kouri, J.C., & Velez-Zuazo, X. (2016b). Situación de los batoideos en el Perú: Lo que sabemos y lo que no sabemos. Libro de resúmenes. V Congreso de Ciencias del Mar del Perú, Lambayeque, Perú.

Gonzalez-Pestana, A., Acuña-Perales, N., Coasaca-Cespedes, J., Córdova-Zavaleta, F., Alfaro-Shigueto, J., Mangel, J.C., & Espinoza, P. (2017). Trophic ecology of the smooth hammerhead shark (*Sphyrna zygaena*) off the coast of northern Peru. *Fishery Bulletin*, **115**, 451–459.

Gonzalez-Pestana, A., Acuña-Perales, N., Córdova, F., Coasaca, J., Alfaro, E., Alfaro-Shigueto, J., & Mangel, J. C. (2018). Feeding habits of thresher sharks *Alopias* sp. in northern Peru: Predators of Humboldt squid (*Dosidicus gigas*). *Journal of the Marine Biological Association UK*, 1-8.

Gonzalez-Pestana, A. (2018). *Habitat Suitability of Juvenile Smooth Hammerhead Shark (Sphyrna zygaena) off northern Peru*. (Master thesis, James Cook University, Townsville, Australia).

Retrieved from

https://www.researchgate.net/publication/330168901_Habitat_Suitability_of_Juvenile_Smooth_Hammerhead_Shark_Sphyrna_zygaena_off_northern_Peru

Gray, A. E., Mulligan, T. J., & Hannah, R. W. (1997). Food habits, occurrence, and population structure of the bat ray, *Myliobatis californica*, in Humboldt Bay, California. *Environmental Biology of Fishes*, **49**(2), 227-238.

Guénette, S., Heymans, S. J. J., Christensen, V., & Trites, A. W. (2006). Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 2495–2517.

Guénette, S., Christensen, V., & Pauly, D. (2008). Trophic modelling of the Peruvian upwelling ecosystem: towards reconciliation of multiple datasets. *Progress in Oceanography*, **79**(2-4), 326-335.

Harris, S. A., Bennett, B. A., & Branch, G. M. (1988). An assessment of the role of the sand shark *Rhinobatos annulatus* as a predator in Langebaan Lagoon. *South African Journal of Marine Science*, **7**, 153–159.

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution*, **23**, 202–210.

Heithaus, M. R., Frid, A., Vaudo, J. J., Worm, B., & Wirsing, A. J. (2010). Unraveling the ecological importance of elasmobranchs. In J. C. Carrier, J. A. Musick, M. R. Heithaus (Eds.), *Sharks and their relatives II: Biodiversity, adaptive physiology, and conservation*. Florida: CRC Press.

Hothorn, T., Hornik, K., & Zeileis, A. (2006a). Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics*, **15**, 651–674.

Hothorn, T., Hornik, K., & Zeileis, A. (2006b). Party: A Laboratory for Recursive Partytioning. R Package Version 0.9-0. <<http://CRAN.R-project.org>>.

Hyslop, E. J. (1980). Stomach content analysis-a review of methods and their application. *Journal of Fish Biology*, **17**, 166-172.

Ibáñez, C. M., González, C., & Cubillos, L. (2004). Dieta del pez espada *Xiphias gladius* Linnaeus, 1758, en aguas oceánicas de Chile central en invierno de 2003. *Investigaciones Marinas*, **32**(2), 113–120.

Jacobsen, I. P., & Bennett, M. B. (2013). A comparative analysis of feeding and trophic level ecology in stingrays (Rajiformes; Myliobatoidei) and electric rays (Rajiformes: Torpedinoidei). *PLoS One*, **8**(8), e71348.

Jahncke, J., Checkley, D. M. Jr., & Hunt, G. L. Jr. (2004). Trends in carbon flux to seabirds in the Peruvian upwelling system: effects of wind and fisheries on population regulation. *Fisheries Oceanography* **13**, 208-223.

Kaplan, I. C., Brown, C. J., Fulton, E. A., Gray, I. A., Field, J. C., & Smith, A. D. (2013). Impacts of depleting forage species in the California Current. *Environmental Conservation*, **40**(4), 380-393.

Kitchell, J. F., Essington, T. E., Boggs, C. H., Schindler, D. E., & Walters, C. J. (2002). The role of sharks and long-line fisheries in a pelagic ecosystem of central pacific. *Ecosystems*, **5**, 202–216.

Kiszka, J. J., Heithaus, M. R., & Quod, J. P. (2015). Stingrays as possible facilitators for foraging trevallies in a nearshore sandflat. *Marine Biodiversity*, **45**, 625–626.

Kogure, K., & Wada, M. (2005). Impacts of macrobenthic bioturbation in marine sediment on bacterial metabolic activity. *Microbes Environment*, **20**, 191–199.

Labropoulou, M., & Eleftheriou, A. (1997). The foraging ecology of two pairs of congeneric demersal fish species: important of morphological characteristic in prey selection. *Journal of Fish Biology*, **50**, 324–340.

Last, P., Naylor, G., Séret, B., White, W., de Carvalho, M., & Stehmann, M. (Eds.). (2016). *Rays of the World*. CSIRO publishing.

Link, J. (1999). (Re) constructing food webs and managing fisheries. In *Ecosystem Approaches for Fisheries Management*. University of Alaska Sea Grant, AK-SG- 99-01, Fairbanks, Alaska.

Link, J.S., Brodziak, J.K.T., Edwards, S.F., Overholtz, W.J., Mountain, D., et al.

(2002). Marine ecosystem assessment in a fisheries management context. *Canadian Journal of Fish Aquatic Science* **59**, 1429–1440.

Livingston, P. A., Aydin, K., Boldt, J., Ianelli, J., & Jurado-Molina, J. (2005). A framework for ecosystem impacts assessment using an indicator approach. *ICES Journal of Marine Science*, **62**, 592–597.

López, S., Meléndez, R., & Barría, P. (2010). Preliminary diet analysis of the blue shark *Prionace glauca* in the eastern South Pacific. *Revista de Biología Marina y Oceanografía*, **45**, 745–749.

Lloor-Andrade, P., Pincay-Espinoza, J., & Rosas-Luis, R. (2017). Diet of the blue shark *Prionace glauca* in the Ecuadorian Pacific Ocean during the years 2013 to 2015. *Journal of Applied Ichthyology*, 1–5.

Löwemark, L. (2015). Evidence for targeted elasmobranch predation on thalassinidean shrimp in the Miocene Taliao Formation, NE Taiwan. *Lethaia*, **48**(2), 227–234.

Lu, C. C., & Ickeringill, R. (2002). Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of southern Australian finfishes. *Museum Victoria Science Reports*, **6**, 1–65.

Lucifora, L. O., García, V.B., Menni, R. C., Escalante, A. H., & Hozbor, N. M. (2009). Effects of body size, age and maturity y stage on diet in a large shark: ecological and applied implications. *Ecology Research*, **24**, 109–118.

Lundberg, J., & Moberg, F. (2003). Mobile link organisms and ecosystem functioning: Implications for ecosystem resilience and management. *Ecosystems*, **6**(1), 87–98.

Manrique, M.R., & Mayaute, L.F. (2017). Hábitos alimentarios de las rayas *Pseudobatos planiceps* (Garman, 1880), *Hypanus dipterurus* (Jordan & Gilbert, 1880) y *Myliobatis chilensis* (Philippi, 1892), en Pisco, Ica, Perú, 2016. Tesis de pregrado. Universidad Nacional —San Luis Gonzagall De Ica, Perú.

Marshall, K. N., Stier, A. C., Samhuri, J. F., Kelly, R. P., & Ward, E. J. (2016). Conservation challenges of predator recovery. *Conservation Letters*, **9**(1), 70–78.

Martins, A. P. B., Heupel, M. R., Chin, A., & Simpfendorfer, C. A. (2018). Batoid nurseries: definition, use and importance. *Marine Ecology Progress Series*, **595**, 253–267.

Marine Stewardship Council (2018). MSC Fisheries Standard. Version 2.01, 31 August 2018. United Kingdom.

Mason, J. G., Alfaro-Shigueto, J., Mangel, J. C., Brodie, S., Bograd, S. J., Crowder, L. B., & Hazen, E. L. (2019). Convergence of fishers' knowledge with a species

distribution model in a Peruvian shark fishery. *Conservation Science and Practice*, **1**(4), e13.

Meyer, J. L., & Schultz, E. T. (1985). Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnology and Oceanography*, **30**(1), 146–156.

Motta, P. J. (2004) Prey capture behaviour and feeding mechanics of elasmobranchs. In J. F. Carrier, J. A. Musick, M. R. Heithaus (Eds.), *Biology of Sharks and their Relatives*. London: CRC Press.

Moscoso, V. (2013). Catalogue decapod and stomatopod crustaceans of Perú. *Instituto Boletín del Mar del Perú*, **27**, 1-2.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, **315** (80), 1846–1850.

Myrick, J. L., & Flessa, K. W. (1996). Bioturbation rates in Bahia La Choya, Sonora, Mexico. *Ciencias Marinas*, **22**, 23–46.

Murphy, R.C. (1925). Bird Islands of Peru. New York, USA: GP Putnams Sons.

Nagy, K., Reiczigel, J., Harnos, A., Schrott, A., & Kabai, P. (2010). Tree-based methods as an alternative to logistic regression in revealing risk factors of crib-biting in horses. *Journal of Equine Veterinary Science*, **30**, 21–26.

Nigmatullin, C. M., Nesis, K. N., & Arkhipkin, A. I. (2001). A review of the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). *Fisheries Research*, 9-19.

Okes, N., & Sant, G. (2019). An overview of major shark traders, catchers and species. TRAFFIC, Cambridge, UK

Oksanen, F. J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). Vegan: Community Ecology Package. R package Version 2.5-6. <https://CRAN.R-project.org/package=vegan>.

O'Shea, O. R., Thums, M., van Keulen, M., & Meekan, M. (2012). Bioturbation by stingrays at Ningaloo Reef, Western Australia. *Marine and Freshwater Research*, **63**, 189–197.

Ortega-Cisneros, K., Yokwana, S., Sauer, W., Cochrane, K., Cockcroft, A., James, N. C., & Pecl, G. (2018). Assessment of the likely sensitivity to climate change for the key marine species in the southern Benguela system. *African Journal of Marine Science*, **40**(3), 279-292.

Pauly, D., Muck, P., Mendo, J., Tsukayama, I. (Eds.) (1989). *The Peruvian upwelling ecosystem: dynamics and interactions*. Manila, Philippines: IMARPE/GTZ/ICLARM, ICLARM.

Pennington, J. T., Mahoney, K. L., Kuwahara, V. S., Kolber, D. D., Calienes, R., & Chavez, F. P. (2006). Primary production in the eastern tropical Pacific: a review. *Progress in Oceanography*, **69**, 285–317.

Pikitch, E., Santora, C., Babcock, E., Bakun, A., & Bonfil, R, et al. (2004). Ecosystem based fishery management. *Science* **305**, 346.

Polis, G. A., Anderson, W. B., & Holt, R. D. (1997). Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecological Systems*, **28**, 289–316.

Ponte, D. D. S., Barcelos, L. M. D., Santos, C. S., Medeiros, J., & Barreiros, J. P. (2016). Diet of *Dasyatis pastinaca* and *Myliobatis aquila* (Myliobatiformes) from the Azores, NE Atlantic. *Cybium*, **40**(3), 209-214.

Powers, J. E., & Monk, M. H. (2010). Current and future use of indicators for ecosystem based fisheries management. *Marine Policy*, **34**(3), 723-727.

Navia, A. F., Giraldo, A., & Mejía-Falla, P. A. (2006). Notas sobre la biología y dieta del toyo vieja (*Mustelus lunulatus*) en la zona central de pesca del Pacífico colombiano. *Investigaciones marinas*, **34**(2), 217-222.

Piatkowski U., Pierce G., & Moraisda Cunha, M. (2001). Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. *Fisheries Research*, **52**, 5–10.

Ramirez, R., Carlos Paredes, C., & Arenas, J. (2003). Moluscos del Perú. *Revista de Biología Tropical*, **51**(3), 225–284.

Rasher, D. B., Hoey, A. S., & Hay, M. E. (2017). Cascading predator effects in a Fijian coral reef ecosystem. *Scientific Reports*, **7**, 15684.

R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/index.html>

Rosas-Luis, R., Salinas-Zavala, C. A., Koch, V., Del Monte Luna, M. V., & Morales-Zárat, M. V. (2008). Importance of jumbo squid *Dosidicus gigas* (Orbigny , 1835) in the pelagic ecosystem of the central Gulf of California. *Ecological Modelling*, **8**, 149–161.

Rosas-Luis, R., Loor-Andrade, P., Carrera-Fernández, M., Pincay-Espinoza, J. E., & Vincés-Ortega, L. C. S. (2015). Cephalopod species in the diet of large pelagic fish (sharks and billfishes) in Ecuadorian waters. *Fisheries Research*, **173**(2), 159-168.

Rosa, R. et al. (2013). *Dosidicus gigas*, Humboldt squid. In: R. Rosa, P. J. Pierce, R. O'Dor (Eds), *Advances in Squid Biology, Ecology and Fisheries*. Nova Science Publishers, USA.

Rosenberger, L. J. (2001). Pectoral fin locomotion in batoid fishes: undulation versus oscillation. *The Journal of Experimental Biology*, **204**, 379–394.

Ruckelshaus, M., Klinger, T., Knowlton, N. & DeMaster, D.P. (2008). Marine ecosystem-based management in practice: scientific and governance challenges. *Bioscience*, **58**, 53–63.

Salvatecci, R., Gutiérrez, D., Field, D., Sifeddine, A., Ortlieb, L., Caqueneau, S., Baumgartner, T., Ferreira, V., & Bertrand, A. (2019). Fish debris in sediments from the last 25 kyr in the Humboldt Current reveal the role of productivity and oxygen on small pelagic fishes. *Progress in Oceanography*, **176**, 102114

Samame, M., Castillo, J., & Espino, M. (1989). El tollo un recurso demersal, algunos aspectos de la biología y pesquería de *Mustelus whitneyi*. *Revista del Pacífico Sur*.

Schindler, D. E., Essington, T. E., Kitchell, J. F., Boggs, C., & Hilborn, R. (2002). Sharks and tunas: fisheries impacts on predators with contrasting life histories. *Ecology Applied*, **12**(3), 735–748.

Schindler, D. E., Carpenter, S. R., Cottingham, K. L., He, X., Hodgson, J. R., Kitchell, J. F., & Soranno, P. A.. (1996). Food web structure and littoral zone coupling to pelagic trophic cascades. In G. A. Polis and K. O. Winemiller, (Eds.), *Food webs: integration of patterns and dynamics*. Chapman and Hall, New York, New York, USA.

Silva-Garay, L., Pacheco, A. S., & Vélez-Zuazo, X. (2018). First assessment of the diet composition and Trophic position of an assemblage of poorly known

chondrichthyans off the central coast of Peru. *Environmental Biology of Fish*, **101**(19), 1525–1536.

Segura-Cobeña, E. (2017). *Composición de la dieta de la Raya Águila Chilena *Myliobatis chilensis* (Philippi, 1892) en la caleta de San José, Lambayeque*. (Bachelor thesis, Universidad Científica del Sur, Lima, Perú).

Silliman, W., & Gruber, S. H. (1999). Behavioral biology of the spotted eagle ray, *Aetobatus narinari*. *Journal of Science*, **7**, 13–20.

Smale, M. J. (1991). Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape coast of South Africa. *South African Journal of Marine Science*, **11**, 31–42.

Sternes, P. C., & Shimada, K. (2020). Body forms in sharks (Chondrichthyes: Elasmobranchii) and their functional, ecological, and evolutionary implications. *Zoology*, 125799.

Sheaves, M. (2009). Consequences of ecological connectivity: the coastal ecosystem mosaic. *Marine Ecology Progress Series*, **391**, 107–115.

Sherman, C. S., Heupel, M. R., Moore, S. K., Chin, A., & Simpfendorfer, C. A. (2020). When sharks are away, rays will play: effects of top predator removal in coral reef ecosystems. *Marine Ecology Progress Series*, **641**, 145–157.

Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., Mackinson, S., Marzloff, M., Shannon, L. J., Shin, Y. J., & Tam, J. (2011) Impacts of fishing low-trophic level species on marine ecosystems. *Science* **333**, 1147–1150.

Staudinger, M. D., Juanes, F., Salmon, B., & Teffer, A. K. (2013). Deep-Sea Research II The distribution, diversity, and importance of cephalopods in top predator diets from offshore habitats of the Northwest Atlantic Ocean. *Deep-Sea Research II*, **95**, 182–192.

Stevens, J. D., Bonfil, R., Dulvy, N. K., & Walker, P. A. (2000). The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science*, **57**, 476–494.

Soberón, J., & Llorente, J. (1993). The use of species accumulation functions for the prediction of species richness. *Conservation Biology*, **7**, 480–488.

Tam, J., Blaskovic'Huayta, V., Goya Sueyoshi, E., Bouchon Corrales, M., Taylor, M., Oliveros Ramos, R., & Purca Cuicapusa, S. (2010). Relación entre anchoveta y otros componentes del ecosistema. *IMARPE Bulletin*, **25** (1-2), 31–37.

Tam, J., Taylor, M. H., Blaskovic, V., Espinoza, P., Ballón, R. M., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quipúzcoa, L., Gutiérrez, D., Goya, E., Ocho, N., & Wolff, M. (2008). Trophic modeling of the Northern Humboldt Current Ecosystem, Part I: Comparing trophic linkages under La Niña and El Niño conditions.

Progress in Oceanography **79**, 352-365.

Taylor, M. H., Tam, J., Blaskovic, V., Espinoza, P., Ballón, R. M., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quipúzcoa, L., Gutiérrez, D., Goya, E., Ocho, N., & Wolff, M. (2008). Trophic modeling of the Northern Humboldt Current Ecosystem, Part II: Elucidating ecosystem dynamics from 1995 to 2004 with a focus on the impact of ENSO. *Progress in Oceanography* **79**, 366-378.

Takeuchi, S., & Tamaki, A. (2014). Assessment of benthic disturbance associated with stingray foraging for ghost shrimp by aerial survey over an intertidal sandflat. *Continental Shelf Research*, **84**, 139–157.

Therneau, T., Atkinson, B., & Ripley, B. (2012). Package ‘rpart’ and ‘rpart.plot’ in URL: <http://cran-r.c3sl.ufpr.br/>

Tripp-Valdez, A., Galvan-Magaña, F., & Ortega-Garcia, S. (2015). Food sources of common dolphinfish (*Coryphaena hippurus*) based on stomach content and stable isotopes analyses. *Journal of the Marine Biological Association of the United Kingdom*, **95**(3), 579-591.

Vanni, M. J. (1996). Nutrient transport and recycling by consumers in lake food webs: implications for algal communities. In G. A. Polis and K. O. Winemiller, (Eds.) *Food webs: integration of patterns and dynamics*. New York, USA: Chapman and Hall.

Vander Zanden, M. J., & Vadeboncoeur, Y. (2002). Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, **83**(8), 2152-2161.

Vaudo, J. J., & Heithaus, M. R. (2011). Dietary niche overlap in a nearshore elasmobranch mesopredator community. *Marine Ecology Progress Series*, **425**, 247–260.

Ward, P., & Myers, R. A. (2005). Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology*, **86**(4), 835–847.

Warzybok, P., Santora, J. A., Ainley, D. G., Bradley, R. W., Field, J. C., Capitolo, P. J., Carle, R. D., Elliott, M., Beck, J. N., McChesney, G. J., & Hester, M. M. (2018). Prey switching and consumption by seabirds in the central California Current upwelling ecosystem: Implications for forage fish management. *Journal of Marine Systems*, **185**, 25-39.

Watters, G.M., Olson, R.J., Field, J.C., & Essington, T.E. (2008). Range expansion of the Humboldt squid was not caused by tuna fishing. *Proceedings of the National Academy of Sciences USA* 105, 3.

Wetherbee, B., Cortés, E., & Bizzarro, J. J. (2012). Food consumption and feedings habits. In: J. C, Carrier, J. A., Musick, M. R. Heithaus (Eds), *Biology of Sharks and their Relatives*. Florida: CRC Press.

Williams, R., Krkošek, M., Ashe, E., Branch, T. A., Clark, S., Hammond, P. S., ... & Winship, A. (2011). Competing conservation objectives for predators and prey: estimating killer whale prey requirements for Chinook salmon. *PloS one*, **6**(11), e26738.

Xavier, J. C., & Cherel, Y. (2009). Cephalopod beak guide for the southern ocean. Cambridge, UK: British Antarctic Survey.

Zabel, R. W., Harvey, C. J., Katz, S. L., Good, T. P., & Levin, P. S. (2003). Ecologically Sustainable Yield. *American Scientist*, **91**, 150-154.

Significance Statement

This study advances our ecological understanding of nine highly exploited, threatened or poorly understood species. The study site is located in one of the most productive ocean ecosystems and in one of the largest elasmobranch fisheries in the Pacific ocean. This research reveals the importance of elasmobranchs as predators of keystone and commercial species, and represents the most comprehensive assessment to date of the ecological role of elasmobranchs in the Northern Humboldt Current Large Marine Ecosystem.

Figure 1. Landing points where the samples of nine elasmobranch species were collected

Figure 2. Randomized cumulative prey curve for the diet sample of nine elasmobranch species, all prey items were pooled into nine main taxa groups. Mean values are plotted; the gray area represents the standard deviation of the plotted mean

Figure 3. Diet quantified by percent by prey-specific index of relative importance (%PSIRI) for nine elasmobranch species off northern Peru. A: *Alopias* spp., PG: *Prionace glauca*, SZ: *Sphyrna zygaena*, CB: *Carcharhinus brachyurus*, TM: *Triakis maculata*, GG: *Galeorhinus galeus*, MC: *Myliobatis chilensis*, MW: *Mustelus whitneyi*, PP: *Pseudobatos planiceps*

Tables and Figures

Table 1. Characteristics of nine elasmobranch species whose diets was analyzed off northern Peru. Sample size of non-empty stomachs. TL: total length; DW: disc width.

Common name	Scientific name	Conservation Status (IUCN Red List)	Sample Size	Body length (cm) Mean (range)
Smooth hammerhead shark*	<i>Sphyrna zygaena</i> L.	Vulnerable	259	104 (55-294) TL
Thresher shark*	<i>Alopias</i> spp. (Bonnaterre, 1788)	Vulnerable and Endangered	110	289 (120-385) TL
Blue shark*	<i>Prionace glauca</i> L.	Near Threatened	121	216 (120-287) TL
Humpback smoothhound*	<i>Mustelus whitneyi</i> , Chirichigno, 1973	Vulnerable	76	80 (36-122) TL
Bronze whaler shark	<i>Carcharhinus brachyurus</i> (Günther, 1870)	Near Threatened	69	98 (73-137) TL
School shark	<i>Galeorhinus galeus</i> L.	Vulnerable	41	125 (78-170) TL
Spotted houndshark	<i>Triakis maculata</i> , Kner & Steindachner, 1867	Vulnerable	43	137 (88-165) TL
Pacific Guitarfish*	<i>Pseudobatos planiceps</i> (Garman, 1880)	Data Deficient	74	88 (49-117) TL
Chilean Eagle ray*	<i>Myliobatis chilensis</i> , Philippi, 1892	Data Deficient	72	140 (74-254) DW

IUCN: International Union for Conservation of Nature
(<https://www.iucnredlist.org/>)

* Among the nine most caught elasmobranch species in Peru (Gonzalez-Pestana *et al.*, 2016 a,b)

Table 2. Trophic position and trophic niche width, according to Levin index, of the diet of nine elasmobranch species off northern Peru.

Species	Levin index	Trophic position
<i>Alopias</i> spp.	0.35	4.4
<i>Prionace glauca</i>	0.06	4.2
<i>Sphyrna zygaena</i>	0.23	4.3
<i>Triakis maculata</i>	0.09	4.1
<i>Mustelus whitneyi</i>	0.42	4.1
<i>Myliobatis chilensis</i>	0.20	4.1
<i>Galeorhinus galeus</i>	0.53	4.2
<i>Carcharhinus brachyurus</i>	0.40	4.4
<i>Pseudobatos planiceps</i>	0.62	3.8

Table 3. SIMPER analysis of the trophic assemblages for the nine elasmobranch species off northern Peru. Avg. Sim: average similarity; Avg. Diss : average dissimilarity, SD : standard deviation, Contrib% : contributing percent, Cum% : cumulative percent. A: *Alopias* spp., SZ: *Sphyrna zygaena*, PG: *Prionace glauca*, MW: *Mustelus whitneyi*, MC: *Myliobatis chilensis*, GG: *Galeorhinus galeus*, TM: *Triakis maculata*, CB: *Carcharhinus brachyurus*, PP: *Pseudobatos planiceps*

Trophic assemblage	Abundance	Avg.Sim	Contrib%	Cum.%
Node 2: A, SZ, PG				
Average similarity = 42.8				
Cephalopods	7.6	40.9	95.6	95.6
Node 3: MW, MC, GG, TM, CB, PP				
Average similarity = 26.2				
Teleosts	1.7	21.3	81.2	81.2
Crabs	0.3	2.9	11.1	92.3
	Abundance	Avg.Diss	Contrib%	Cum.%
Node 2 – Node 3				
Average dissimilarity = 87.6	Node 2	Node 3		
Cephalopods	7.6	0.5	54.5	62.2
Teleosts	0.8	1.7	20.6	85.7
Crabs	0	0.3	5.3	91.8

Table 4. Prey composition in stomach contents of nine elasmobranch species off northern Peru. Index of relative importance: %IRI, prey-specific index of relative importance: PSIRI%.

	<i>Sphyrna zygaena</i>		<i>Alopias spp.</i>		<i>Prionace glauca</i>	
	IRI	PSIRI	IRI	PSIRI	IRI	PSIRI
Teleosts						
Unidentified teleosts	17.4	16			1.9	6.1
<i>Anchoa nasus</i>	0.4	0.4				
<i>Auxis thazard</i>					<0.1	<0.1
<i>Coryphaena hippurus</i>					0.2	1.0
<i>Coryphaenoides</i> sp.					<0.1	<0.1
Engraulids	0.4	0.7				
<i>Engraulis ringens</i>	<0.1	0.3	0.1	0.6	0.3	1.3
Exocoetidae eggs					0.4	<2.2
Fistulariidae	<0.1	0.1	0	0		
<i>Merluccius gayi</i>	0.7	2	4.5	5	<0.1	0.3
<i>Myctophum aulateratum</i>					<0.1	<0.1
<i>Odontesthes regia</i>	0	<0.1	0	0		
<i>Sardinops sagax</i>	<0.1	0.3	0	0		
<i>Sphyrna idiaestes</i>					<0.1	<0.1
Tetrodontidae	0	0	0.02	0.3		
Cephalopods						
Unidentified cephalopods	<0.1	0.3	8.3	10.7	6.9	31.3
<i>Abraliopsis affinis</i>					<0.1	0.4
<i>Ancistrocheirus lesueuri</i>	2.1	3.1	2.4	4.7	12.8	6.2
<i>Thysanoteuthis rhombus</i>	0.1	0.4	0	0		
<i>Argonauta</i> sp.					54.5	16.06
<i>Chroteuthis veranyi</i>					0.1	1.2
<i>Dodiscus gigas</i>	33.1	30.3	74.5	63.9	5.6	2.8
<i>Doryteuthis gahi</i>	35.2	30.9	5.8	7	0.4	0.9
<i>Eledone</i> spp.					<0.1	<0.1
<i>Galiteuthis pacifica</i>					<0.1	1.0
<i>Gonatus antarcticus</i>	3.5	4.6	1.3	2.7	7.1	5.8
<i>Grimalditeuthis bonplandi</i>					1.6	0.9
<i>Histioteuthis cerasina</i>					<0.1	0.1
<i>Histioteuthis hoylei</i>	1.1	2.5	0.9	1.6		
<i>Japetella diaphana</i>					0.9	3.4
<i>Japetella heathi</i>					<0.1	0.2
<i>Leachia danae</i>					0.2	0.6
<i>Mastigoteuthis dentata</i>	3.4	4.5	0.9	1	<0.1	1.2
<i>Muusoctopus</i> sp.					<0.1	<0.1
Octopoda	2.2	2.7	1	1.2		
<i>Octopoteuthis sicula</i>	0.4	0.8	<0.1	0.4	0.3	1.5

Oegopsida					<0.1	0.1
<i>Ommastrephes bartramii</i>	<0.1	0.1	0.1	0.8	0.4	0.9
<i>Onychoteuthis banksii</i>					0.1	0.5
<i>Pholidoteuthis massyae</i>					<0.1	0.2
<i>Stigmatoteuthis hoylei</i>					2.4	2.5
<i>Thysanoteuthis rhombus</i>					1.4	5.9
<i>Tremoctopus violaceus</i>					<0.1	<0.1
<i>Vampyroteuthis infernalis</i>					1.8	2.7
<i>Vitreledonella richardi</i>					<0.1	<0.1
Crustaceans						
<i>Pleuroncodes monodon</i>					0.1	0.8
Unidentified crustaceans					0.1	0.4
Marine mammals						
<i>Delphinidae</i>					0.1	0.8

	<i>Mustelus whitneyi</i>		<i>Myliobatis chilensis</i>		<i>Pseudobatos planiceps</i>	
	IRI	PSIRI	IRI	PSIRI	IRI	PSIRI
Teleosts						
Unidentified teleosts	7.5	6.7	18	18.3	36.5	23
<i>Axilis</i> sp.	1.6	2.2	0	0	0	0
<i>Scomber japonicus</i>	0	0	0.8	0.6	0	0
<i>Paralichthys</i> sp.	0	0	1	0.8	0	0
<i>Xenomystax atrarius</i>	0	0	1.3	1.3	0	0
<i>Cynoscion analis</i>	0	0	0	0	0	0
<i>Merluccius gayi</i>	3.1	3.6	4.6	4.5	0	0
<i>Engraulis ringens</i>	23.9	22.1	20.7	19.6	0	0
Crustaceans						
Unidentified crustaceans	4.9	5.2	6.8	6.1	0	0
<i>Pagurus perlatus</i>	0	0	1.4	1.4	0	0
<i>Palinuridae</i>	1.3	1.3	0	0	0	0
Crabs						
<i>Brachyura</i>	10.4	10	0	0	18.7	14.9
<i>Hepatus chiliensis</i>	2.2	2	1.4	1.5	0	0
<i>Hepatus kossmanni</i>	0	0	4.7	4.3	0	0
<i>Platymera gaudichaudii</i>	2.9	3	6	6.2	0	0

<i>Cancer porteri</i>	4.6	5.4	6.4	5.7	0	0
<i>Calappidae</i>	0	0	<0.1	0.2	0	0
<i>Pinnaxodes chilensis</i>	0	0	0	0	0.9	3.4
Shrimps						
<i>Caridae</i>	0	0	0	0	11	5.4
<i>Litopenaeus vannamei</i>	0	0	0	0	0.1	1.7
<i>Farfantepenaeus californiensis</i>	0	0	0	0	6.1	7.1
Stomatopods						
Unidentified stomatopods	0	0	1.1	0.7	15.1	12.7
<i>Goodeactylidae</i>					0.8	4.2
<i>Squilla</i> sp.	0	0	0.2	0.4	0	0
<i>Squilla aculeata aculeata</i>					<0.1	0.8
<i>Squilla parva</i>	0	0	1.5	1.7	0	0
<i>Scymnites peruvianus</i>	0.6	1.6	0	0	<0.1	0.6
<i>Pseudosquilla lessonii</i>	0	0	1.4	1.4	0.1	1.7
<i>Hemisquilla ensigera ensigera</i>	0	0	0	0	1.6	3.4
Gastropods						
Unidentified gastropods	15.5	13.8	12	14	0	0
<i>Maroidae</i>	0.1	0.6	0.1	0.4	0	0
<i>Naticidae</i>	6.8	6.5	6.9	6.9	0	0
Bivalves						
Unidentified bivalves	0.9	1.3	1.4	1.3	6	10.1
<i>Nuculana</i>	0	0	0	0	<0.1	0.5
<i>Ensis macha</i>	0	0	0	0	0.2	1.7
Cephalopods						
Unidentified cephalopods	1.6	2.5	1.8	1.6	1.6	4.8
<i>Doryteuthis gahi</i>	11.9	10.7	0.8	1.1	0	0
<i>Dodiscus gigas</i>	0.1	0.7	0	0	0	0
<i>Octopoda</i>	0.1	0.8	0	0	0	0
Annelids						
Unidentified annelids	0	0	0	0	1	3.9

	<i>Triakis maculata</i>		<i>Carcharhinus brachyurus</i>		<i>Galeorhinus galeus</i>	
	IRI	PSIRI	IRI	PSIRI	IRI	PSIRI
Teleosts						
Unidentified teleosts	80.1	61.1	19.8	19.3	37.1	30.6
<i>Auxis</i> sp.	0	0	1	2.5	0	0
<i>Aphos porosus</i>	1.1	2.5	0.1	0.8	0	0
<i>Scorpaena</i> sp.	0		4.1	4.3	0	0
<i>Trachurus pallensis</i>	0	0	3.1	3.8	0	0
Scombridae	0	0	0.1	0.8	0	0
<i>Scomber japonicus</i>	0	0	2.9	3	0	0
<i>Devalabrax humeralis</i>	0	0	0	0	0	0.4
<i>Sciaena deliciosa</i>	0.8	1.4	0	0	0	0
<i>Stellifer minor</i>	0.1	0.9	0	0	0	0
<i>Cynocion analis</i>	0	0.7	0	0	0	0
<i>Galeichtys peruvianus</i>	0.4	1	0	0	0	0
<i>Merlucius gayi</i>	0	0.4	5.5	5.7	9	10.7
<i>Mugil cephalus</i>	0	0.4	0	0	0	0
<i>Sphyraena ensis</i>	0.1	1	0	0	0	0
<i>Engraulis ringens</i>	0.3	1.3	45.5	42.9	7.5	7.5
<i>Micropogonias</i> sp.	0.1	1.2	0	0	0	0
<i>Stromateus stellatus</i>	3.2	6.1	0	0	0	0
Chondrychtyans						
<i>Urotrygon aspidura</i>	0	0.2	0	0	0	0
Crustaceans						
Unidentified crustaceans	9	9.5	0	0	8.1	6.9
Crabs						
<i>Paraxanthus barbiger</i>	1.2	1.7	0	0	0	0
<i>Portunus asper</i>	0.6	0.5	0	0	0	0
<i>Cronius ruber</i>	2.1	2.3	0	0	0	0
<i>Cancer porteri</i>	0.2	1.7	0	0	0	0

<i>Peloeus armatus</i>	0.1	1	0	0	0	0
Stomatopods						
Unidentified stomatopods	0	1.4	0	0	2.9	5.6
<i>Squilla</i> sp.	0	0.3	0	0	0	0
Gastropods						
<i>Nassarius dentifer</i>	0.4	1.2	0	0	0	0
<i>Stramonita chocolata</i>	0.2	1.5	0	0	0	0
Cephalopods						
Unidentified cephalopods	0	0.5	0.2	1.4	4.8	4.9
<i>Doryteuthis gahi</i>	0	0	17.7	15.5	16	16.5
<i>Octopoteuthis sicula</i>	0	0	0	0	3.2	3.4
<i>Loligo gigas</i>	0	0	0	0	0.5	1
<i>Mastigoteuthis dentata</i>	0	0	0	0	0	0
<i>Histioteuthis hoylei</i>	0	0	0	0	0.5	0.9
<i>Archistrocheirus leeuweni</i>	0	0	0	0	1.5	2.8
Octopoda	0	0	0	0	8.7	8.9
Annelids						
Pectinariidae	0	0.2	0	0	0	0





