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Evaluating the Trophic Habits and Dietary Overlap of Two Deep-Sea Catsharks (Apristurus brunneus and Parmaturus xaniurus) in Central California, USA

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Evaluating the trophic habits and dietary overlap of two deep-sea catsharks (*Apristurus brunneus* and *Parmaturus xaniurus*) in central California, USA

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Matthew Jew
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Thesis of Matthew Jew:

EVALUATING THE TROPHIC HABITS AND DIETARY OVERLAP OF TWO DEEP-SEA CATSHARKS (*APRISTURUS BRUNNEUS* AND *PARMATURUS XANIURUS*) IN CENTRAL CALIFORNIA, USA

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ABSTRACT

Evaluating the trophic habits and dietary overlap of two deep-sea catsharks (*Apristurus brunneus* and *Parmaturus xaniurus*) in central California, USA

by
Matthew Jew
Master of Science in Marine Science
California State University Monterey Bay, 2021

In marine communities, there are often multiple species that occupy the same or similar niches. When resources are in short supply, competitive interactions can negatively affect the survival of one or both of the species involved. Understanding the trophic habits and interactions of species helps explain their role in a given ecosystem. Additionally, knowing the trophic habits of targeted or bycaught species captured in fisheries can help to influence management decisions on an ecosystem level. *Apristurus brunneus* and *Parmaturus xaniurus* (Family: Pentachidae) are abundant deep-sea predators native to the Northeastern Pacific Ocean. Central California offers a unique opportunity to study these sympatric species in a location where they have large populations and the potential to compete for dietary resources. This study identifies: (1) the dietary composition of each predator; (2) the biological and environmental factors associated with variation in their trophic habits; (3) the trophic level of each species; and (4) the level of trophic overlap and potential for interspecific competition between the two species. To investigate the trophic habits of these two predators, this study used two complimentary techniques: stomach content analysis (SCA) and stable isotope analysis (SIA). Specimens from both species were collected during fishery-independent trawl surveys along the central California coast. Stomachs (for SCA) and dorsal white muscle tissue (for SIA) were removed from sharks after biological and catch data were recorded for each individual, including potential explanatory variables (e.g. depth, latitude, longitude, maturity, season, sex, trawl composition, and total length). Trophic habits and trophic position were calculated for each species independently and the level of trophic overlap between each species were calculated for SCA and SIA. Both shark species consumed the same three major prey groups (shrimp, squid, and fishes), however *A. brunneus* exhibited a similar preference for all three prey categories, while *P. xaniurus* exhibited a preference for shrimp. *Apristurus brunneus* diet composition varied with sampling season, latitude, sex, and total length. In contrast, the diet of *P. xaniurus* only varied with sampling season and total length. The results of the SIA indicated similar results. In *A. brunneus*, δ^{15}N varied with latitude, sex, and total length while δ^{13}C varied with latitude and total length. *Parmaturus xaniurus*' SIA variation was as a function of total length, latitude, and season for δ^{15}N and δ^{13}C varied with latitude and season. SCA and SIA metrics indicated that the size of dietary niche was consistently smaller for *P. xaniurus*. Species with a smaller niche size are considered to implement specialist feeding strategy, whereas a much larger niche (like *A. brunneus*) would indicate generalist diet. Despite the differences in the size of the dietary niche, both SCA and SIA found significant trophic overlap between the two species, such that *P. xaniurus* samples are nearly completely contained within the isotopic space of *A. brunneus*. While there is significant dietary overlap, in order for there to be competition between species resources must be limiting. In central California, resources are likely not limiting and these two species have implemented feeding strategies that maximize their net energy gain even when a strong co-competitor is present. Ultimately, the knowledge gained on the dietary and competitive habits of these two species improves our understanding of their role in the deep-sea ecosystem of central California and this new knowledge will aid managers in the implementation of ecosystem-based fisheries management.

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Introduction

The rapid expansion of commercial fishing and the exploitation of deep-sea fish stocks has renewed interest in understanding species distributions, population dynamics, and species interactions in the deep-sea (Devine et al. 2006; Haedrich 2007). To understand the potential impacts of fisheries on the deep-sea ecosystems and improve management, we need more data on life-history traits and predator-prey interactions of impacted species, including information on growth rates, timing of maturation, reproductive traits, and diet (Adams 1980; Heupel et al. 2007). Determining the trophic habits of a species can answer questions related to the species' location within a food web and how resources are used within their environment. Diet studies can also help predict how community structure and resource allocation will change in response to population changes. Examining the trophic habits and overlap of resident species can lead to better predictions of future ocean changes, but these studies can be logistically challenging to conduct in the deep-sea.

Competition is a species interaction where both parties are negatively impacted (Dayton 1971; Shurin and Allen 2001). Interspecific competition occurs when two species utilize the same limited resource (e.g. food, water, or space) (Colinvaux 1973; McIntosh 1985; Grant 1986). Competitive interactions can take the form of either interference competition or exploitative competition. Interference competition is the active process of preventing another species from accessing or utilizing a shared resource (e.g. territorial behavior of the damselfish, *Stegastes planifrons*, limits access of weaker competitors to algal resources) (Case and Gilpin 1974; Robertson 1996; Smallegange et al. 2006). In contrast, exploitative competition is a form of indirect competition where two species utilize the same resources and can deplete them to the detriment of the other species, but they do not interact directly to exclude each other from access (e.g. canopy-forming kelps limiting access to light resources by shading understory species) (Connell 1961; Bertness 1981; Hsu et al. 1981; Dean and Connell 1987; Watanabe et al. 1992; Smallegange et al. 2006). Exploitative competition can take many different forms, depending on the resource (i.e. prey, space or compounds necessary for life) being utilized (Ferguson et al. 2013).

Most often, we think of exploitative competition as a predator consuming a prey resource before another predator has the opportunity (Matsuda et al. 1993; Holt et al. 1994). However, two similar species occupying the same habitat and using the same resources may not experience the effects of competition unless resources become limiting (Grant 1986). When resources are limited, natural selection can act to reduce competition by partitioning resource use into different niches, so two similar species can coexist in the same habitat (Schoener 1974; Pacala and Roughgarden 1982; Josefson 1989). Reducing competitive effects through the partitioning of resources helps organisms efficiently meet daily metabolic needs, build energetic reserves for reproduction, or support demands during times of resource scarcity (van Valen 1965; Roughgarden 1972; Bearhop et al. 2004). Trophic overlap theory predicts that resource partitioning in time and space will allow two (or more) species with similar dietary habits to coexist in the same habitat (Gonzalez-Solis et al. 1997; Cardona 2001; Bizzarro et al. 2007). A high degree of trophic overlap implies that two species are consuming similar diets and thus competition is more likely (Gonzalez-Solis et al. 1997). Low trophic overlap indicates that the diets of the two species are different and natural selection has partitioned resources to allow species to fill different trophic niches, much like Darwin’s finches (Grant and Grant 2002). Dietary partitioning, therefore, has a large impact on the amount of prey available and the metabolic cost of resource acquisition.

Although Darwin's finches are the most notable example of trophic overlap leading to dietary specialization, trophic overlap is also common in the marine environment (Connell 1961; Reynoldson and Bellamy 1970; Peterson and Andre 1980; Robertson 1996). In fact, many of the classic examples of competition are from marine environments (Paine 1966; Targett 1981; Menge 1992; Edgar and Shaw 1995; Trites et al. 1997). Despite numerous examples of competition in the marine environment, most examples occur in the nearshore coastal environment, with a severe lack of attention to other marine habitats. The ecological paradigm developed in kelp forest, coral reef and other coastal ecosystems about the importance of competition in regulating community structure can help us develop questions about the potential influence of competition in other less studied areas of the ocean, such as the deep-sea.

The deep-sea (typically defined as deeper than 200 meters) is the largest habitat on Earth (Marshall 1979). The ecosystem is characterized by low food availability and stable environmental conditions that do not promote changes in community composition (Thiel 1983; Pèrés 1985). Although vast, this habitat is understudied compared to its nearshore and epipelagic counterparts, primarily due to the extreme logistical challenges of studying the deep-sea (Herring 2002; Devine et al. 2006). These logistical challenges often result in studies with low statistical power due to low sample size (Carrassón et al. 1992; Navarro et al. 2014). Existing information on competitive interactions in the deep-sea indicates that competition can be difficult to detect due to the relatively high environmental stability of the ecosystem (Gage and Tyler 1991), however questions regarding trophic overlap and competition remain unresolved.

The family Pentanchidae is the most specious family of the Chondrichthyans, with over 100 species inhabiting every ocean across the world, and with the highest diversity occurring in the deep-sea (Springer 1979; Eschmeyer et al. 2018). Sharks in this family are small (no larger than 1.5 meters in length) and are characterized by similarities in jaw morphology (Springer 1979). While the family is broadly distributed, species typically have small geographic ranges that overlap with other species in the family (Ebert et al. 2013). Studying the trophic habits of these mid-level predators may allow us to use their diet as a predictor for changes occurring in the deep-sea ecosystem (Olaso et al. 2004).

Two species from the Family Pentanchidae, the brown catshark (*Apristurus brunneus*) and the filetail catshark (*Parmaturus xaniurus*), have similar morphology and inhabit the same depths throughout most of their respective ranges. Both species are found in waters offshore from central California, making this the ideal location to investigate the potential for competition for dietary resources between these two species (Lee 1969; Cross 1988; Olaso et al. 2004). The limited diet data available reveals that small teleosts, crustaceans and cephalopods are important components of both species' diets (Jones and Green 1977; Cross 1988). However, these studies were conducted in British Columbia, Canada (*A. brunneus*, Jones and Green 1977), and Southern California (*A. brunneus* and *P. xaniurus*, Cross 1988), where geographic overlap of both species is low. For my thesis, I will conduct a detailed study comparing the trophic ecology between these species to test whether there is the potential for trophic competition on the central coast of California, a location where both species have large historical population sizes. This will allow for extrapolation to areas around the world where other members of this family overlap in geographic range and likely overlap in diet.

Two methods were implemented to assess the trophic ecology and diet of *A. brunneus* and *P. xaniurus*: stomach content analysis (SCA) and stable isotope analysis (SIA). Historically, SCA was the primary method for assessing trophic habits of different species or individuals. SCA provides a quantitative assessment of the relative contribution of different species or groups of prey to a predator's overall diet (Hyslop 1980). Prey items found in the digestive tract of an individual are identified to the lowest taxonomic level and then counted and weighed (Hyslop 1980). The relative contributions can be calculated by looking at the number of individuals from a prey group found in the digestive tract, the weight of all individuals from a prey group, or a combination of both. By looking at the diet through multiple facets (number and weight), the likelihood of a prey group being overlooked due to its morphology will be reduced. SCA is powerful tool for assessing trophic ecology due to the ability to identify prey with high taxonomic resolution, however it has a few shortcomings: it only provides an instantaneous snapshot of the diet, digestion times can lead to the amplification of one species over another, and it often requires lethal sampling (Beukers-Stewart and Jones 2004; Hussey et al. 2011). Pairing SCA with SIA enables the ability to paint a more complete picture of the diet, with each method complimenting the other.

The easiest way to understand the workings of SIA is the maxim: *You are what you eat*. As predators consume dietary resources, the isotopic signatures of those resources are incorporated into the tissue of the predator through isotopic fractionation. Stable isotope analysis provides estimations of trophic position and habitat utilization by using the ratios of heavier isotopes $^{13}C/^{12}C$ (or $\delta^{13}C$) and $^{15}N/^{14}N$ (or $\delta^{15}N$), relative to international standards (Peterson and Fry 1987; Fry 2007). Nitrogen-15 increases relative to Nitrogen-14 as trophic level increases through biomagnification at approximately 3-4‰ for every trophic level (Fry 2007; Post 2002). Isotopic carbon does not change in the same way; ratios remain relatively constant across trophic levels (~0.5‰ increase in Carbon-13 relative to Carbon-12 as trophic level increases), but vary depending on the source of primary production at the base of the food chain (Fry 2007). In the marine environment, enriched $\delta^{13}C$ values often indicate the source of primary production is from benthic/coastal zone while depleted $\delta^{13}C$ values often represent a source of primary production from the offshore/pelagic system (Deniro and Epstein 1978; Fry 2007). SIA integrates prey consumption over the span of weeks to years depending on the type of tissue examined as different tissues have different turnover times (Hussey et al. 2012). Studies of deep-sea elasmobranchs have shown that turnover times for white muscle tissue occurs on the order of months to a year (Van Dover et al. 1992; Post 2002). Extensive sampling of the isotopic composition of prey tissues is required to provide clarity on the relative importance of different prey types in the diet.

This study used SCA and SIA to assess the trophic ecology of *A. brunneus* and *P. xaniurus* where the species co-occur in central California, a geographic region where both species are abundant and unstudied. Both analysis methods were used to address the following objectives: 1) To characterize the diet of *A. brunneus* and *P. xaniurus*; 2) To determine how diet varies as a function of depth, latitude, longitude, maturity, season, sex, trawl composition, and total length within each species; 3) To determine the tropic level of each species; and 4) To determine the degree of trophic overlap between the two species. Based on previous studies, it is predicted that *A. brunneus* will feed primarily on penaeid/carid shrimp, teuthid squid, and teleosts and *P. xaniurus* will feed on penaeid/carid shrimp and teleosts (Jones and Geen 1977; Cross 1988). Of the eight environmental and biological factors collected, it is predicted that the diets of these species will vary as a function of depth, maturity, sampling season, total length, and trawl composition (Specziár and Erős T. 2014; Yurkowski et al. 2016; Giraldo et al. 2017; Ratcliffe et al. 2018). Significant variations within each species' diet would be a result of changes in prey population size and availability (depth, sampling season, and trawl composition) or ability to consume variable sized prey (maturity and total length). Conversely, trophic habits will not vary as a function of latitude, longitude, or sex because of the relatively restricted geographic sampling range (latitude and longitude) and due to these species not sexually segregating. Based on the predicted important prey groups, it is predicted that both analysis methods will show that the trophic level of *A. brunneus* and *P. xaniurus* will be that of a tertiary predator (trophic level≈4). Finally, it is predicted that *A. brunneus* and *P. xaniurus* have significant overlap in their diets. Their diets may not be identical, but these two species will be occupying a similar trophic niche.

Materials and Methods

Study Species Natural History

This study focuses on two species in the Family Pentanchidae that inhabit the central California coast. *A. brunneus* ranges from Alaska, U.S.A., to Baja California, Mexico, and possibly down to Ecuador (Ebert 2003; Flammang 2005; Ebert et al. 2013), but field observations indicate that the species is most common between Washington and Point Conception, California, U.S.A. (Kamikawa pers. com. 2017; NOAA NWFSC). *Parmaturus xaniurus* has been reported from Oregon, U.S.A. to the Gulf of California, Mexico (Ebert et al. 2013), but most commonly found from Point Reyes to San Diego, California, U.S.A (Northwest Fisheries Science Center 2018). Both species are found in demersal habitat over the outer continental shelf to the upper continental slope, inhabiting maximum depths of 1200-1300 m (Ebert 2003; Ebert et al. 2013). *Apristurus brunneus* reaches a maximum recorded total length of 69 cm and both males and females mature at approximately 50 cm (Flammang et al. 2008; Ebert et al. 2013). *Parmaturus xaniurus* is a slightly smaller species that only reaches a maximum recorded total length of 61 cm and males reach maturity between 37 and 45 cm, while females mature between 42 and 50 cm (Balart et al. 2000; Ebert et al. 2013). Aging studies for both species have not been performed due to poorly calcified hard parts; thus, it is unclear at what age these sharks mature or how quickly they grow (Cailliet et al. 1983; Tieszen et al. 1983).

While neither species is economically important, they are often taken as bycatch in sablefish traps, longline and trawl fisheries. Other related species occur primarily in different habitats. *Apristurus kampae* (Longnose Catshark) is typically found in deeper water than the targeted sampling habitat and *Cephaloscyllium ventriosum* (Swell Shark; Family Scyliorhinidae) occurs in much shallower water and over rocky, high relief habitat.

Study Area and Sample Collection

Samples of *A. brunneus* and *P. xaniurus* were collected between June 2017 and October 2017 off the coast of central California, between Pescadero Point (Latitude: 37.2°) and just north of Point Conception (Latitude: 34.9°). Samples were collected on board chartered commercial fishing vessels through the West Coast Groundfish Bottom Trawl Survey (WCGBTS) conducted by the Fishery Resource Analysis and Monitoring (FRAM) Division of the National Oceanic and Atmospheric Administration’s (NOAA) Northwest Fisheries Science Center (NWFSC). The WCGBTS uses fishery independent sampling to assess groundfish population status along the entire West Coast of the United States (Keller et al. 2017). Depths between 55 and 1280 m were split into adjacent grid cells (2 latitudinal nautical miles by 1.5 longitudinal nautical miles) and cells were selected by stratified random sampling design then sampled using standardized Aberdeen trawl and warp fishing gear. Specimens were collected from trawls conducted primarily over soft-bottom, low-relief habitat. The average working dimensions of the trawl while fishing were 13.5 meters wide and 5.1 meters tall with 5.5 inch mesh and 1.5 inch codend mesh liner. Twenty stations were sampled in the central California region and information was recorded on the location (latitude and longitude), depth, and date (Figure 1). When the trawl net came on board the vessel, fish were sorted by species, enumerated, and trawl composition (the proportion of each species in relation to the total number of *A. brunneus* and *P. xaniurus* caught), and specimens of the study species were retained for this study. Specimens were frozen in bags with sharks of the same species from the same trawl location and then were transported back to Moss Landing Marine Laboratories for dissections.

Specimens were thawed in room temperature water (~20°C), given a unique identifier, and measured for total length and body girth (measured just posterior to the pelvic fins) to the nearest millimeter, then weighed to the nearest 0.1 gram. During dissections, stomachs were removed for gut content analysis, a piece of white muscle tissue was collected for stable isotope analyses, the liver was removed to assess body condition, and gonads were removed to assess maturity. To ensure all stomach contents were collected, I extracted material from the esophagus (posterior to the heart) to the beginning of the spiral valve. All internal parts of the reproductive system were grouped into the term gonads. The stomach, liver, and gonads were weighed to the nearest 0.01gram. Two 2 mL vials were filled with white muscle tissue taken from the vertebral region. Stomachs and muscle tissue were refrozen for later gut content or stable isotope analysis.

The stage of maturity was assigned to each specimen using a numeric ranking system. Maturity was assessed externally for males and internally for females (Ebert 1996; Ebert 2005; Ebert et al. 2006). The ranking system was described as follows: (1) Newborn pup: males possess flexible, short claspers (total length typically less than half of the pelvic fin inner margin) and females’ ovaries show no development of eggs or structure. (2) Juveniles: males have clasper total length that is just less than the pelvic fin inner margin and are still flexible. Females possess ovaries that show some development, but the oviducts remain thin and string-like. (3) Adolescent: males' claspers surpassed the pelvic fin free rear tip, but lack calcification of the terminal edge. Females have developed ovaries with small, underdeveloped oocytes. (4) Mature: male claspers surpass the pelvic fin free rear tip and are firm with a calcified terminal edge. Females have fully developed ovaries with large, yellow, yolky oocytes. (5) Pregnant: this classification was only used on females and was when egg cases were present in one or both of the uteri of the individual.

Stomach Content Analysis (SCA)

Stomachs were thawed in cold water and the contents were sorted and identified to the lowest taxonomic level. Each prey item was blotted dry using paper towels and weighed to the nearest 1 mg. Under a dissecting scope at 10-50x power, items were sorted and the minimum number of unique prey individuals were determined for each stomach. In cases where contents were partially digested, hard parts (e.g. beaks and otoliths) were used to determine the minimum number of individuals. Digested material that could not be identified to any taxonomic level was weighed and classified as "unidentified prey" to compensate for the total weight of prey items in the whole stomachs. This category was excluded from the counts and other analyses described below. Parasites and inorganic material were also excluded because they are not targeted prey items of the predator.

The required sample sizes were calculated with cumulative prey curves (Ferry and Cailliet 1996) using values from Cohen (1988) (α=0.05 and β=0.20, Figure 2). Cumulative prey curves evaluate whether the number of stomach samples is sufficient to describe differences between prey categories observed in the diet. The observed prey categories were plotted against the cumulative number of viable stomachs sampled in the study (Bigman 2013). Prey curves with 95% confidence intervals were generated to verify that the collected sample size was large enough to identify differences in the prey categories using the "Vegan Community Ecology package" in R (Oksanen et al. 2011; Bigman 2013).

Stomach content analyses followed Brown et al. (2012), and focused on prey-specific abundances (for both the fourth root transformed number and weight data) as opposed to the historical metrics of percent number and percent weight (Hyslop 1980; Amundsen et al. 1996; Cortes 1997). Prey-specific abundances are considered a better metric to characterize stomach content data because they represent the average abundances of each prey category over all the samples in which the prey category is present (Brown et al. 2012). This eliminates potential zeros from the analysis, thus giving a better representation of the importance (or lack thereof) of prey categories in the diet. Prey-specific metrics move away from describing diet on a population level and move toward describing diet on an "inter-individual" level (Brown 2010; Brown et al. 2012; Bigman 2013).

To characterize the diet of each species, the following indices were used to describe the diet of *A. brunneus* and *P. xaniurus*:

Index 1. Prey-specific abundances for both number and weight (%PN and %PW):

$$PA_i = \frac{\sum_{j=1}^{n} A_{ij}}{n_i}$$

Where A_{ij} is the proportional abundance (number or weight) of each prey category *i* in stomach sample *j*. n_i is the number of stomachs that contain the prey category *i*.

Index 2. Average percent abundance for both number and weight (%N and %W):

$$A_i = \frac{\sum_{j=1}^{n} A_{ij}}{n}$$

Where A_{ij} is the proportional abundance (number or weight) of each prey category i in stomach sample j and n is the number of stomachs sampled.

Index 3. Frequency of Occurrence (FO):

$$FO = \frac{n_i}{n}$$

Where n_i is the number of stomachs that contain the prey category i and n is the number of stomachs sampled.

Index 4. Prey-specific index of relative importance (PSIRI):

$$PSIRI_i = \frac{\%FO_i * (\%PN_i + \%PW_i)}{2}$$

Where $\%FO_i$, $\%PN_i$, $\%PW_i$ are all expressed as percentages of the proportional indices above.

To determine which environmental or biological factors contribute to differences in the diet within each species, a series of permutational multivariate analysis of variance (PERMANOVA) models were run on the fourth root transformed number and weight data for each shark species (Anderson 2001, Anderson 2014). Stepwise model selection criteria identified the best fit PERMANOVA model using a forward selection approach. Results from single factor PERMANOVA models determined the strength of each factor on an individual basis. Then factors were added to the model in the order of largest F-statistic from the single factor PERMANOVA models. Stepwise selection criteria terminated when the model met two standards: 1) all included factors and interactions were significant and 2) the model had the highest combined F-statistic amongst all other model combinations. The following factors were tested in the models: depth, latitude, longitude, season, sex, trawl composition, and total length (maturity was excluded because it significantly covaries with total length). The PERMANOVA models identify where differences occur within a factor, but it does not identify the trends in diet between levels in a significant factor (Anderson 2014). Additionally, stacked bar plots (categorical variables) and simple linear regressions (continuous variables) were used to identify the drivers of dietary differences within the two shark species.

Trophic level was calculated for each species from the stomach content data using an adaptation of Cortes' (1999) equation to include both weight and number data:

Index 5. Prey proportion in the diet

$$P_j = \left(\sum_{i=1}^{n} P_{ij} * N_i\right) / \left(\sum_{j=1}^{5}\left(\sum_{i=1}^{n} P_{ij} * N_i\right)\right)$$

Where P_j is the proportion of prey category j in the diet. P_{ij} is the proportion of prey category j in stomach i, N_i is the number of sampled stomachs with identified prey items, n is the number of stomachs and j is the number of prey categories. P_j was calculated for both number and weight data and the average of those two values was called $\overline{P_j}$.

Index 6. Trophic level

$$TL = 1 + \left(\sum_{j=1}^{5} \overline{P_j} * TL_j\right)$$

Where TL_j is the trophic level of prey category j. Trophic levels for prey categories were taken from several sources (Sydeman et al. 1997; Cortes 1999).

To test the degree of dietary overlap between the two species of catsharks, Zaret and Rand's (1971) dietary overlap coefficient was used.

Index 7. Dietary overlap coefficient

$$\hat{C}\lambda = \frac{2\sum_{i=1}^{S} X_i Y_i}{\sum_{i=1}^{S} {X_i}^2 + \sum_{i=1}^{S} {Y_i}^2}$$

Where S is the total number of food categories, X_i is the proportion of prey item, i, in the diet of species X and Y_i is the proportion of prey item, i, in the diet of species Y. The dietary overlap coefficient produces values between 0 and 1. Values at 0 represent dietary compositions with no overlap and values at 1 indicate species with identical diets in terms of proportionality. According to Zaret and Rand (1971), any value greater than 0.60 is considered significant overlap.

Non-metric multidimensional (nMDS) scaling plots using a Bray-Curtis dissimilarity matrix were used to visually identify how the diets of the two species differed. These plots show the prey categories as vectors from the origin and ellipses of the predators' 95% confidence trophic region (Dixon 2003). Prey categories that fall closer to the centroid of the predator ellipses are more important to that species diet. Visualizing the overlap in the 95% confidence regions along with the prey vectors helps identify which dietary resources are more commonly shared between the two species.

Stable Isotope Analysis (SIA)

Stable isotope levels in white muscle tissue samples were analyzed following the methods of Kim and Koch (2012), which recommends using petroleum ether to remove lipids more efficiently and minimize the loss of amino acids, which contain nitrogen (Dobush et al. 1985). Because most elasmobranch species retain high levels of urea and trimethylamine oxide for osmoregulation, the samples were rinsed with DI water to remove urea from the muscle tissue, as the presence of urea can inflate isotopic nitrogen values (Fisk et al. 2002; Hussey et al. 2012; Kim and Koch 2012). DI water was added to the sample vials, the vials were placed in a sample shaker for 15 minutes, and finally the water was decanted. The process was repeated twice to ensure residual urea had been removed. All DI rinsed samples were freeze-dried using a Labconco FreeZone Freeze Dryer for 48 hours at -50°C at 0.002 mBar. Once dried, the sample was crushed to a powder using 5 mm stainless steel grinding balls and ball mill. Once in powdered form, petroleum ether was used to extract lipids, instead of the traditional ethanol or methanol, because ethanol and methanol can alter carbon isotope results (Kim and Koch 2012). Petroleum ether was added to each sample, shaken for 15 minutes, spun in a centrifuge for 10 minutes to pack the powdered sample to the bottom of each vial, and then the petroleum ether was decanted. The process was completed a second time and then the samples were left in a fume hood overnight to allow residual petroleum ether to vaporize.

In addition to the predator white muscle samples, isotopic analysis was conducted on minimally decomposed prey items that were found in the stomachs of either species. The prey isotopic data was used to give insight to the trophic ecology of the two predator species (Layman et al. 2012). To prepare prey samples for isotopic analysis, prey tissue was cleaned with DI water, indigestible parts removed from the sample, freeze fried under the same standard as the shark tissue, and crushed to a powder using a DI-water-rinses mortar and pestle. Indigestible parts, such as squid beaks, were excluded from the analysis because although they are consumed, they are not digested, thus the isotopic nitrogen and carbon are not incorporated into the predator tissue.

Tissue samples of the two catsharks and prey were analyzed at the Center for Stable Isotopes at the University of New Mexico, using a Thermo Scientific Delta V mass spectrometer with a Costech 4010 elemental analyzer. The results of the mass spectrometer are expressed in standard δ notation, calculated using the following equations (Peterson and Fry 1987):

$$\delta^{13}\mathrm{C} = \left[\frac{C_{sample}}{C_{std}} - 1\right] \times 1000 \qquad \delta^{15}\mathrm{N} = \left[\frac{N_{sample}}{N_{std}} - 1\right] \times 1000$$

Where C_{sample} is the measured isotopic carbon ratio in the sample and C_{std} is the isotopic ratio of the carbon ($^{13}C/^{12}C$) from PeeDee belemnite, N_{sample} is the measured isotopic nitrogen ratio ($^{15}N/^{14}N$) in the sample and N_{std} is the isotopic ratio of the nitrogen taken from nitrogen gas in the atmosphere (Peterson and Fry 1987). The $\delta^{13}\mathrm{C}$ and $\delta^{15}\mathrm{N}$ isotope values were expressed per mil (‰) and used in the following analyses to determine the trophic habits of each species. To calculate the trophic level of each species, Post's (2002) trophic level equation was used:

$$TL_{predator} = \frac{\delta^{15}\mathrm{N}\ _{predator} - \delta^{15}\mathrm{N}_{prey}}{3.4} + TL_{prey}$$

Where TL indicates the trophic level of an animal and the prey values are a composite means based on proportional contribution to the diets found in the SCA (PSIRI). $\delta^{15}\mathrm{N}_{prey}$ values were found from the tissue taken from prey items found in the stomachs of the two predators. The trophic levels of the prey were taken from Cortes (1999) and Sydeman et al. (1997).

To determine which environmental or biological factors contribute to significant differences in the $\delta^{13}\mathrm{C}$ and $\delta^{15}\mathrm{N}$ values within each species, PERMANOVA models were used similarly as described for the SCA analysis. Once again, the PERMANOVA models identify which factors contribute to differences, but do not identify the trends in response variables between levels in a significant factor (Anderson 2014). Final models were selected using the same criteria described earlier for SCA. The factors that were included in the models were: depth, latitude, longitude, season, sex, trawl composition, and total length (maturity was excluded because it significantly covaries with total length). The PERMANOVA models further investigated using Stable Isotope Bayesian Ellipses in R (SIBER) (categorical factors) and/or simple linear regressions models (continuous factors) to identify how the isotopic data changed as a result of the eight factors tested. SIBER analysis takes the isotopic values (δ^{15}N, δ^{13}C) for every individual in a group and plots them on a bivariate plane (Jackson et al. 2011; Madigan et al. 2012; Syväranta et al. 2013). An ellipse is overlayed and represents the 95% confidence interval of δ^{15}N and δ^{13}C for the distinct groups. If the intervals do not overlap, the dietary niche areas are considered to be distinct. To compliment the SIBER ellipses, standard ellipse area (SEA) plots were created to display the difference in ellipse area between the levels within the categorical factors. These SEA plots represent the true species area contained by the 95% confidence interval ellipses and details the spread of the individuals in each group by displaying the 50%, 75%, and 95% credible intervals of standard area. By viewing these SIBER ellipses along with SEA plots, the differences between groups can be identified.

To further understand the characteristics of each species' trophic region and to determine the degree of isotopic trophic overlap, spatial isotopic metrics were used to quantify the size, spread, and evenness of the two isotopic niches (Layman et al. 2007). The 6 metrics include: range of δ^{13}C and δ^{15}N, mean distance to the centroid (CD), mean nearest neighbor distance (NND), standard deviation of nearest neighbor distance (SDNND), and total convex hull area (TA). CD is used to depict the amount of spread of isotope values within a species; NND is used to measure the density of isotopic samples within the species; SDNND is used to show the level of evenness in isotopic values within the species; and TA is used to show the total amount of trophic niche space occupied. Individuals from both species was plotted on a 2-dimensional isotopic plot and the standard isotopic niche area was calculated for each species using the R package Stable Isotope Bayesian Ellipses in R (SIBER). SIBER was used to visualize the degree of trophic overlap between the two species, with the assumption that populations of generalist feeders will have larger ellipses while populations with less dietary diversity will have smaller ellipses (Jackson et al. 2011).

To statistically determine the degree of overlap between the two species, the R package nicheROVER implemented a probabilistic approach to determine the overlap of ecological niches (Swanson et. al 2015). This method plots the niche region of multiple species and puts their trophic overlap into quantifiable probabilities. nicheROVER can examine multiple species and multiple elemental stable isotopic ratios, but for this research nicheROVER was used for the two predator species on a 2-dimensional isotopic plane. In nicheROVER, 1000 random SIBER standard isotopic niche ellipses were generated by the Bayesian analysis and overlap metrics were calculated from 1000 Monte Carlo draw which results posterior probability frequency distribution of an *individual of Species A* falling into the niche region of *Species B* (Swanson et al. 2015). Finally, a 95% confidence interval was constructed within the probability distribution. Thus, there is a quantifiable measure of the degree of trophic niche overlap between the two species.

Results

Specimen Characteristics

There were a total of 304 *A. brunneus* and 303 *P. xaniurus* collected on the WCGBTS during 2017. The total lengths of *A. brunneus* ranged between 48 mm and 700 mm with a mean of 392 mm (±7.96 standard error). Total lengths of *P. xaniurus* were more narrowly distributed between 205 mm and 570 mm with a mean of 327 mm (±3.30 standard error). Two boats sampled in the fall and only one collected in the summer which resulted in a higher percentage of samples being collected during the fall (*A. brunneus*: 64%, *P. xaniurus*: 67%) than the summer.

The percentage of female to male samples was nearly even for both species (*A. brunneus*: 53% F: 47% M, *P. xaniurus*: 52% F: 48% M)

Stomach Content Analysis (SCA)

Of the total number of sharks collected, I sampled 229 (75%) *A. brunneus* and 258 (85%) *P. xaniurus* stomachs that contained identifiable prey items (Table 1). Only non-empty stomachs were included in the following results. There were a total of 1675 prey items identified between both species that fell into 18 unique prey categories, 8 of which were identified down to the species level. These 18 prey categories were grouped into 5 functional groups (Table 2). Taxonomic resolution varied across prey functional groups. Hard parts, such as beaks and otoliths, made identification more accurate when present in the stomachs. 78.7% of squid found in stomachs were identified to the species level compared to only 21.5% of fishes and 10.2% of shrimp. The digestion process of shrimp was rapid which led to highly digested individuals making taxonomic identification challenging. Despite digestion, 40.5% of shrimp individuals found in the stomach were able to be identified to the orders listed in Table 2 (Caridea, Euphausiacea, Sergestoidea, Mysida, and Isopoda).

Apristurus brunneus

Apristurus brunneus stomach contents were dominated by three functional groups: squid (46.73% PSIRI), shrimp (28.39% PSIRI), and fishes (24.59% PSIRI) (Figure 3; Table 3). Pyrosomes were observed in this study, however none were found in the stomachs of *A. brunneus*. The hierarchy of frequency of occurrence followed the same patterns as PSIRI; squid were the most commonly found item in stomachs (FO=70%), followed by shrimp (FO=43%), and fishes (FO=38%). The single species that contributed to the highest level of importance across all taxa was *Stigmatoteuthis dofleini* (30.15% PSIRI) (nested in squid functional group), which occurred in 48% (FO) of the stomachs sampled. In general, the diet of *A. brunneus* exhibited uniformity across the 3 main prey taxa groups in terms of %PSIRI, %PN, and %PW. Although uniform, shrimp was most important by weight and squid was most important by number. This difference between number and weight data could be attributed to the slower digestion rate and high taxonomic resolution of squid beaks found in the stomachs.

The diet of *A. brunneus* varied as function of the following factors: season, latitude, sex, total length and an interaction between season and total length (Table 4). Season and latitude were included as significant factors in the PERMANOVA models for both the %N and %W datasets. Sex was only a significant factor for the %N data and total length and the interaction between season and total length were found to be significant in the %W data. The dietary variation by season showed that *A. brunneus* consumed more squid in the fall by number and more fishes in the fall by weight (Figure 4; Figure A1). The proportion of shrimp between the two seasons sampled did not change significantly and the difference between the two seasons can be attributed to the differences in consumption of squid and fishes. The interaction gave much insight to the differential diet between seasons and total length. There was no significant difference between small and large sharks across all four prey functional groups for sharks caught in the fall. Nearly all the variability observed in season and total length was a result of the variability in diet from sharks captured in the summer sampling season. The trends for latitude were similar between %N and %W for *A. brunneus*. As latitude increased (from south to north), *A. brunneus* consumed fish species at an increasing rate, while shrimp were consumed at a decreasing rate (Figure 4; Figure A1). The importance of squid did not change across the latitudinal gradient, and were the most important functional prey group (in terms of %N and %W) across all latitudes sampled. Sex differences in the diet were only significant for *A. brunneus* in the %N data. Males consumed proportionally higher number of squid while females consumed proportionally higher number of fishes. No differences in the importance of shrimp and crabs occurred between the two sexes. Finally, total length explained significant changes in the %W diet data of *A. brunneus*. Fishes comprised a larger proportion of the diet in larger sharks, while smaller sharks fed more on shrimp and squid (Figure 4; Figure A1). The PERMANOVA for the %W data produced a significant interaction between season and total length. The interaction revealed that there was little variability in diet across the size distribution for sharks caught in the fall season, but much bigger differences in dietary composition between large and small sharks in the summer. The calculated trophic level for *A. brunneus* through the use of stomach content analysis is 4.01 (Table 5). This means that *A. brunneus* would be classified as a tertiary consumer.

Parmaturus xaniurus

The diet of *P. xaniurus* contained all five groups of identifiable prey from Table 2, however the diet was dominated by shrimp (64.3% PSIRI) (Figure 3; Table 3). The other four groups of prey contributed less to the overall composition of the diet, in decreasing order: squid (21.99% PSIRI), fishes (9.96% PSIRI), crabs (3.45% PSIRI), and pyrosomes (0.30% PSIRI). Fishes had a relatively low frequency of occurrence (FO=25%), but when fishes were present in the stomach of a single individual, they often contributed most to the diet in both number and weight. A similar trend was also seen in pyrosomes; they were observed in very few stomachs, but occupied a large proportion of the stomachs they were present in. The %PN, %PW, and FO data indicate that shrimp were the most dominant prey species in the diet of *P. xaniurus* (FO=85%). *Euphausia pacifica* (family Euphausia) was the most common species in the diet of *P. xaniurus* (8.14% PSIRI) and occurred in 9.7% (FO) of the stomachs sampled.

Due to the dominance of shrimp, the diet of *P. xaniurus* was less variable among individuals than I observed in *A. brunneus*. The factors that contributed to dietary differences for *P. xaniurus* in the PERMANOVA models were season and total length (Table 4). Because shrimp were the most important prey group, proportional differences in the other functional groups lead to differences between factors. *P. xaniurus* fed on higher proportions of squid (both %N and %W) in the fall season, which explained seasonal differences in diet (Figure 5; Figure A2). Additionally, the pyrosomes were only observed in the fall season. Diet also varied as a function of total length for both the %N and %W data sets. As the total length of the *P. xaniurus* increased, the diet was still dominated by shrimp, however other prey groups (fishes, squid, and pyrosomes) were also incorporated into the diet (Figure 5; Figure A2). Finally, there was an overall decrease in the proportion of crabs consumed as total length increased. The calculated trophic level of *P. xaniurus* from the stomach content analysis data was 3.72 (Table 5). This means that *P. xaniurus* falls between a secondary and tertiary consumer.

Trophic Overlap

Overall, both species consumed the same general taxonomic prey groups, however difference in the importance of certain groups to their respective diets resulted in different dietary niches (Figure 6; Figure A3). According to the nMDS, the dietary niche of *A. brunneus* is much larger and this species tends to feed on multiple prey groups in relatively equal proportions, whereas the niche of *P. xaniurus* is much more restricted and consists primarily of shrimp (Figure 6; Figure A3). The dietary overlap coefficient between *A. brunneus* and *P. xaniurus* was 0.62 (%N) and 0.87 (%W), indicating high overlap in prey categories. Although the dietary niche of *A. brunneus* is much larger than that of *P. xaniurus,* there is significant overlap between the two species. These results indicate there is less variation between individuals within *P. xaniurus* (i.e., all individuals eat the same prey), while individual *A. brunneus* appear to exhibit more inter-individual specificity in their diet.

Stable Isotope Analysis (SIA)

There were 297 *A. brunneus* and 296 *P. xaniurus* muscle tissue samples analyzed for δ^{13}C and δ^{15}N stable isotope analysis. The grouping of samples by depth, region, sex, and body size were similar to those for SCA (Table 1). The average δ^{13}C and δ^{15}N (with standard deviation) for *A. brunneus* was -17.79 ‰ (±0.27) and 17.21 ‰ (±0.65) respectively and for *P. xaniurus*, the values were -17.39 ‰ (±0.18) and 17.40 ‰ (±0.36) (Table 6). The stable isotope values for both species are similar, but the lower standard deviation for *P. xaniurus* indicates less inter-individual variability in the diet, as those samples are more tightly grouped around the average δ^{13}C and δ^{15}N values (Figure 7).

Apristurus brunneus

PERMANOVA models were used to identify biological and environmental factors that contributed to significant differences in the δ^{13}C and δ^{15}N values. The significant factors for *A. brunneus* were total length, sex, latitude, and an interaction between total length and sex (Table 7). There was a significant decrease in δ^{13}C as total length increased ($\delta^{13}C = -0.0004 * TL - 17.62$, p<0.001), however, in contrast, there was a significant positive relationship between total length and δ^{15}N ($\delta^{15}N = 0.29 * TL + 6.79$, $p<0.001$), indicating that larger sharks are feeding at higher trophic levels (Figure 8). Differences in diet as a function of sex are explained by the overall larger isotopic niche size of males compared to females (Figure 8). The interaction between total length and sex occurred because females did not exhibit a change in δ^{15}N with total length, whereas δ^{15}N increased significantly in males with increasing total length. Both δ^{13}C ($\delta^{13}C = 0.08 * °N - 20.53$, $p=0.005$) and δ^{15}N ($\delta^{15}N = 0.29 * °N + 6.79$, $p<0.001$), exhibited a significant increase as latitude increased (from south to north) (Figure 8). The calculated trophic level of *A. brunneus* for the stable isotope data is 3.76 (Table 5). This is similar to the calculated trophic level found using SCA, supporting the notion that *A. brunneus* is a tertiary consumer.

Parmaturus xaniurus

The PERMANOVA models for *P. xaniurus* produced the following significant factors: total length, latitude, season, and an interaction between total length and season (Table 7). There was not a significant linear trend for δ^{13}C as total length increased ($p=0.566$), but δ^{15}N did increase significantly as individuals increased in size ($\delta^{13}N = 0.003 * TL + 16.37$, $p<0.001$) (Figure 9), indicating that larger individuals feed at higher trophic levels. Both δ^{13}C ($\delta^{13}C = 0.04 * °N + 18.94$, $p=0.003$) and δ^{15}N ($\delta^{15}N = 0.19 * °N + 10.77$, $p<0.001$) increased with increasing latitude, similar to the pattern observed in *A. brunneus*. Both species appear to feed at higher trophic levels and on prey with more coastal isotopic signatures in the northern range in this study. Season influenced the isotopic levels of *P. xaniurus*, with individuals collected in the summer exhibiting a wider range of δ^{15}N values. δ^{13}C levels were similar in both summer and fall, but the larger range of δ^{15}N in the summer resulted in a larger trophic niche (Figure 9).

There was also an interaction between season and total length. The interaction between the terms showed that sharks in the summer did not show a difference in $\delta^{13}C$ across the size spectrum, but there was a significant enrichment of $\delta^{13}C$ as sharks got larger in the fall. Additionally, larger sharks in the summer saw a more dramatic enrichment of $\delta^{15}N$ in the summer that was not seen in the fall. The calculated trophic level of *P. xaniurus* using the SIA dataset was 3.45 (Table 5). This agrees with the calculated trophic level found using the SCA dataset that indicated the *P. xaniurus* sits between a secondary and tertiary consumer.

Trophic Overlap

Consistent with the SCA, the overlap analysis indicated that there was high niche overlap, but that the two species exhibited a different range of niche sizes. First, the standard ellipse area of *A. brunneus* (0.54‰^{2}) was over twice the size of *P. xaniurus'* (0.21‰^{2}) (Figure 10), which is also supported by calculated Layman spatial isotopic metrics (Table 8). The total convex hull area (TA) of *A. brunneus* is 2.7 times larger than *P. xaniurus'* TA (*A. brunneus*: 4.4‰^{2}, *P. xaniurus*: 1.7‰^{2}). The observed range in $\delta^{13}C$ were similar between the two species (*A. brunneus*: 1.6‰, *P. xaniurus*: 1.2‰), thus the twofold difference in niche size was largely driven by the range of $\delta^{15}N$ values (*A. brunneus*: 4.2‰, *P. xaniurus*: 2.1‰). The CD (0.35‰) and the NND (0.01‰) show that individuals of *P. xaniurus* are more tightly packed into a smaller niche range than *A. brunneus* (CD = 0.56‰; NND = 0.04). However, both species show similar evenness in spread between other individuals within their species (*A. brunneus*: 0.06‰, *P. xaniurus*: 0.04‰)

Secondly, there is high overlap for the $\delta^{15}N$ values between the two species but they show less overlap in the $\delta^{13}C$ (Figure 11). Finally, nicheROVER produced the 95% probabilistic likelihood of the two species falling into the other’s niche region. There is between a 31% and 45% chance of a randomly selected *A. brunneus* individual falling into the niche region of *P. xaniurus* (Figure 12). Whereas, there is between an 81% and 94% chance of a randomly selected *P. xaniurus* individual falling into the niche region of *A. brunneus* (Figure 12). Overall, there is high trophic overlap between the two species with the niche region of *P. xaniurus* nearly falling completely inside the niche region of *A. brunneus*.

Discussion

Diet

Apristurus brunneus and *P. xaniurus* are high trophic level consumers that live in a complex deep-sea food web that is largely understudied. The goal of this project was to further the basic life history knowledge of both species and to inform fisheries management decisions. While these two species are in the same family, are similar size, and reside in the same habitat, they may exhibit different feeding strategies. There are two broad categories of feeding strategies: specialists and generalists (Hyatt 1979; Amundsen et al. 1996); however, it is more common that a species occupies a space along the spectrum between these categories (Boyes and Perrin 2009). The implemented feeding strategy can indicate a species’ ability to adapt as the community composition around them changes. A generalist will be able to adapt with shifts in available prey, while a specialist could face challenges adapting to a lack of preferred prey.

The diet of *A. brunneus* contained three dominant prey groups that were relatively evenly distributed throughout the diet, with the most common prey item being *Stigmatoteuthis dofleini*. Additionally, both SCA and SIA showed that the dietary niche of *A. brunneus* was broad, which indicates that individuals within this species show much more variability in the prey that they consume. The increased variability and the evenness of prey selectivity implies that *A. brunneus* implements more of a generalist feeding strategy. Conversely, the diet of *P. xaniurus* consisted of prey from the same three prey groups, however the majority of the diet came from prey in the Shrimp category. The single most important prey species was *Euphausia pacifica* which had a PSIRI of 8.14%, however this value is likely much higher due to the challenges of identifying shrimp species. Again, the SCA and SIA results were consistent, demonstrating that *P. xaniurus* has a much more restricted dietary niche than *A. brunneus*. The smaller dietary niche implies that there is less inter-individual variability within this species. Due to the importance of a single species/ group and relatively low inter-individual variability, this implies that *P. xaniurus* exhibit more of specialist feeding strategy. Because *P. xaniurus* incorporates other prey into their diet, this suggests that the species selects their preferred prey when it is available and abundant (Boyes and Perrin 2009), but, when times are tough, they may shift their diet to incorporate less desirable prey. The calculated trophic level using SCA and SIA showed that both species are a tertiary consumer. The trophic level of *P. xaniurus* was slightly lower, primarily because of their specialization on prey in the shrimp functional group which is a lower trophic level than the other two prey categories that are heavily incorporated into the diet of *A. brunneus*: fishes and squid.

Two previous studies were conducted on the feeding habits of these two species in different geographic regions. Jones and Green (1977) used FO for *A. brunneus* samples collected off the coast of British Columbia and found that shrimp and fishes occurred with regularity in the diet and squid were present in some individuals. Cross (1988) conducted a SCA study on both species in waters between Santa Catalina Island and Orange County, CA. They found that both species heavily consumed crustaceans, but also consumed squid and shrimp with some regularity. Similar to this study, *A. brunneus* consumed the three prey categories relatively evenly, while *P. xaniurus* did not place very much importance on squid and fish prey categories. Other species of catsharks have been found to have similar trophic habits within their respective geographic ranges. Fishes, shrimp and squid are important components in the diet of many catshark species (Ebert et al. 1996, Barnett et al. 2013, Lopez et al. 2013). Most catsharks exhibit a generalist feeding strategy across the three dominant prey groups, but some members of the family exhibit relatively even distributions of importance across the three main prey categories, while other species show specialist tendencies. For example, the diet of *A. saldanha* on the west coast of southern Africa is comprised almost completely by fishes (Ebert et al. 1996). While most species did not deviate from fishes, shrimp, and squid, there are a few exceptions where a species tends to specialize on a more uncommon prey item. For example, nearly 70% of the diet of *Bythaelurus canescens* is siphonophores, but the remainder of the diet was composed of squid and fishes (Lopez et al. 2013). Overall, the diet of *A. brunneus* and *P. xaniurus* consists of similar prey groups as other species in the family, but the high occurrence of squid in the diet of *A. brunneus* may be regionally driven.

Biological and environmental factors influencing trophic variation

Both species show the same general trends in how their diet varies in response to biological and environmental factors. It was found that the most common factors (for both SCA and SIA) for dietary variation were sampling season, latitude and total length. Individuals were only collected in summer and fall of 2017 so it is impossible to determine if the species exhibit different dietary trends throughout the year. The central coast of California experiences three different oceanographic seasons: 1) upwelling from March to July caused by strong southerly winds, 2) ocean current season from August to November which occurs when the southerlies relax and the southward California Current moves closer to shore, and 3) the northward Davidson Current strengthens from December to February bringing warmer water up from Southern California (Skogsberg 1936, Skogsberg and Phelps 1946; Dawson 2001). These different oceanographic seasons contribute to differences in prey abundance and availability, which lead to changes in diet composition of these two species of predators (Broitman et al. 2008). The increase in shrimp in the diet during the summer season is consistent with greater abundance of euphausiids as a result of the effect of the upwelling season (Brinton and Townsend 2003; Rinewalt 2007).

Variation due to latitude was not expected due to the relatively small geographic sampling range. However, variations in habitat and associated prey availability contributed to differences in diet as sharks were captured from two different regions. The two regions sampled, (1) San Luis Obispo (SLO) from 34.92-36°N and (2) Monterey Bay/Big Sur (MBBS) from 36-36.94°N, are broadly characterized as having distinct habitat structure. The ecosystem of the SLO region is characterized by very low relief, shallow, soft-bottom habitat, while just a bit further north, the MBBS is characterized by large submarine canyons (National Centers for Coastal Ocean Science 2020). These submarine canyons create habitats with high vertical relief, exposed rocky reefs, and a large range of depths. These differences in ecosystem characteristics are likely contributors to spatial differences in prey abundance and ultimately the dietary composition of predators used in this study. In the SCA data, fish contributed more to dietary composition in MBBS while invertebrates (shrimp and squid) contributed more heavily in SLO. In isotopic analysis, $\delta^{13}C$ (significant) and $\delta^{15}N$ (non-significant) showed positive trends as a function of latitude. In MBBS, the network of deep submarine canyons enhances nutrient exchange between shallow, coastal and deep-sea water masses (Burton and Koch 1999). Shallow, coastal waters are more enriched in $\delta^{13}C$ and $\delta^{15}N$ (Reich et al. 2010, Snover et al. 2010, Olson et al. 2010) which illustrates the stronger connection that sharks caught in the MBBS region have to the shallow, coastal ecosystem. Sharks caught in the SLO region do not receive the same magnitude of coastal input which results in the depleted levels of both $\delta^{13}C$ and $\delta^{15}N$.

Maturity was removed from all analyses because it was correlated with total length. It was expected that both maturity and total length contributed to dietary differences but for the same reason: larger predators are capable of eating larger, higher tropic level prey. Larger sharks consumed greater proportions of higher trophic level prey (squid and fish) and had elevated $\delta^{15}N$, an indication of trophic level. The positive association between body size and $\delta^{15}N$ has been observed in numerous deep-sea isotopic studies. For example, larger myctophid fishes have higher $\delta^{15}N$ (Cherel et al. 2010), however, each genus occupies only one trophic level (~3.7 $\delta^{15}N$ ‰), similar to what was observed for both *A. brunneus* and *P. xaniurus*. Deep-sea elasmobranchs also follow this trend throughout the world's oceans. *Centrophorus granulosus* and *Squalus cubensis* in the Gulf of Mexico and *Dasyatis lata* in Hawaii all showed positive relationships between body size and $\delta^{15}N$, but again, never having a range greater than 3.7 $\delta^{15}N$‰ from the smallest to the largest individuals (Dale et al. 2011; Churchill et al. 2015). Ultimately, it is unclear whether maturity or total length is the driving factor for increased trophic level. The difference could be due to sharks at different sizes consuming different prey or the observed differences are a result of smaller sharks having a more rapid tissue turnover rate (resulting from metabolic replacement and new tissue growth). A more in-depth look at the metabolic needs for sharks at various maturity and sizes is necessary to determine why $\delta^{15}N$ values are higher in larger individuals.

SCA and SIA revealed that trophic habits did not vary as a function of longitude and depth. Longitude was included as a proxy for distance to shore, but that significantly covaried with depth. Neither of these factors contributed to differences in dietary composition nor isotopic differences. In conclusion, differences in the dietary composition and isotopic makeup of these two predators appear to be due to prey availability and predator size. Both sampling season and latitude likely contribute to cyclical prey populations throughout the year. Predator total length enables larger sharks to select and consume larger, higher trophic level prey.

Dietary overlap and the potential for competition

Both SCA and SIA support the observation that *P. xaniurus* has a smaller dietary niche than *A. brunneus*. *Parmaturus xaniurus*, as a species, feeds on a more restricted range of prey and has less inter-individual variability which leads to the much smaller trophic niche (Figure 6, Figure 10). The SCA showed that *P. xaniurus* feeds heavily on shrimp, while the *A. brunneus* show less of a rigid prey selection criterion. It is possible that individuals of *A. brunneus* may show individualistic specialization, meaning that some individuals may choose to specialize on a more restricted scope of prey items (much like some humans prefer vegan foods), but, as a species, there is a lot more inter-individual variability leading to larger trophic niche ranges. Based on the results from both analyses, *A. brunneus* would fall into a more opportunistic or generalist feeding strategy, while *P. xaniurus* would fall further away from that strategy on the spectrum.

SIA demonstrated a similar trend in niche size. First, the SEA and TA for *A. brunneus* was over 2.5 times larger than the ellipse size of *P. xaniurus* ($SEA_{A.\ brunneus}$ = 0.54‰^{2}; $SEA_{P.\ xaniurus}$ = 0.21‰^{2}; $TA_{A.\ brunneus}$ = 4.4‰^{2}; $TA_{P.\ xaniurus}$ = 1.7‰^{2}). The twofold difference in the range of $\delta^{15}N$ primarily drove the differences in the niche sizes for both species (Range $\delta^{15}N_{A.\ brunneus}$ = 4.2‰; Range $\delta^{13}N_{P.\ xaniurus}$ = 2.1‰), whereas the ranges of $\delta^{13}C$ were similar in size (Range $\delta^{13}C_{A.\ brunneus}$ = 1.6‰; Range $\delta^{13}C_{P.\ xaniurus}$ = 1.2‰), but just offset. Secondly, CD shows the average distance from an individual to the average coordinate value for the species and was 1.6 times larger for *A. brunneus* ($CD_{A.\ brunneus}$ = 0.56‰; $TA_{P.\ xaniurus}$ = 0.35‰). These differences, along with other metrics for dispersion support the idea that *A. brunneus* feeds closer on the spectrum to an opportunistic feeding strategy while *P. xaniurus* shows more species level specialization feeding strategy.

Although the two species implement different feeding strategies, there is still significant overlap in their diets. The dietary overlap index of Zaret and Rand (1971) indicates a high degree of overlap with values >0.6. In this study, I calculated overlap coefficients between *A. brunneus* and *P. xaniurus* at 0.62 for %PN and 0.87 for %PW. For SIA, nicheROVER also identified significant overlap, with the probability of *P. xaniurus* overlapping with *A. brunneus* to be between 81% and 94%. There is high overlap in the $\delta^{15}N$ values between the two species and less overlap in the $\delta^{13}C$. This implies that the two sharks feed on similar type prey but likely forage in different habitats. While these two species occupy the same geographic area, Ebert et al. (2013) hypothesized that these they are using the water column differently. Flammang et al. (2011) stated that *P. xaniurus* uses the water column more regularly while *A. brunneus* associates with rocky benthic substrate. This study did not sample any midwater or rocky habitat, so both these species associate with soft-bottom, benthic habitat. The difference in the utilization of foraging habitat is supported by both analysis techniques. *P. xaniurus* forages on more pelagic prey (i.e., squid, Sergestidae, Mysida, and Euphausiacea) and have more enriched δ^{13}C values (a signature of a benthic organisms) in comparison to *A. brunneus* which incorporated both pelagic and benthic prey (i.e., fishes- *Merluccius productus* and Carid shrimp) into its diet while having depleted δ^{13}C values (Reich et al. 2010). Ultimately, it is unclear why the isotopic carbon does not align with the prey found in the stomachs, but it is clear that these two sharks are utilizing the habitat differently. There are multiple reasons that could explain why these two similar sharks feed in different habitats, but the two most likely reasons stem from the assumption of competition: *are resources limited?*

If dietary resources are limited, then competition must be acting upon these two species because there is significant trophic overlap (Schoener 1983). The competitive exclusion principle has been explored by many, but Darwin is often thought to be the individual who first developed this theory (Hardin 1960; Grant and Grant 2002). The competitive exclusion principle (for trophic ecology) states that two species cannot occupy the same trophic niche over a long period of time. If one species has a competitive advantage over the other, the weaker species will shift toward a different trophic niche or go extinct (Gause 1932; Hardin 1960).

First, I will explore the possibility that *P. xaniurus* is the stronger competitor. Because it occupies the smaller trophic niche, *P. xaniurus* could be forcing *A. brunneus* to expand it dietary niche because *A. brunneus* is being outcompeted for resources. By forcing *A. brunneus* out of its preferred foraging habitat (the water column where pelagic crustaceans are abundant), they need to search for prey on the seafloor to complement their diet. The shift in habitat is likely why *A. brunneus* incorporates higher proportions of fishes and Carid shrimp into its diet. Because *P.*

xaniurus is the stronger competitor, it has continued to forage in its preferred habitat and thus has a smaller trophic range than that of *A. brunneus*.

Conversely, *A. brunneus* could be viewed as the stronger competitor. In Connell's (1961) groundbreaking asymmetric competition experiment, he showed that competition for space was evident between two barnacle species: *Chthamalus stellatus* and *Balanus crenatus*. In this study, *Balanus* outcompeted *Chthamalus* for space, forcing *Chthamalus* to a smaller, more restrictive, and less desirable space in the rocky intertidal. The effects of *Chthamalus* on *Balanus* were insignificant; regardless of whether or not *Chthamalus* was present, *Balanus* occupied that same zone in the rocky intertidal. The paradigm that this experiment presents could be applied to *A. brunneus* and *P. xaniurus*. To explore this, it is assumed that *A. brunneus* is the stronger competitor. Because it has a much larger trophic niche than *P. xaniurus*, *A. brunneus* is competitively forcing *P. xaniurus* to occupy a trophic niche that is smaller and less desirable, much like *Chthamalus* being forced into a more restricted spatial range.

To explore an alternative reason for why these sharks are feeding differently, we must look at the second answer to the competitive assumption question: *are resources limited?* If dietary resources are not limited, it means that competition is not acting upon these two species. This scenario does not exclude the possibility that competition has already acted upon these two species and they have already partitioned resources to ensure survival. Optimal foraging theory helps explore why these species have the observed diets. Optimal foraging theory focuses on the feeding strategies implemented by predators to maximize their net energy gained (Schoener 1971; Pyke et al. 1977; Smith 1978). Net energy gained is the energy gained from prey consumption minus the energy expended capturing prey. Of the common prey types found in this study, squid and fishes not only have larger caloric value per body weight, but they also grow to larger sizes than shrimp (Wacasey and Atkinson 1987; Eder and Lewis 2005). This means that fish and squid have more energetic value than shrimp per capita. These species have likely adapted their morphology over time to maximize their net energy gain in their commonly used foraging habitat.

The body types of these two species are noticeably different; the body of *A. brunneus* is elongated and slender while the body of *P. xaniurus* is shorter and rounder (Ebert et al. 2013). Furthermore, the snouts of these two sharks are morphologically different; the snout of *A. brunneus* is elongated and dorso-ventrally compressed which allows for the species to search for prey on a two-dimensional plane (i.e., the seafloor) (Kajiura 2001). The snout of *P. xaniurus* is much shorter and rounder, which implies that this species likely uses its electrosenses to detect prey in a three-dimensional space around its head (i.e., the water column) (Hueter et al. 2004). Due to these differences, *P. xaniurus* is likely spending more time feeding in the water column, but that means that they must consume more prey to offset the energetic costs of increased levels of movement. This could be why I found 4.33 prey items per non-empty stomach for *P. xaniurus*, but only 2.42 per non-empty stomach for *A. brunneus*. *Apristurus brunneus* spends more time near the seafloor foraging on prey that is larger and more energetically beneficial (e.g. squid and fishes) while expending relatively lower energy. However, if shrimp are abundant and readily available, they will incorporate them into their diet as well. Because *P. xaniurus* must expend more energy to swim, it relies more on the lower energetic value, but easier to capture, shrimp. This implies that *A. brunneus* is better suited to adapt to disturbances in the community structure because of its ability to feed evenly on demersal and pelagic prey. *P. xaniurus* has a more restricted trophic niche which would be of concern if their primary prey were to undergo large changes.

While we can't conclude which species is the better competitor or if competition is currently occurring between the two species, this study does support that dietary resource partitioning is common in deep-sea fishes (Ross 1986; Carrassón and Cartes 2002; Valls et al. 2017). Vertical distribution of dietary resources off the seafloor has been shown as a significant contributor to dietary resource partitioning (Cartes 1988). *Apristurus brunneus* and *P. xaniurus* have partitioned their resources from benthic and water column resources. Ultimately, if dietary resources are limited, it is nearly impossible to distinguish which species is the stronger competitor. An experimental study similar to Connell's (1961) would need to be conducted in the species' natural environment, but, due to the logistic restrictions of studying the deep-sea, this may not be possible at this time.

Deep-sea community of elasmobranch predators

Now that the diets of *A. brunneus* and *P. xaniurus* have been characterized, we have a better idea the role of these catsharks as predators in the deep-sea demersal ecosystem in central California. Other elasmobranch predators that reside in this ecosystem are: *A. kampae*, *Squalus suckleyi*, *Beringraja binoculata*, *Raja inornata*, *Beringraja rhina*, and *Bathyraja kincaidii*. There have not been any diet studies conducted on *A. kampae* anywhere in the world, although Ebert et al. (2013) hypothesized that this species feeds on deep-sea shrimp, squid and bony fishes. Bigman (2013) conducted a trophic study on *S. suckleyi* off the coast of central California and found that the SCA aligned with the feeding strategies of *A. brunneus*. Similar to *A.* brunneus, *S. suckleyi* forages both in the water column and near the seafloor while feeding uniformly on shrimp, squid, and fishes. Finally, Bizzarro et al. (2007) characterized the diet of the four skate species in central California. Surprisingly, Bizzarro et al. (2007) found that these four different species of skate do not feed similarly to each other; they all exhibit variations in their diet to fit into their own niche within the food web. *Bathyraja kincaidii* displayed similar prey selection habits as *P. xaniurus*. Both species place high importance on shrimp species while consuming noticeable proportions of fishes and squid. The difference here is that *B. kincaidii* is likely feeding more on benthic shrimp-like crustaceans whereas *P. xaniurus* feeds on more pelagic shrimp. The other 3 species of skate form their own functional group that place importance on fishes, squid and crab. These 3 different functional groups of elasmobranch predators have partitioned the low-relief, soft-bottom habitat on the shelf and upper slope of central California.

Of the six other elasmobranch species found in this ecosystem, SIA has been conducted on *S. suckleyi, Beringraja binoculata,* and *Beringraja rhina*. Although the SCA showed that there were similarities in the implemented feeding strategies between these deep-sea elasmobranchs, the SIA from Bigman (SIA) showed that *S. suckleyi* had depleted levels of δ^{13}C (-18.3±0.9 ‰) and δ^{15}N (14.6±0.5 ‰) when compared to both *A. brunneus* and *P. xaniurus* (Figure 13). As stated earlier, *S. suckleyi* feeds primarily in the water column which can account for the differences in the δ^{13}C values, but feeds at nearly one whole trophic level below *A. brunneus* and *P. xaniurus*. Because all three species are carnivorous deep-sea sharks, this is unusual because *S. suckleyi* grows to larger overall sizes (total length and weight) than the two catshark species, so it was expected that they feed at a higher trophic level. Shrimp/euphausiids had the highest %PSIRI in the diet of *S. suckleyi* (Bigman 2013). Bigman (2013) found that the average δ^{15}N value for euphausiids (n=4) in their study were 8.1±1.3‰, while this study found the average δ^{15}N value to be 14.45±0.90 for shrimp. The unexpected difference in trophic level is likely due to the difference of isotopic values for prey species that contribute to the diet of the predator.

Carlisle et al. (2017) conducted the SIA for *Beringraja binoculata* and *Beringraja rhina* (among others) but these samples were taken from the Gulf of Alaska (Figure 13). Skates, with their dorso-ventral compression, forage on prey that are on or within a close proximity to the seafloor. These two species likely show differences in $\delta^{13}C$ values because they both were caught in the Gulf of Alaska. However, their depletion of $\delta^{15}N$ relative to *A. brunneus* and *P. xaniurus* is likely due to feeding exclusively on the seafloor. These differences should be interpreted with caution because isotopic signatures vary depending on the ecosystem. Overall, compared to other elasmobranch predators in central California, *A. brunneus* and *P. xaniurus* may occupy a more prominent role as a top predator.

Management

Apristurus brunneus and *P. xaniurus* are frequently bycaught in the U.S. west coast groundfish commercial fishery. Past studies leave unanswered questions about the life-history of each species (Jones and Green 1977; Cross 1988; Cailliet 1990; Balart et al. 2000; Flammang 2005). Previous studies provide insight into the diet and life-history but the information was limited and the studies were done in a region where there is little geographic overlap between the two species. No dietary studies had been conducted on these species in the central and northern California regions, where NMFS WCGBTS encountered the highest abundance of both species over the past decade (Northwest Fisheries Science Center 2018). To properly manage the groundfish fishery on the west coast of the United States, it is imperative that the diet and life histories are incorporated into management schemes so we can predict the full extent of the effects of fishing on the deep-sea environment. Understanding the trophic linkages and the role that species play in their environment (i.e., how they affect both prey and competitive species) will help make accurate predictions about the changes in the community composition if one species is removed from the ecosystem.

As of 2006, the International Union for Conservation of Nature (IUCN) listed both species as Data Deficient (DD) (Flammang et al. 2015; Huveneers et al. 2015). In 2015, both species were reassessed; *P. xaniurus* was upgraded to Least Concern (LC) and *A. brunneus* remained as DD. Although the status of *P. xaniurus* was changed to LC, this decision was made without new species-specific data; the change was made because of the creation of marine protected areas (MPAs) and the reduction of the number of bottom trawlers in central and northern California (Flammang et al. 2015). Due to the lack of data, there were objections to the decision. Both these species are lacking in life history studies and this study filled a much-needed gap to understand the trophic ecology of these species. This information can be used in the coming years when the threat level is assessed for both species.

West coast fisheries management groups (Pacific Coast Management Council and National Marine Fisheries Service) have made the push in recent years to focus on ecosystem-based fisheries management. Interactions between species (especially predator-prey interactions) within a community need to be considered when assessing the overall health of the deep-sea, soft-bottom ecosystem in California (and along the U.S. West Coast). These species interactions and their prey sources are not constant; they can change latitudinally, seasonally, temporally, etc. NOAA has data on long term population trends of these species, as well as their prey abundance, which can be used to understand the complex linkages that occur in ecosystems where commercially important species are present. Understanding species interactions can help fishery managers regulate the health of an ecosystem as a whole, not just the commercially important species.

Conclusions

Apristurus brunneus and *P. xaniurus* are two tertiary consumers in the deep-sea, soft-bottom ecosystem off the coast of central California. While these two species are not economically important, they do play an important role as an abundant top predator in the deep-sea ecosystem and fine scale changes in their trophic habits could be detected both spatially and temporally. While the two species exhibit significant trophic overlap, the difference in the diet indicate they use the ecosystem differently. In order for ecosystem-based fisheries management to be successful, it requires a greater understanding of the life histories of all the species residing in that ecosystem, not just a chosen few. Knowledge on the trophic ecology of *A. brunneus* and *P. xaniurus* brings us one step closer to fully understanding the deep-sea ecosystem off the coast of central California.

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Table 1. Sample sizes for stomach content analysis and stable isotope analysis by species for each factor being analyzed. Numerical values are totals after removing empty stomachs.

		Stomach Content Analysis		Stable Isotope Analysis	
Factor	Level	*A. brunneus*	*P. xaniurus*	*A. brunneus*	*P. xaniurus*
Depth in meters (100m bins)	<400	0	64	1	68
	400 to 500	16	104	23	121
	500 to 600	38	30	50	33
	600 to 700	88	56	116	69
	700 to 800	70	4	80	5
	>800	17	0	27	0
Region	Monterey Bay	75	35	87	42
	Big Sur	75	55	109	68
	San Luis Obispo	79	168	101	186
Season	Summer	75	79	110	93
	Fall	154	179	187	203
Sex	Female	122	103	158	117
	Male	107	155	139	179
Total Length in millimeters (50 mm bins)	≤200	8	0	11	0
	201 to 250	13	6	19	11
	251 to 300	38	82	46	98
	301 to 350	45	92	66	99
	351 to 400	28	49	43	56
	401 to 450	19	18	24	21
	451 to 500	8	9	7	9
	501 to 550	18	2	21	2
	551 to 600	27	0	34	0
	>600	25	0	26	0
Trawl Composition	All A. brunneus	87	0	131	0
	Mixed	142	180	166	212
	All P. xaniurus	0	78	0	84
	Total	**229**	**258**	**297**	**296**

Table 2. A list of prey and prey groups that were included in each of the five functional prey categories used for this study.

Functional Group	Subgroups included
Crab	Brachyura, Anomura
Fishes	*Engraulis mordax*, *Merluccius productus*, *Sebastes*, unknown fish parts
Shrimp	*Euphausia pacifica*, Sergestoidea, Caridea, Mysida, Isopoda, unknown shrimp, unknown krill
Squid	*Doryteuthis opalescens*, *Gonatus onyx*, *Histioteuthis heteropsis*, *Hyaloteuthis pelagica*, *Stigmatoteuthis dofleini*, unknown squid parts
Pyrosome	*Pyrosoma atlanticum*

Table 3. Diet composition indices for each functional prey category (in bold) and for the lowest taxonomic level identified for *A. brunneus* (n=229) and *P. xaniurus* (n=258). There were no pyrosomes found in the gut contents for *A. brunneus*.

		Apristurus brunneus						*Parmaturus xaniurus*					
Group	Category	%N	%PN	%W	%PW	FO	%PSIRI	%N	%PN	%W	%PW	FO	%PSIRI
CRAB		**0.22**	**25.00**	**0.37**	**42.10**	**0.01**	**0.29**	**2.89**	**41.43**	**4.00**	**57.35**	**0.07**	**3.45**
FISHES		**24.05**	**64.04**	**25.14**	**66.94**	**0.38**	**24.59**	**8.16**	**32.37**	**11.77**	**46.70**	**0.25**	**9.96**
	Merluccius productus	3.71	60.71	5.38	87.93	0.06	4.54	1.29	25.51	3.76	74.69	0.05	2.52
	Teleost Other	20.34	62.94	19.76	61.16	0.32	20.05	6.87	34.08	8.00	39.70	0.20	7.44
SHRIMP		**25.49**	**59.57**	**31.32**	**73.17**	**0.43**	**28.40**	**65.34**	**76.98**	**63.26**	**74.53**	**0.85**	**64.30**
	Euphausiacea	1.06	40.46	1.38	52.58	0.03	1.22	7.73	79.75	8.55	88.26	0.10	8.14
	Shrimp Other	24.43	60.81	29.94	74.52	0.40	27.18	57.62	75.84	54.71	72.01	0.76	56.16
SQUID		**50.24**	**71.46**	**43.18**	**61.42**	**0.70**	**46.71**	**23.29**	**44.18**	**20.69**	**39.25**	**0.53**	**21.99**
	Doryteuthis opalescens	0.76	28.93	0.89	33.82	0.03	0.82	1.52	32.76	1.77	37.98	0.05	1.65
	Gonatus onyx	5.30	48.58	3.09	28.26	0.11	4.19	5.73	43.51	5.17	39.22	0.13	5.45
	Stigamatoteuthis dofleini	32.34	67.94	27.97	58.76	0.48	30.15	7.69	39.66	5.08	26.20	0.19	6.38
	Squid Other	11.84	73.27	11.24	69.55	0.16	11.54	8.35	37.12	8.67	38.59	0.22	8.51
PYROSOME	*Pyrosoma atlanticum*							**0.32**	**41.67**	**0.29**	**36.89**	**0.01**	**0.30**

Table 4. PERMANOVA results identifying the biological and environmental factors that contribute to differences in the diet for both *A. brunneus* and *P. xaniurus* in terms of %N and %W.

Species	Data	Factor	df	F-stat	R^2	p-value
Apristurus brunneus	%N	Season	1	6.05	0.025	0.0061
		Sex	1	4.10	0.017	0.0277
		Latitude	1	3.64	0.015	0.0463
		Residuals	225		0.942	
	%W	Season	1	6.65	0.028	0.0007
		Total Length	1	3.78	0.016	0.0132
		Latitude	1	2.97	0.012	0.0377
		Season x Total Length	1	3.07	0.013	0.0324
		Residuals	224		0.960	
Parmaturus xaniurus	%N	Total Length	1	5.69	0.021	0.0008
		Season	1	5.04	0.019	0.0015
		Residuals	255		0.949	
	%W	Season	1	5.12	0.019	0.0019
		Total Length	1	4.89	0.018	0.0031
		Residuals	255		0.962	

Table 5. Trophic levels for prey species taken from published literature and calculated trophic levels of *Apristurus brunneus* and *Parmaturus xaniurus* for both stomach content analysis (SCA) and stable isotope analysis (SIA).

Prey Species	Published Trophic Level	Catshark species by trophic analysis	Calculated Trophic Level
Crab (Cortes 1999)	2.52	*Apristurus brunneus* (SCA)	4.01
Fishes (Cortes 1999)	3.24	*Parmaturus xaniurus* (SCA)	3.72
Shrimp (Sydeman et al. 1997)	2.25	*Apristurus brunneus* (SIA)	3.76
Squid (Cortes 1999)	3.20	*Parmaturus xaniurus* (SIA)	3.45

Table 6. Mean and standard deviation for δ^{13}C (‰), δ^{15}N (‰), and C:N ratio for predator and prey tissue samples collected and processed by this study. Below each functional group are breakdowns of the category by species.

Species/ Group	Mean δ^{13}C ± SD (‰)	Mean δ^{15}N ± SD (‰)	Mean C:N ± SD (‰)
Apristurus brunneus (n=297)	-17.79 ± 0.27	17.21 ± 0.65	3.23 ± 0.11
Parmaturus xaniurus (n=296)	-17.39 ± 0.18	17.40 ± 0.36	3.20 ± 0.11
Crab (n=3)	-20.47 ± 0.70	13.47 ± 0.51	3.83 ± 0.71
Anomura (n=2)	-20.8 ± 0.57	13.25 ± 0.49	3.90 ± 0.99
Brachyura (n=1)	-19.80	13.90	3.70
Fishes (n=7)	-19.47 ± 0.45	14.51 ± 0.13	4.13 ± 0.41
Merluccius productus (n=3)	-19.73 ± 0.45	14.43 ± 0.06	4.27 ± 0.61
Sebastes spp.(n=1)	-18.80	14.40	4.4
Shrimp (n=23)	-19.49 ± 0.84	14.45 ± 0.90	3.85 ± 0.83
Squid (n=13)	-19.37 ± 0.87	14.35 ± 0.70	4.08 ± 0.76
Doryteuthis opalescens (n=4)	-19.13 ± 0.88	14.10 ± 1.00	4.28 ± 1.07
Gonatus onyx (n=3)	-19.87 ± 0.45	14.20 ± 0.72	4.60 ± 0.72
Stigmatoteuthis opalescens (n=5)	-19.48 ± 1.03	14.66 ± 0.51	3.72 ± 0.37

Table 7. PERMANOVA results identifying the biological and environmental factors that contribute to differences in δ^{13}C and δ^{15}N values for both *A. brunneus* and *P. xaniurus.*

Species	Factor	df	F-stat	R^2	p-value
Apristurus brunneus	Total Length	1	32.18	0.088	0.0001
	Sex	1	7.04	0.020	0.0027
	Latitude	2	6.4971	0.037	0.0003
	Total Length x Sex	1	12.92	0.036	0.0002
	Residuals	291		0.816	
Parmaturus xaniurus	Total Length	1	65.56	0.163	0.0001
	Latitude	2	18.45	0.092	0.0001
	Season	1	4.29	0.011	0.0216
	Total Length x Season	1	5.69	0.014	0.0068
	Residuals	290		0.721	

Table 8. Spatial isotopic metrics for *Apristurus brunneus* and *Parmaturus xaniurus* (following Layman et al. 2007). The 6 metrics include: range of $\delta^{13}C$ and $\delta^{15}N$, mean distance to the centroid (CD), mean nearest neighbor distance (NND), standard deviation of nearest neighbor distance (SDNND), total convex hull area (TA).

Species	Range $\delta^{13}C$	Range $\delta^{15}N$	CD	NND	SDNND	TA
Apristurus brunneus	1.6	4.2	0.56	0.04	0.06	4.4
Parmaturus xaniurus	1.2	2.1	0.35	0.01	0.04	1.7

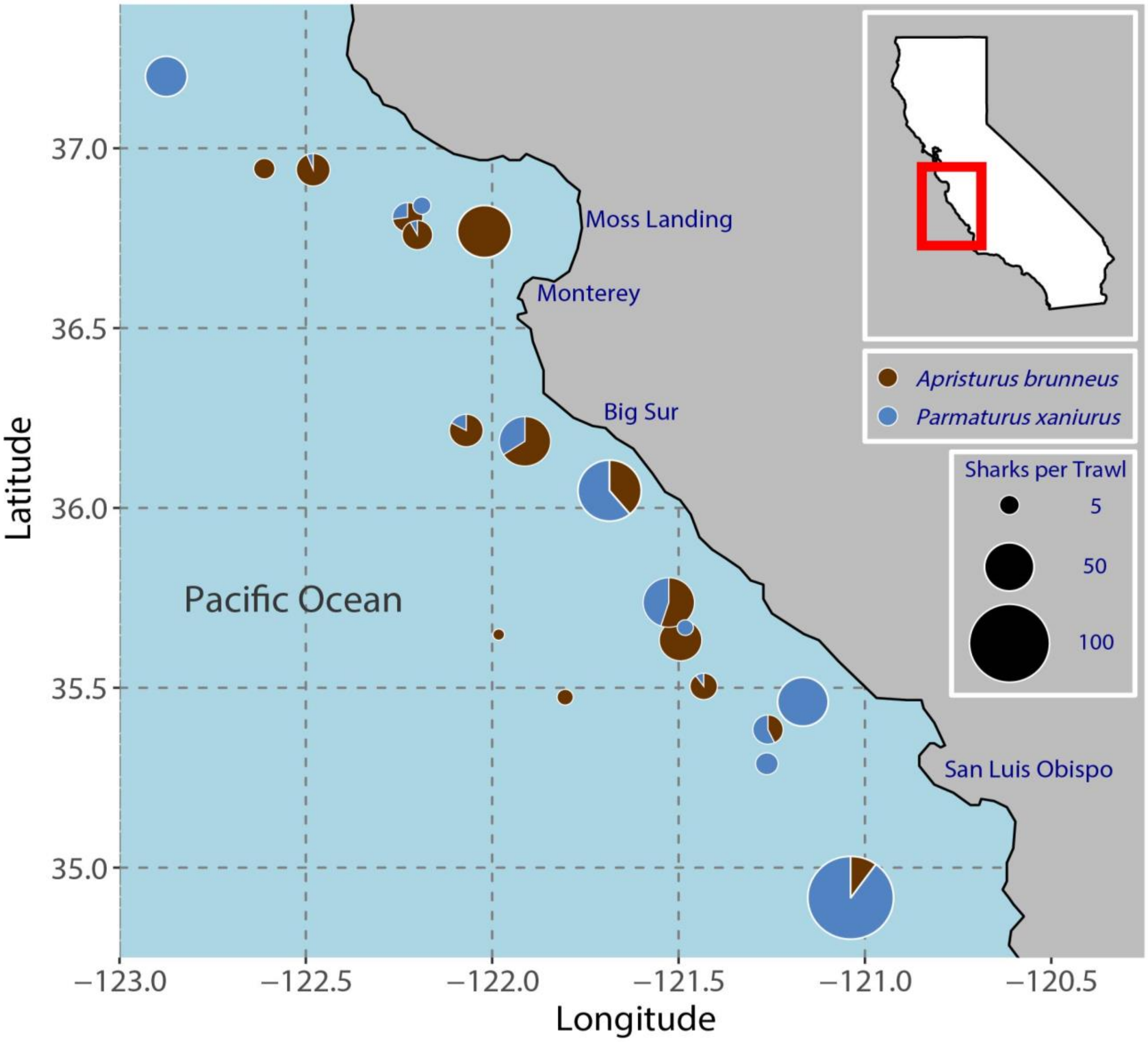

Figure 1. Map of the 20 sampling stations from which shark specimens were collected. The size of the points corresponds to the total number of sharks collected from that location.

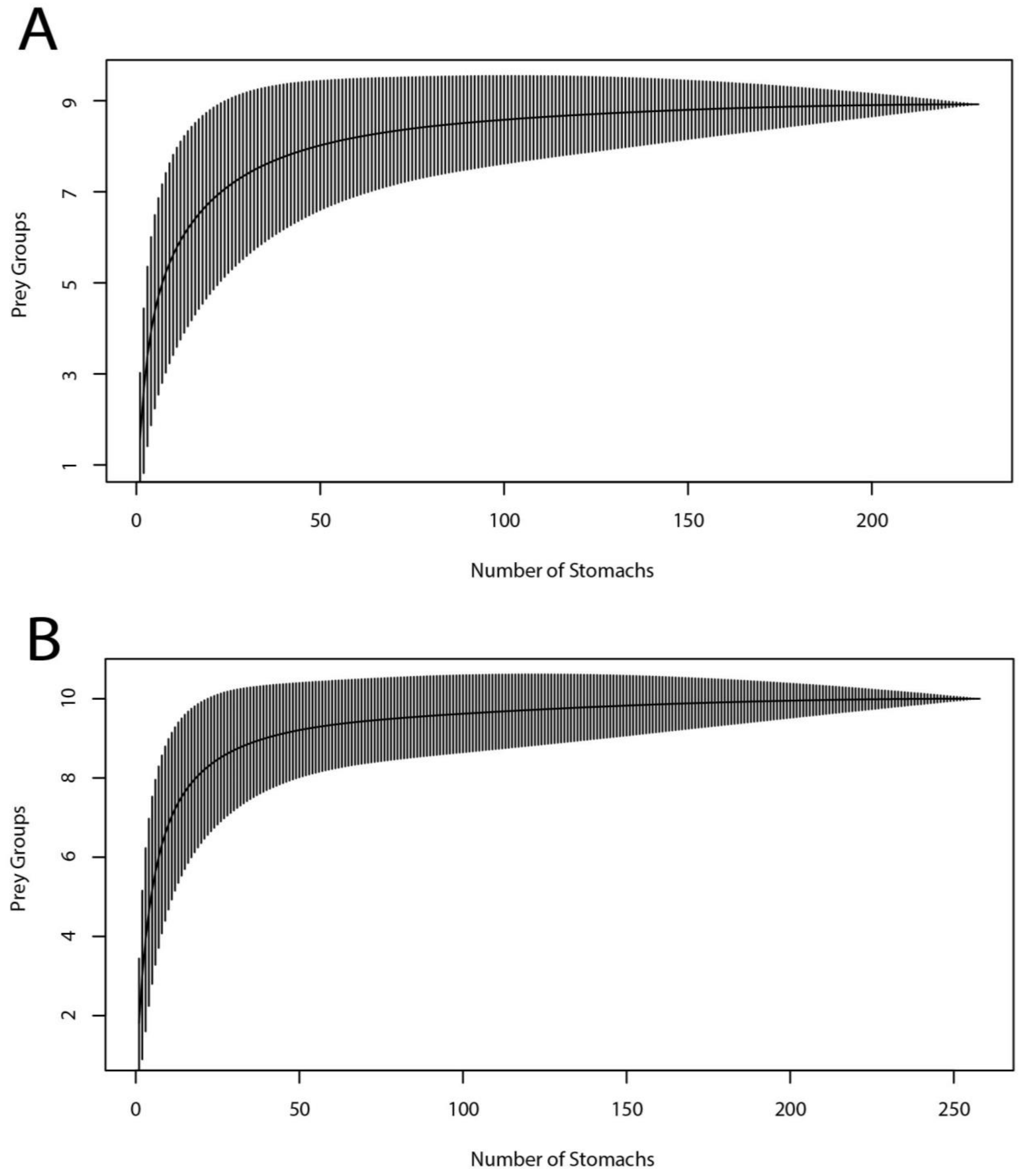

Figure 2. Prey accumulation curves for *Apristurus brunneus* (A) and *Parmaturus xaniurus* (B). Vertical lines represent the 95% confidence intervals around the mean values.

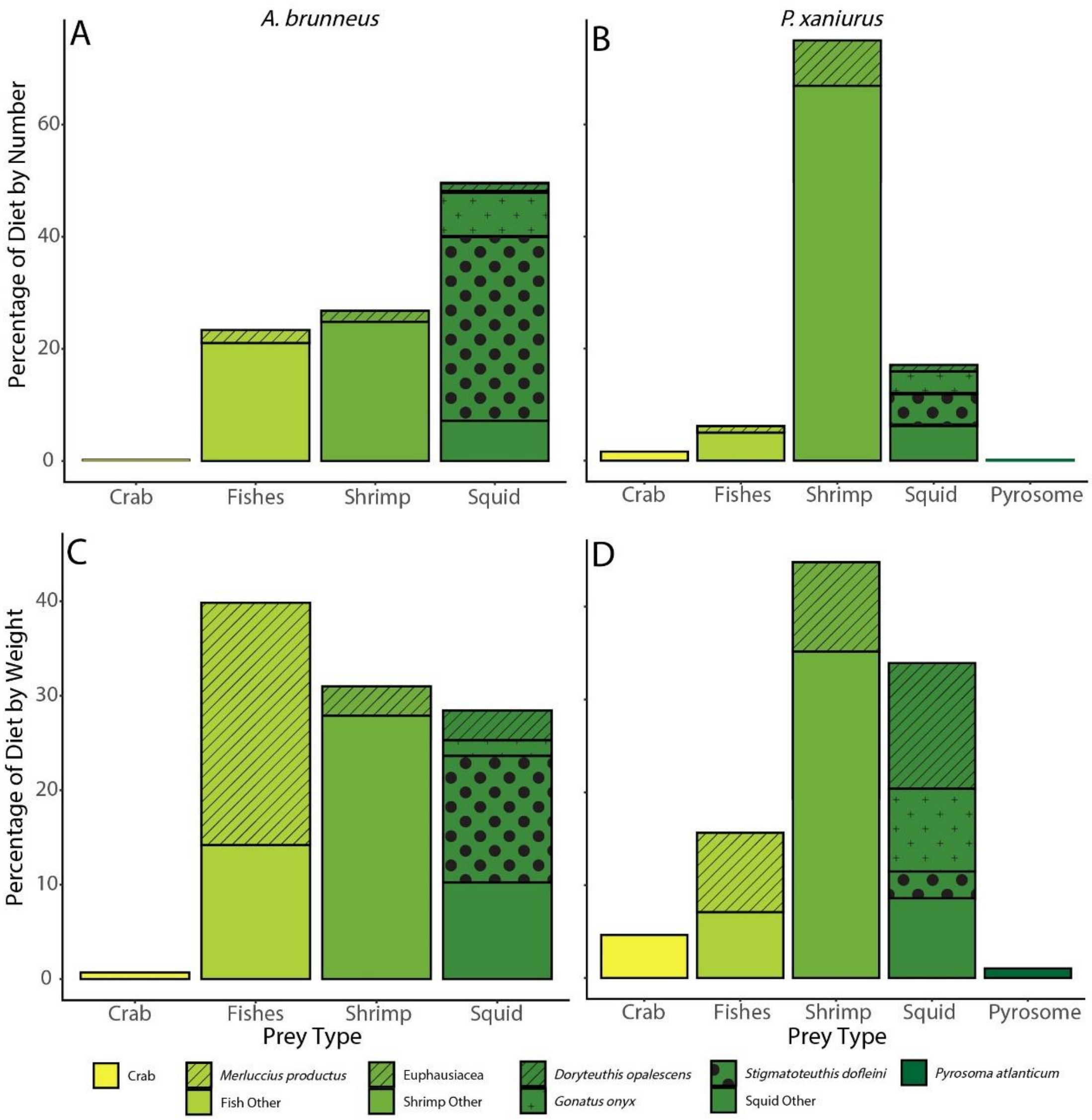

Figure 3. Contributions to overall diet by number (%N) and weight (%W) by prey functional category for the two shark species. Each of the five functional prey categories are broken down further by the most common prey species in the diet. (A) Percentage of the diet by number of prey individuals for *A. brunneus*. (B) Percentage of the diet by number of prey individuals for *P. xaniurus*. (C) Percentage of the diet by weight of prey for *A. brunneus*. (D) Percentage of the diet by weight of prey for *P. xaniurus*.

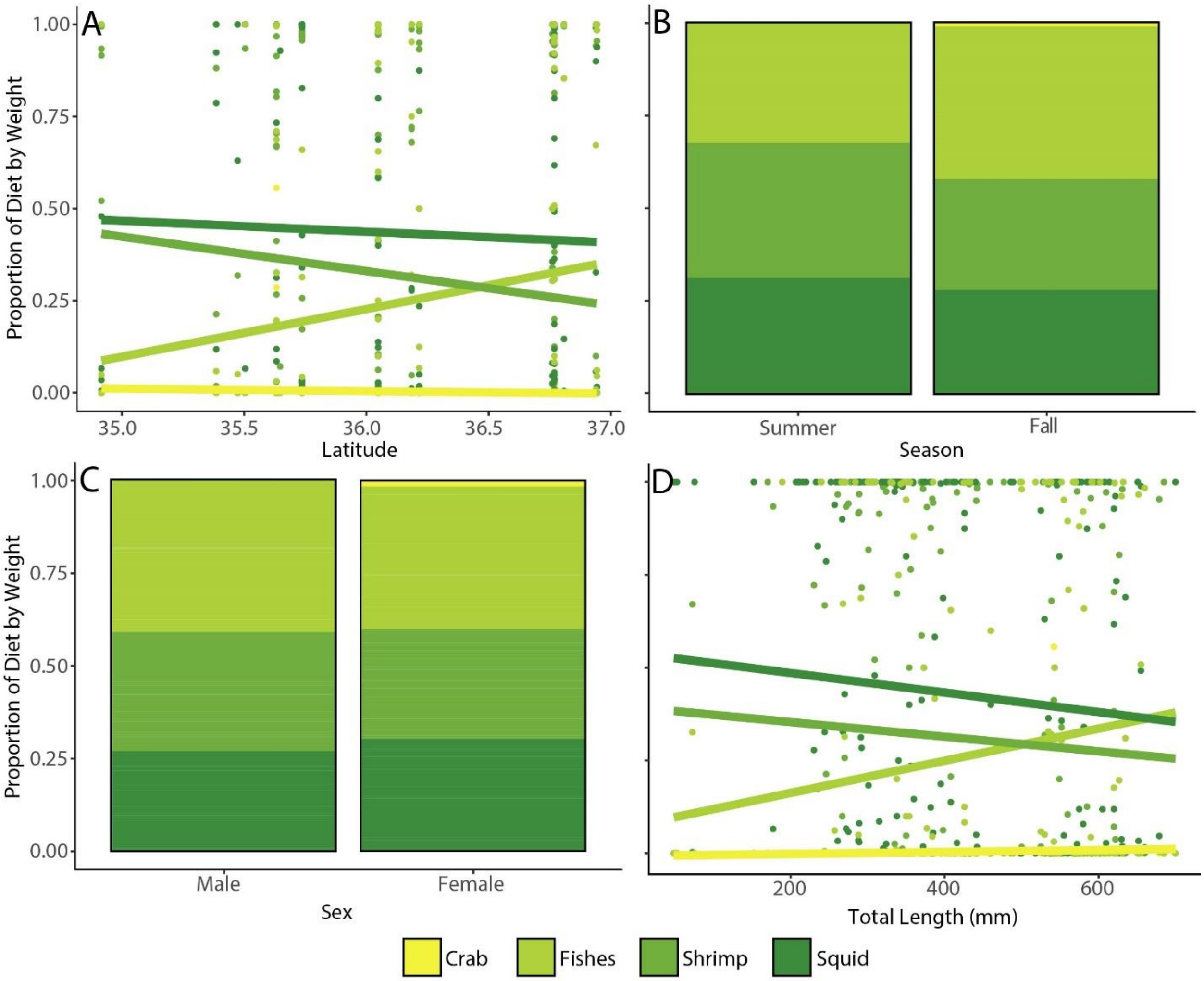

Figure 4. Dietary differences for *Apristurus brunneus* by functional prey category weight for factors that were statistically significant in PERMANOVA models. Continuous factors are displayed as simple linear regressions while categorical factors are displayed as adjacent stacked bar plots. Changes in proportion of dietary prey weight as a factor of (A) latitude, (B) sampling season, (C) sex, and (D) predator total length.

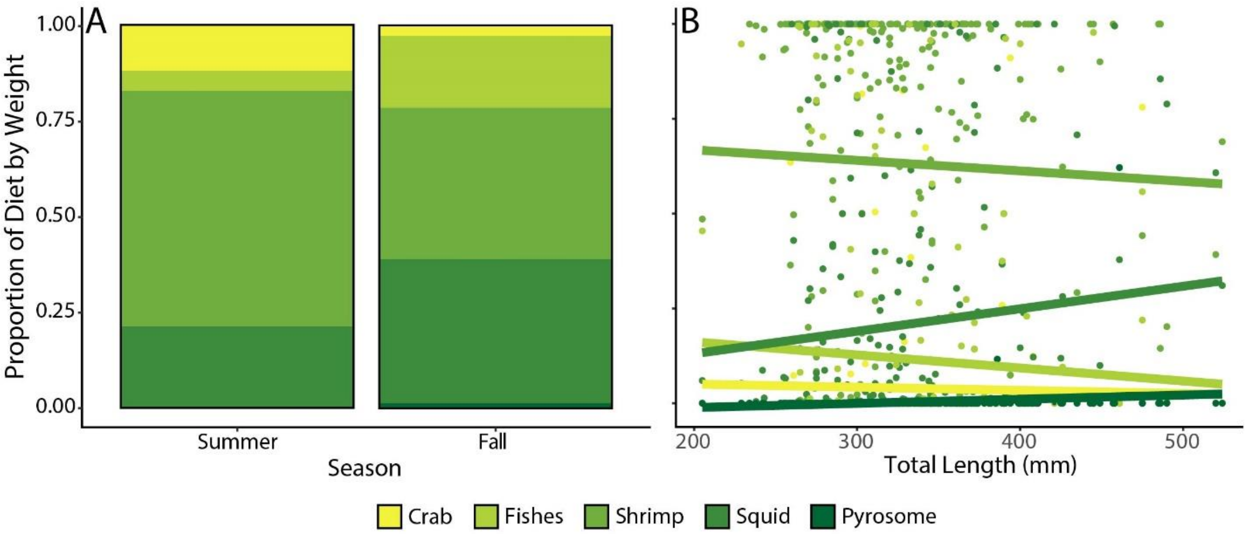

Figure 5. Dietary differences for *Parmaturus xaniurus* by functional prey category weight for factors that were statistically significant in PERMANOVA models. Continuous factors are displayed as simple linear regressions while categorical factors are displayed as adjacent stacked bar plots. Changes in proportion of dietary prey weight as a factor of (A) sampling season and (B) predator total length.

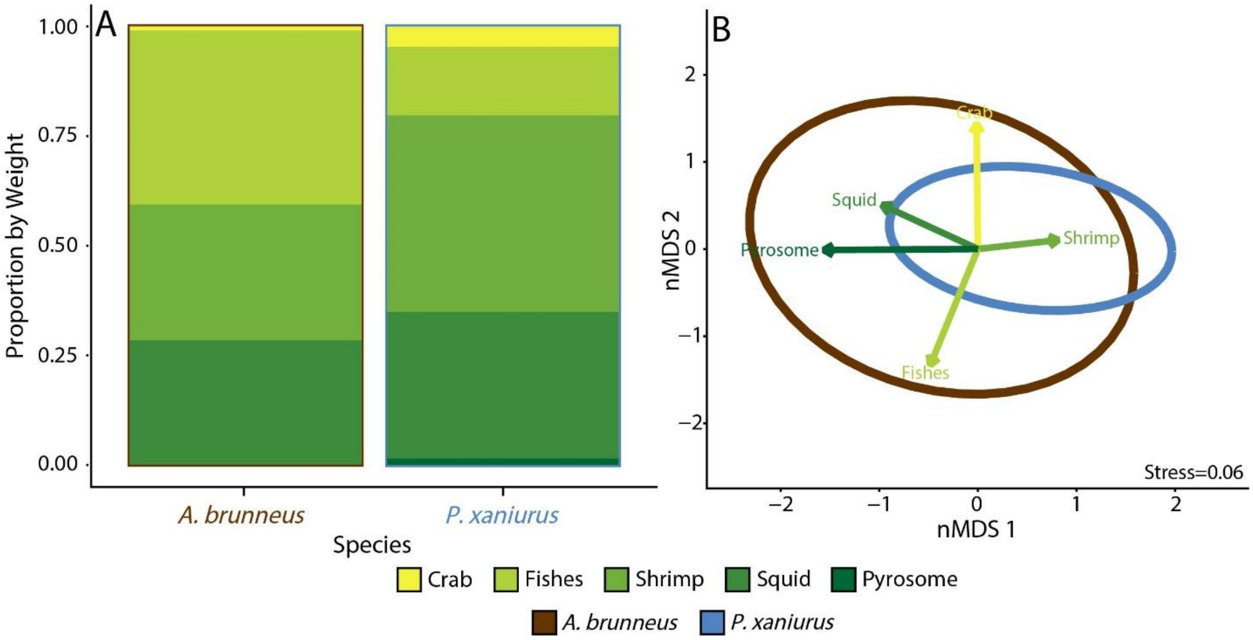

Figure 6. Differences in trophic habits between *Apristurus brunneus* and *Parmaturus xaniurus* through stomach content analysis by weight. Categories are broken down by the 5 most common prey groups. (A) Stacked bar plots showing the proportional difference between the two species. (B) A non-metric multi-dimensional scaling (nMDS) plot highlighting the dietary trends of both species. The proximity from the end of each prey vector to the centroid of each species ellipses shows the importance of that prey group to the diet of that predator species. Prey more centrally located in the predator ellipse are more important to the predator's diet.

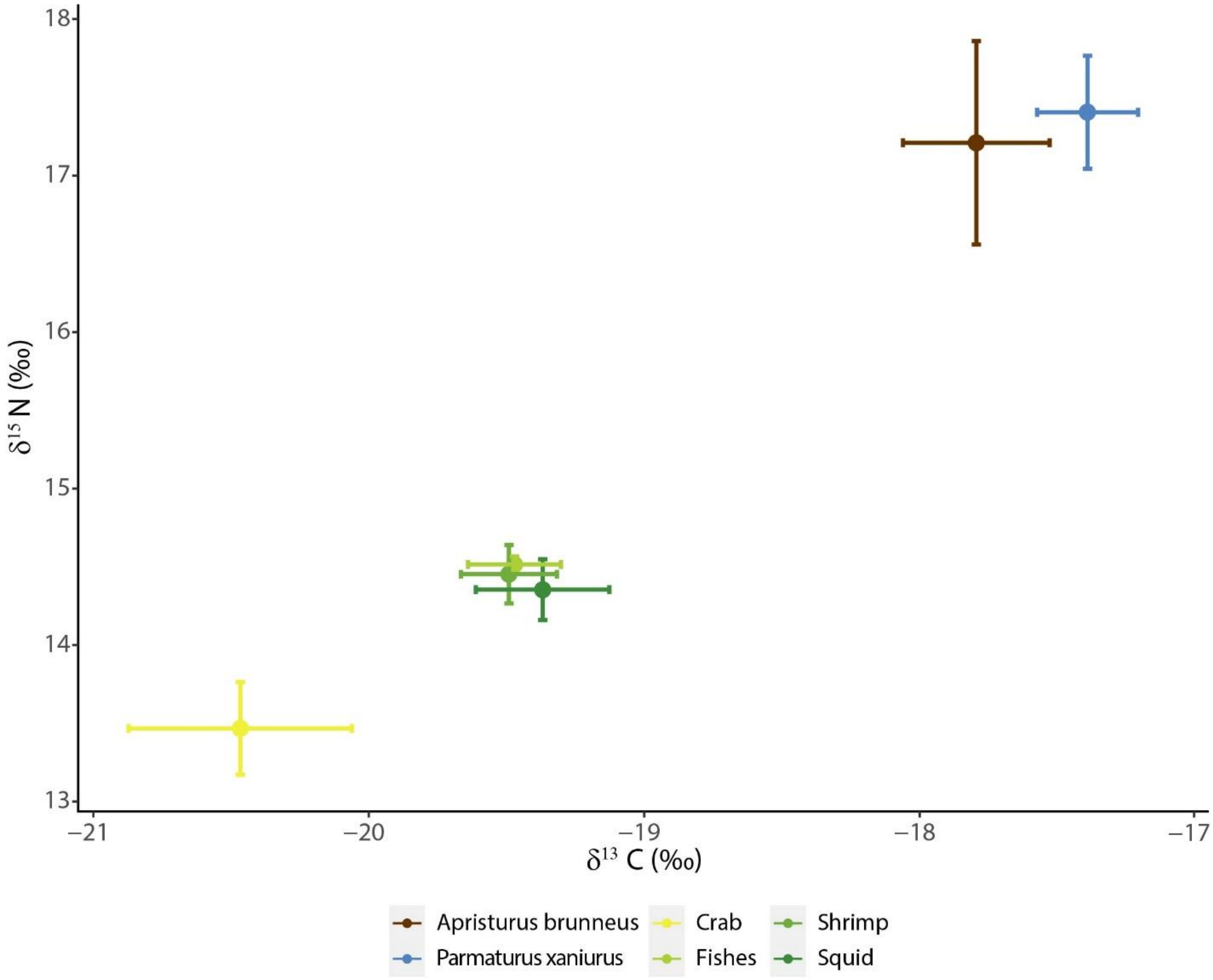

Figure 7. Isotopic biplot for δ^{13}C and δ^{15}N for *Apristurus brunneus*, *Parmaturus xaniurus*, and the prey groups found in the stomachs of the predators. The values plotted are means of the individuals in the group with ± 1 standard deviation.

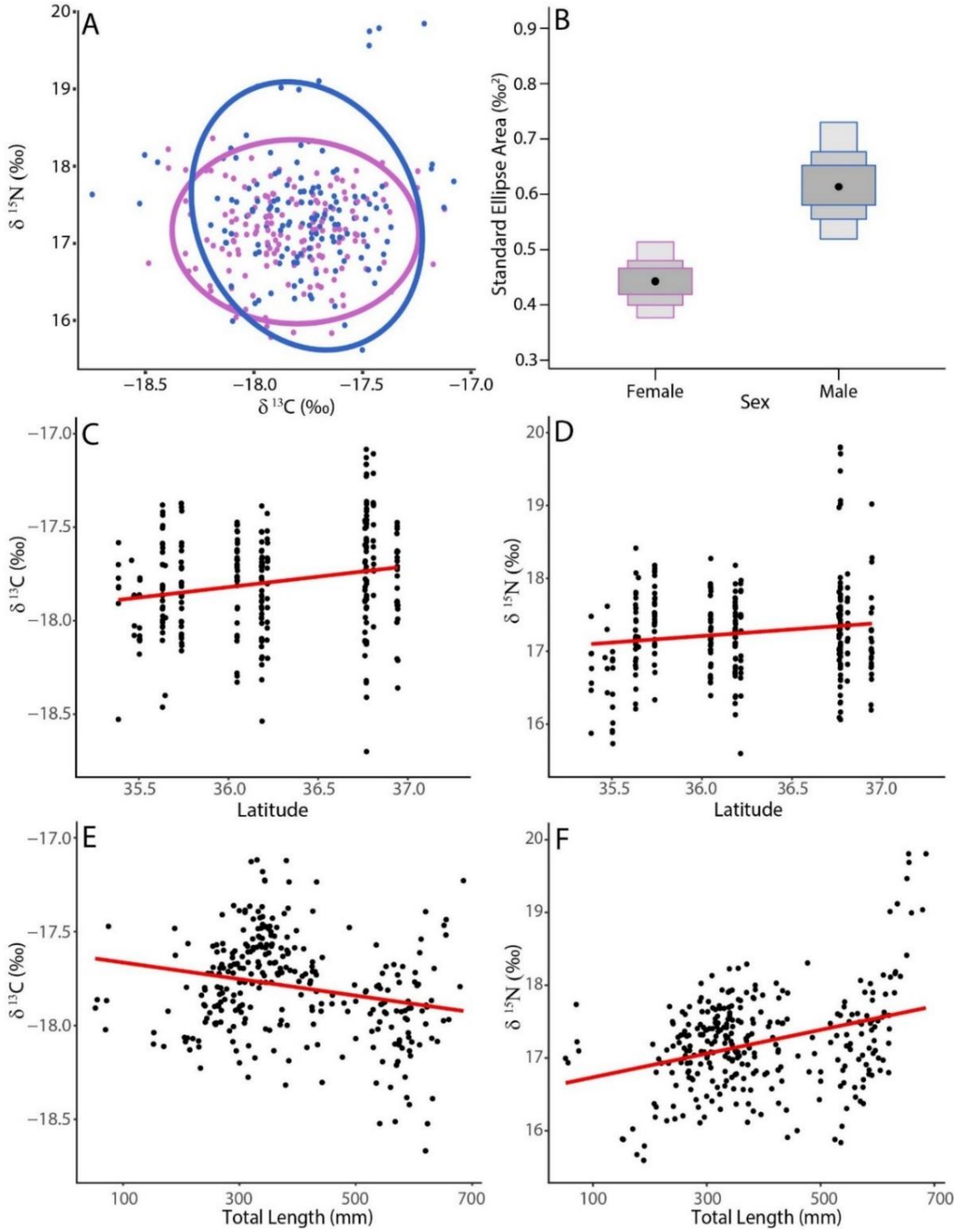

Figure 8. Isotopic differences for *Apristurus brunneus* as a function of the significant factors identified in the PERMANOVA models. Continuous factors are displayed as linear regressions of both $\delta^{13}C$ and $\delta^{15}N$ separately. Categorical variables are displayed as SIBER ellipses plots with corresponding standard ellipse area (SEA) plots. SIBER ellipses plots represent the 95% CI bivariate ellipses and SEA plots show the true population value (black dot) on top of the 50%, 75%, and 95% credible intervals (boxes

from dark to light). Changes in isotopic ratio as function of (A and B) sex, (C and D) latitude, and (E and F) total length.

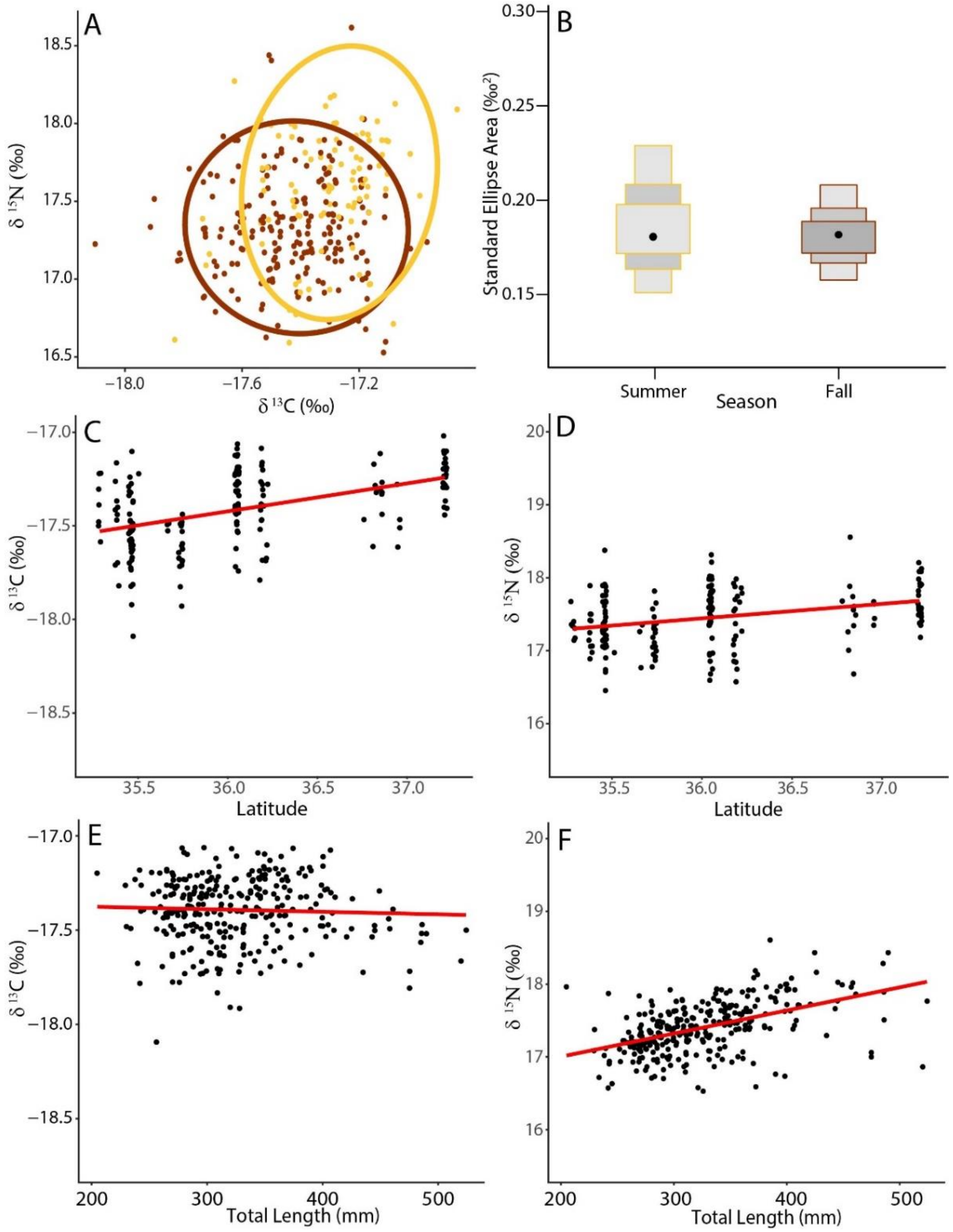

Figure 9. Isotopic differences for *Parmaturus xaniurus* as a function of the significant factors identified in the PERMANOVA models. Continuous factors are displayed as linear regressions of both δ^{13}C and δ^{15}N separately. Categorical variables are displayed as SIBER ellipses plots with corresponding standard ellipse area (SEA) plots. SIBER ellipses plots represent the 95% CI bivariate ellipses and SEA plots show the true

population value (black dot) on top of the 50%, 75%, and 95% credible intervals (boxes from dark to light). Changes in isotopic ratio as function of (A and B) sampling season, (C and D) latitude, and (E and F) total length.

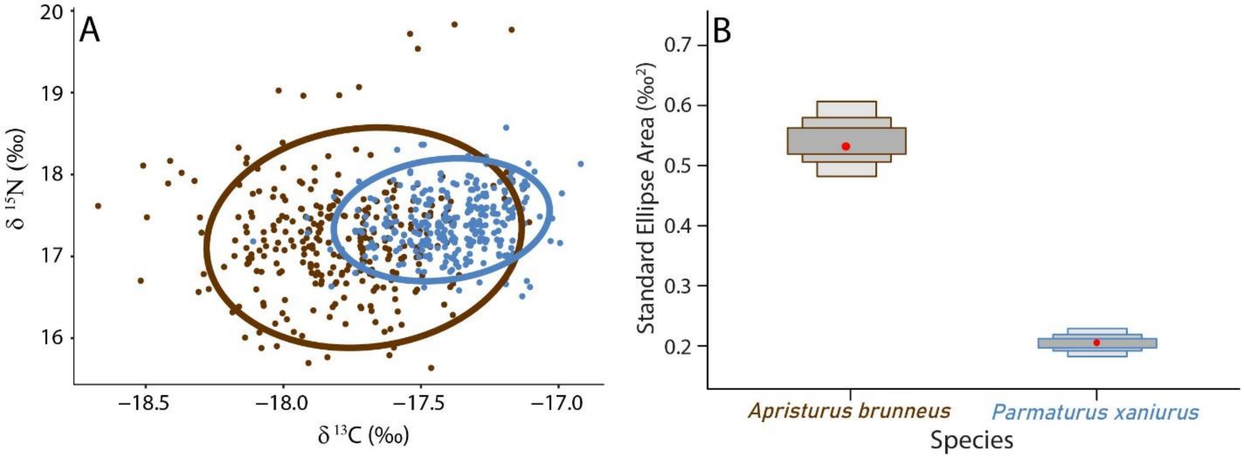

Figure 10. Differences in isotopic values, niche width, and dietary overlap in *Apristurus brunneus* and *Parmaturus xaniurus*. (A) Isotopic biplot with SIBER ellipses to show the trophic niche of both species. (B) Standard ellipse areas (SEA) depict trophic niche breadth of each species. Shown are the true population values (red dot) on top of the 50%, 75%, and 95% credible intervals (boxes from dark to light)

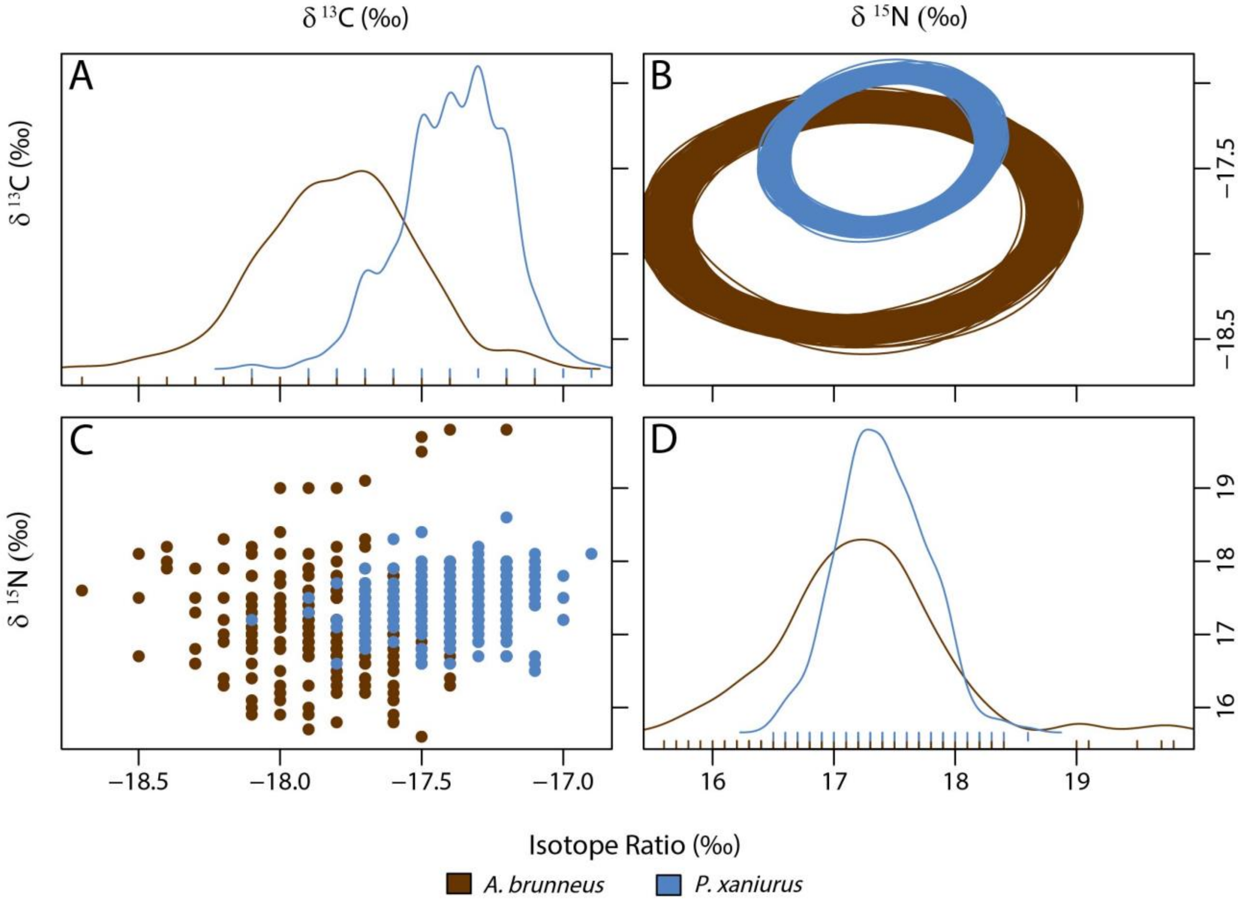

Figure 11. nicheROVER results depicting the degree of dietary overlap in *Apristurus brunneus* and *Parmaturus xaniurus* using stable isotope data. (A) A one-dimensional density plot of the average $\delta^{13}C$ values from the 1000 projected niche regions. (B) A two-dimensional scatterplot that shows the 1000 projected niche regions for both species. (C) A two-dimensional scatterplot that shows the isotopic values of the sampled individuals. (D) A one-dimensional density plot of the average $\delta^{15}N$ values from the 1000 projected niche regions.

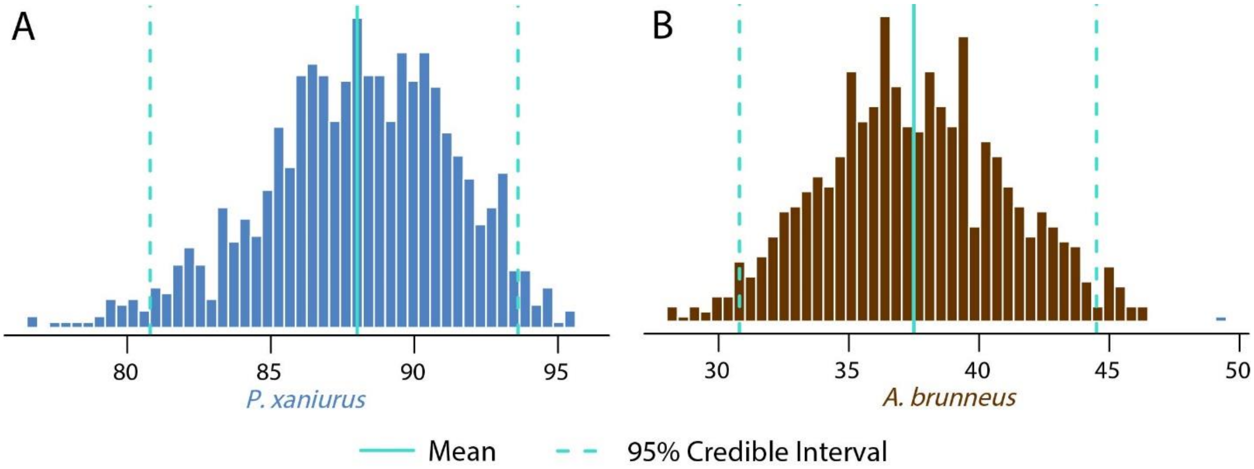

Figure 12. Posterior probability distributions for the niche region overlap metrics between *Apristurus brunneus* and *Parmaturus xaniurus* using nicheROVER. (A) There is between an 81% and 94% probability that a randomly selected *P. xaniurus* will fall into the trophic region of *A. brunneus*. (B) There is between a 31% and 45% probability that a randomly selected *A. brunneus* will fall into the trophic region of *P. xaniurus*.

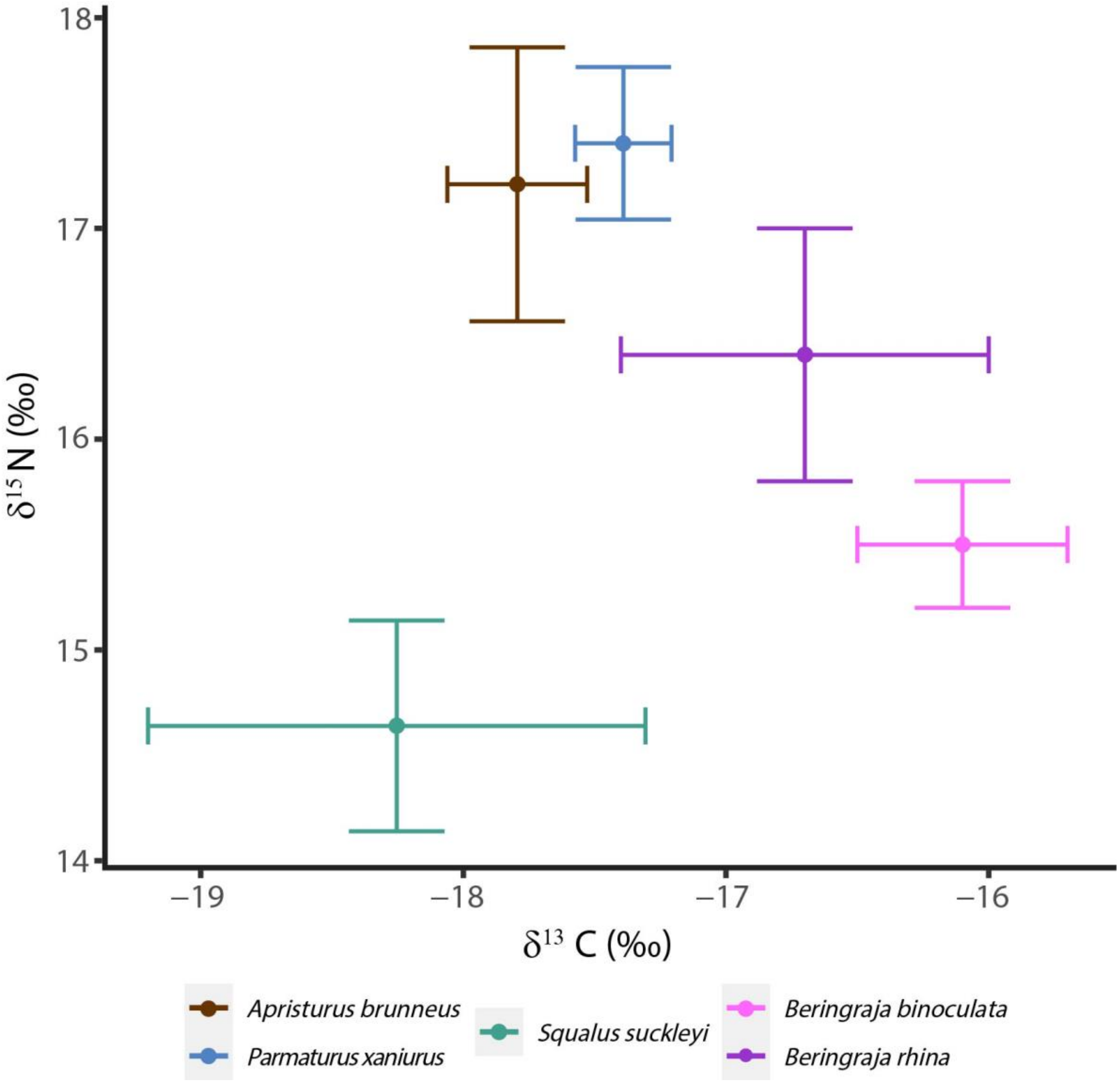

Figure 13. Isotopic biplot for δ^{13}C and δ^{15}N for *Apristurus brunneus*, *Parmaturus xaniurus*, and other elasmobranch predators that inhabit the deep-sea ecosystem in the eastern Pacific. The values plotted are means of the individuals in the group ± 1 standard deviation. Data for *Squalus suckleyi* taken from Bigman (2013) and data for *Beringraja binoculata* and *Beringraja rhina* taken from Carlisle et al. (2017).

APPENDIX A

STOMACH CONTENT ANALYSIS BY NUMBER

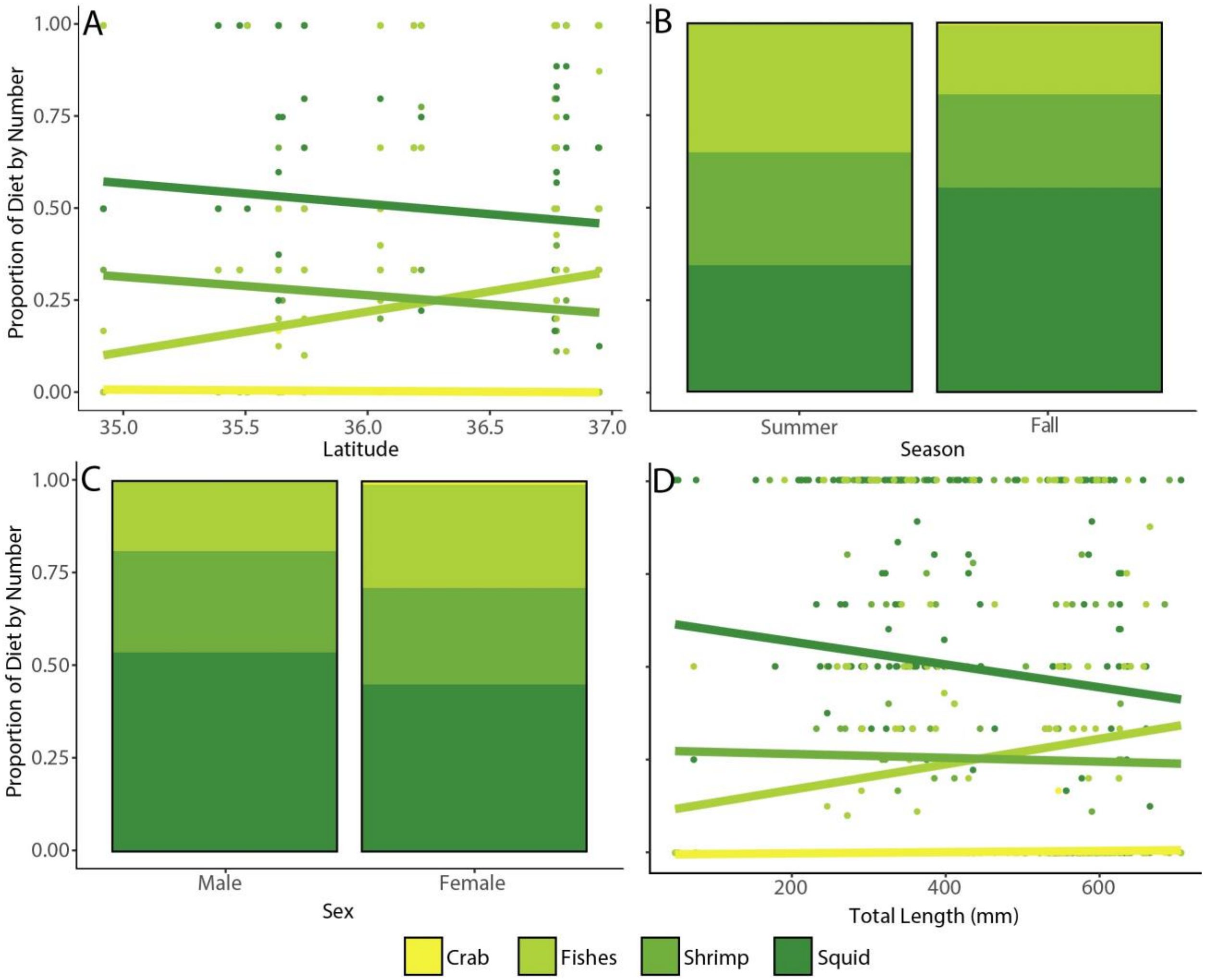

Figure A1. Dietary differences for *Apristurus brunneus* by functional prey category number for factors that were statistically significant in PERMANOVA models. Continuous factors are displayed as simple linear regressions while categorical factors are displayed as adjacent stacked bar plots. Changes in proportion of dietary prey weight as a factor of (A) latitude, (B) sampling season, (C) sex, and (D) predator total length.

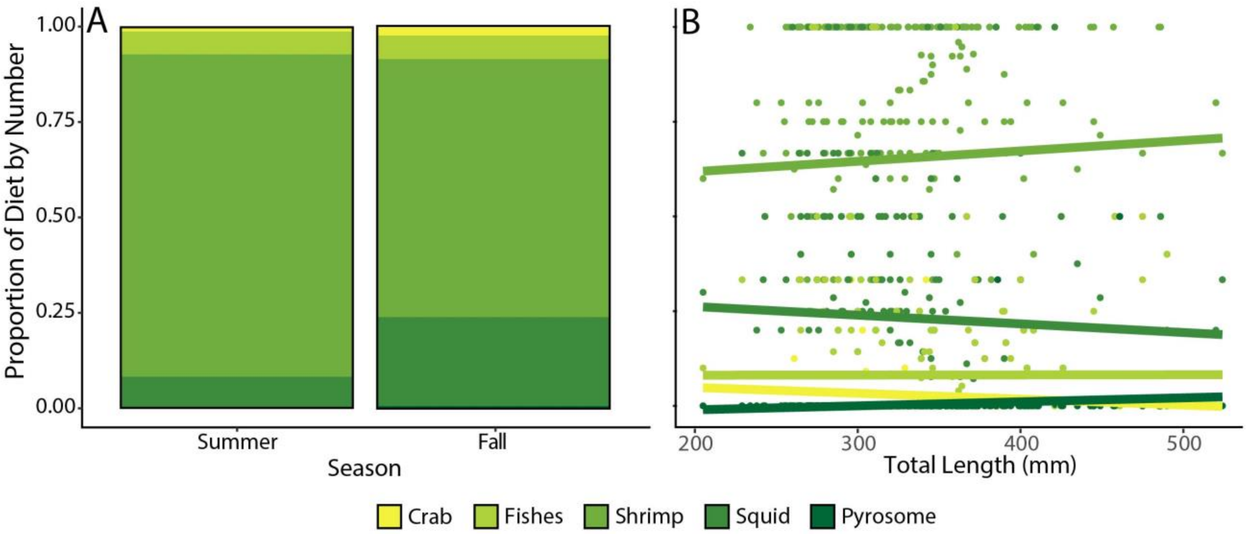

Figure A2. Dietary differences for *Parmaturus xaniurus* by functional prey category number for factors that were statistically significant in PERMANOVA models. Continuous factors are displayed as simple linear regressions while categorical factors are displayed as adjacent stacked bar plots. Changes in proportion of dietary prey weight as a factor of (A) sampling season and (B) predator total length.

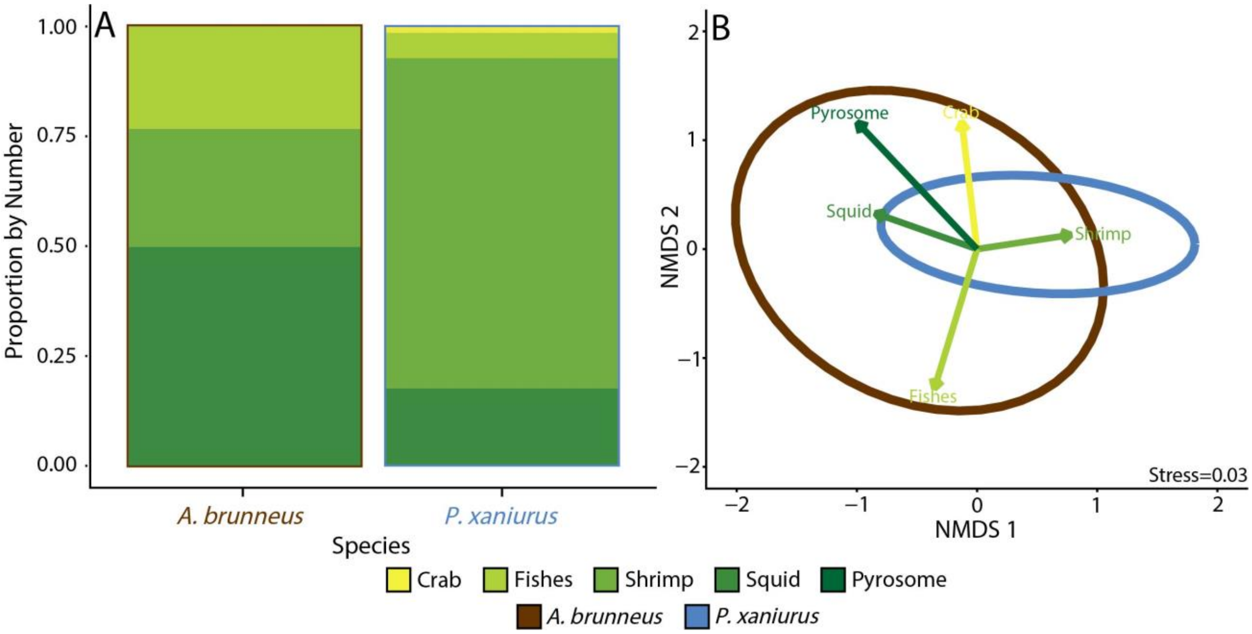

Figure A3. Differences in trophic habits between *Apristurus brunneus* and *Parmaturus xaniurus* through stomach content analysis by number. Categories are broken down by the 5 most common prey groups. (A) Stacked bar plots showing the proportional difference between the two species. (B) A non-metric multi-dimensional scaling (nMDS) plot highlighting the dietary trends of both species. The proximity from the end of each prey vector to the centroid of each species ellipses shows the importance of that prey group to the diet of that predator species. Prey more centrally located in the predator ellipse are more important to the predator's diet.