Spring 2023

Trophic Ecology and Mercury Concentrations of Canary Rockfish (Sebastes Pinniger) in the California Current System

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Recommended Citation

Melanson, Michaela M., "Trophic Ecology and Mercury Concentrations of Canary Rockfish (Sebastes Pinniger) in the California Current System" (2023). *Master's Theses*. 5411.
DOI: https://doi.org/10.31979/etd.q5hh-8mf5
https://scholarworks.sjsu.edu/etd_theses/5411

TROPHIC ECOLOGY AND MERCURY CONCENTRATIONS OF CANARY ROCKFISH (*SEBASTES PINNIGER*) IN THE CALIFORNIA CURRENT SYSTEM

A Thesis

Presented to

The Faculty of the Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Michaela M. Melanson

May 2023

The Designated Thesis Committee Approves the Thesis Titled

TROPHIC ECOLOGY AND MERCURY CONCENTRATIONS OF CANARY ROCKFISH (*SEBASTES PINNIGER*) IN THE CALIFORNIA CURRENT SYSTEM

by

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SAN JOSÉ STATE UNIVERSITY

May 2023

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ABSTRACT

TROPHIC ECOLOGY AND MERCURY CONCENTRATIONS OF CANARY ROCKFISH (*SEBASTES PINNIGER*) IN THE CALIFORNIA CURRENT SYSTEM

by Michaela M. Melanson

Canary rockfish are a profitable fishery resource that has failed and successfully recovered in the 21st century. This study aimed to evaluate their trophic ecology through stomach content and stable isotope analysis and relate these to their mercury concentrations, biological traits, and environmental conditions. Canary rockfish consume mostly krill and teleosts with their geographic location affecting the proportion of prey items, suggesting regional environmental effects: chlorophyll-a, relief, port, and depth impact dietary choices. Mean $\boldsymbol{\delta}^{13}$C values (-17.18 ± 0.54) significantly increased in individuals residing in deeper depths, higher latitudes, higher productivity, and higher temperatures, and in sexually mature individuals. Mean $\boldsymbol{\delta}^{15}$N values (15.26 ± 0.63) increased in individuals within higher latitudes, hotter temperatures, and elevated productivity. Mean calculated trophic level (3.52 ± 0.64) significantly increased in larger individuals, and those residing in more complex and cooler environments. Total mercury concentrations (0.04-0.50 ppm) significantly increased with ontogenetic development, weight, Fulton's K, and latitude. Individuals that consumed higher proportions of teleosts and were larger, sexually mature, and resided in productive, nearshore, or northern environments possessed higher mercury concentrations. Future research should explore if resource allocation changes throughout the year for Canary rockfish, and if mercury concentrations do pose a threat to regional commercial and recreational fisheries.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the hard work and dedication of Rachel Brooks. She spent two summers on the road collecting all of these samples for her own thesis. Starting grad school in 2020 was an enormous struggle due to the uncertainty of research and field work. She was gracious enough to have given me her stomach and tissues samples and isotope data for me to create my own thesis. I am extremely grateful for her time and energy to help me in this process, and this would not have been possible without her.

I also want to thank Jessica Heath of the Moss Landing Marine Laboratories Marine Pollution Studies Lab. She taught me the entire mercury analysis process, and allowed me to take over her machine on a weekly basis to run all of my samples. I completely invaded her work space, and she was nothing but kind, helpful, and gracious towards me while learning all about the mercury analysis process. She spent many of her own work hours helping me, and without her kindness, this thesis would not have been possible.

My thesis committee has also been extremely integral to this process. Their timely feedback and constructive criticism has allowed me to grow as a scientist, writer, researcher, and overall person. I came to grad school with many intentions in mind, but to grow as a person and scientist was paramount, and without their help I do not think I could have accomplished these feats. I am leaving Moss Landing Marine Laboratories different from how I entered, and to me that is what life is about: personal growth. Specifically, Scott Hamilton, thank you for providing me opportunities to work for the National Oceanographic and Atmospheric Administration and The Nature Conservancy, as these jobs have completely shaped my career path. Scott is also responsible for writing the grant and securing the

funding for Rachel's project, thus thank you additionally for the time and effort put forth on your behalf as Rachel and I's theses would not have been possible without it. You have constantly pushed me to be a better scientist, writer, and interpreter and I have learned so much under your guidance. Lastly, thank you for allowing me to graduate in three years, during a global pandemic, a true feat for the both of us.

Lastly, I would like to thank my parents, family, and friends as they have been there for me through the extreme ups and downs of grad school. The late nights, the stressful mornings, and the times when I didn't believe in myself that I would persevere. They were always there to pick me up and remind me of why I wanted to be a marine biologist in the first place. A special shout out to the staff of Dust Bowl Brewing Company who have acted as a second family to me as my place of employment during graduate school. Through this job I have been able to pay all of my tuition and personal bills and I am so proud to say that I will be graduating from graduate school, debt free! Specifically, my dad, the wildlife biologist of the family and the one who has constantly pushed me and inspired me to follow a career in marine biology. Some parents would not approve of such an uncertain career and future, but he has done nothing but be supportive. Whether it meant proofing my lab reports, or showing up for my thesis defense he has been through it all with me!

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LIST OF ABBREVIATIONS

AIC - Akaike Information Criterion
CCS - California Current System
CD - mean distance to centroid
CR - carbon range
dbRDA - distance-based redundancy analysis
ENSO - El Niño-Southern Oscillation
FO - frequency of occurrence
GLM - generalized linear model
GSI - gonadosomatic index
HIS - hepatosomatic index
IQR - interquartile range
IS - individual specialization
MLML - Moss Landing Marine Laboratories
MSA - Magnuson-Stevens Act
MPAs - marine protected areas
NMDS - non-metric multidimensional scaling
NND - mean nearest neighbor distance
NOAA - National Oceanographic and Atmospheric Administration
NR - Nitrogen range
PCA - principal component analysis
PERMANOVA - permutational multivariate analysis of variance
PPM - parts per million
PSIRI - prey-specific index of relative importance
RCA - Rockfish Conservation Areas
SDNND - standard deviation of nearest neighbor distance
SEA - standard ellipse area
SIBER - stable isotope bayesian ellipses
SIMPER - similarities percentages
SST - sea surface temperature
TA - total area of convex hull
TL - trophic level
VIF - variance inflation factor

Introduction

Marine Food Webs and Species Interactions

The study of trophic interactions that comprise marine food webs is essential for understanding energy flow and ecosystem function. Predator-prey relationships are the foundation of food web structure and are influenced by anthropogenic factors such as fishing pressure (Fu et al., 2020; Philippsen et al., 2019), climate change (Chiba & Sato, 2016; Kossak, 2006), variability in oceanography and primary productivity (Fu et al., 2020), or biological factors such as individual specialization (Musseau et al., 2020). Predators can have direct effects on prey populations through consumption, which decreases prey abundance, or through indirect effects that alter the abundance of food resources or competitors for that prey (Bax, 1998). Since these interactions can change over time, consistent documentation is required to identify shifts in organismal abundances or predator-prey interactions that result in trophic cascades or other compounding effects. Trophic cascades can cause semi-permanent phase shifts to ecosystems and entirely alter or render marine food webs and ecosystems unstable (Ripple et al., 2016). Unbalanced or unstable ecosystems can create challenges for sustainable management strategies.

Marine food webs consist of economically and ecologically valuable resources at each trophic level (TL). Therefore, identifying how commercially fished species interact with one another can help support more productive fisheries and holistic management strategies. A detailed understanding of a species' role in the food web allows managers to recognize the resources required to perpetuate the stock and determine possible ecological consequences of overfishing. This classification requires identification of prey resources, foraging strategies, and the scope of the trophic niche. The identification of trophic niches for multiple species in a food web reveals the degree of resource competition amongst species and how populations may be altered in response to changes in those resources. Competition for resources can modify foraging strategies, resulting in specialization, generalization, or opportunistic foraging strategies (Gerking, 2013). Specialization refers to an organism that consumes a select group of prey and rarely deviates from those items. Generalists typically eat a wide variety of prey items and are typically not limited in dietary options. Opportunists do not eat a consistent type of prey, but consume prey that temporally fluctuate in abundance likely due to biotic or abiotic factors. Specifically, there are four fish foraging strategies categorized by generalized TLs: plant and detritus feeders (TL I), planktivory (TL II), benthic carnivores (TL III), and piscivores and pelagic predators (TL IV) (Gerking, 2013).

Many food webs rely heavily on mid-trophic level species to transfer energy from low to high TLs (Rice, 1995). These mid-trophic levels are typically abundant, causing competition for resources, but by displaying dietary plasticity they provide functional redundancy (Beaudoin et al., 1999). For mid-trophic level species or species with generalized diets, any sort of intraspecific variability can alter food web interactions both from the top-down and bottom-up, therefore impacting the overall function of the ecosystem. For many species that occur over broad geographic ranges, it is unknown how spatial variability can also alter their trophic ecology and role in the food web. Therefore, trophic studies occurring over large geographic ranges facilitate a better understanding of the roles and services an organism provides in a regional ecosystem, and how their abundance and distribution may fluctuate in response to environmental or biological characteristics.

Canary rockfish (*Sebastes pinniger*) (Gill, 1864) have a distribution that extends from the Pribilof Islands in the Bering Sea and Western Gulf of Alaska to Punta Colnett, Baja California (Love et al., 2002). They are most common between British Columbia and Central California (Love et al., 2002). The broad distribution of Canary rockfish makes them an ideal species to examine variation in trophic ecology within the highly dynamic California Current System (CCS). The CCS transports cold, nutrient rich water south from Alaska, along the West Coast of the United States, over highly variable bathymetry and habitat types (Checkley & Barth, 2009). This contributes to many oceanographic, environmental, and biological regimes, allowing for dynamic life histories and intraspecific trophic variability (Checkley & Barth, 2009). Additionally, this system is highly dependent on decadal oscillations of the El Niño-Southern Oscillation (ENSO) and seasonal variation in productivity due to oceanographic conditions. ENSO events have significant effects on temperature and productivity with the potential to greatly influence population dynamics, community structure, and ecosystem function from the bottom-up (Chelton et al., 1982; McGowan et al., 1998). The Sebastidae family is highly abundant, diverse (over 70 species), and widespread throughout the CCS, with most species foraging at a mid-trophic level. The adaptive radiation of rockfish over the last 15 million years (Kolora et al., 2021) raises the question of how trophic niches have evolved to permit coexistence and limit interspecific competition? Studies both at the individual species and community level are required to understand how the entire food web functions

The diet of Canary rockfish was described previously (Brodeur et al., 1987; Love et al., 2002), but typically in aggregate with other rockfish species, without focusing on the potential for individual specialization or geographic variation in their trophic ecology. Their diets typically consist of copepods, amphipods, euphausiids, decapods, and small fish (Brodeur et al., 1987; Love et al., 2002). Despite this, Brodeur et al. (1987) characterized rockfish as specialists, while Love et al. (2002) characterized them as generalists. This discrepancy highlights the importance of an updated and more detailed trophic ecology study of *S. pinniger*. My thesis aims to accomplish this task and test whether various biological or environmental factors influence prey consumption and dietary niche diversity in *S. pinniger*. These findings can be used as inputs in future ecological models, references for parts of the CCS food web, and information for resource selection among species within the Sebastidae family. Currently, researchers can integrate dietary data in food web models to anticipate changes to predator or prey populations, which can be valuable information for fisheries managers (Loury, 2011; Tinus, 2012). However, predator-prey relationships are always changing and can be a function of individual choices within a broader population, the outcome of which may alter regional food web dynamics.

Intraspecific Trophic Variability and Individual Specialization

Foraging strategies and trophic preferences are influenced by long-term evolutionary and short-term biological and environmental processes. Intraspecific variability in diets has allowed some fish species to better respond to a changing environment by occupying new ecological niches, outcompeting competitors, or as a consequence of bottom-up changes in prey resources (Beaudoin et al., 1999; Bolnick et al., 2003, 2011; Kernaléguen et al., 2015; Yurkowski, Ferguson, Semeniuk, et al., 2016). Analyzing the trophic ecology of a single species over large spatial scales helps to identify whether biological or environmental characteristics are the predominant drivers of this variability. This is especially true of species occupying geographic distributions with large habitat and oceanographic variability.

Intraspecific differences define the cumulative trophic niche of a species and determine the level of individual or sub-population specialization in the larger population. Van Valen (1965) defined the niche variation hypothesis, suggesting populations with wider niches are more variable than populations with narrower niches. The prediction is that those populations with wider niches can serve the ecosystem in a multitude of ways, while being more tolerant to environmental change. Van Valen further discussed how the niche can be used to determine the degree of individual specialization in resource use (i.e., differences in trophic preferences and feeding methods). Other studies have reinforced these paradigms by identifying species that appear to be ecological generalists, but in reality are a heterogeneous collection of specialized individuals (Bolnick et al., 2003; Rudolf & Lafferty, 2011).

Individual specialization can originate via interspecific competition, intraspecific competition, or in response to predation pressure (Kernaléguen et al., 2015). Individual specialization likely occurs when individuals of similar sex and age classes use a small subset of the entire population's resources (Bolnick et al., 2003; Rudolf & Lafferty, 2011). How species partition and specialize in resource use, especially as it relates to their biological development or environment, helps identify how to best conserve a species throughout different stages of the life cycle and across various locations. Overlooking individual specialization may result in errors when classifying a species' role within a food web, which can have broad ecological consequences for scientists and fisheries managers.

Intraspecific variability in resource use allows for species to occupy broad spatial ranges. Wimberger (1994) argues this is most common among fishes that exhibit the following characteristics: utilizing only the mouth for foraging, possessing multiple prey types that require different modes of extraction, demonstrating behavioral flexibility, possessing stable prey types, and occupying food webs with empty niches. This phenomenon is even more widely observed in species at low to intermediate TLs, as they tend to display a large degree of dietary plasticity (Beaudoin et al., 1999). This variability is heavily influenced by a number of different factors, both biological: gender (Shine, 1991), ontogenetic development stage (Polis, 1984; Rudolf & Lafferty, 2011; Yurkowski, Ferguson, Choy, et al., 2016), length (Olson et al., 2020), and weight (Raffard et al., 2020) and environmental: depth (Basnett, 2021), habitat (Flaherty & Ben-David, 2010), and latitude (Conover & Present, 1990; Yurkowski, Ferguson, Choy, et al., 2016). Any one of these factors can cause high degrees of intraspecific trophic variability and several of these are characteristics of Canary rockfish.

Biological differences in trophic position and prey preferences result from the various metabolic requirements of different life stages (Zhao et al., 2014), or changing environmental conditions (Bergmann, 1847; Conover & Present, 1990). Gender and sexual maturity are two factors routinely identified to explain changes in trophic ecology throughout ontogenetic development (Polis, 1984; Rudolf & Lafferty, 2011; Shine, 1991; Yurkowski, Ferguson, Choy, et al., 2016; Zhao et al., 2014). Notably, females increase their niche during their reproductive period to access more diverse foraging grounds (Kernaléguen et al., 2015), or by foraging higher on the food chain to support the increased metabolic processes related to gestation and egg production (Basnett, 2021). Body size is intimately linked to metabolic processes and the capabilities utilized for acquiring and processing prey; thus trophic interactions frequently change with size (Basnett, 2021; Rice, 1995). Larger individuals within a species generally forage at higher TLs in comparison to juveniles, therefore displaying a positive relationship between size and TL (Di Lorenzo et al., 2020; Olson et al., 2020; Rice, 1995). However, the degree to which this is a function of metabolic requirements versus improved foraging with greater age and size is still debated.

Both genders of *S. pinniger* experience ontogenetic life history changes, thereby altering resource and habitat use throughout their life cycle (Love et al., 2002; Thorson & Wetzel, 2015). For example, many species of rockfish, including *S. pinniger*, inhabit shallower benthic habitats after the end of the pelagic state and migrate to deeper waters with more complex and higher relief habitats as they age and mature (Love et al., 2002; Methot & Stewart, 2005; Vestfals, 2009; Vetter & Lynn, 1997). Additionally, females tend to grow larger in size upon maturation than their male counterparts. Adults primarily inhabit rocky reefs and customarily form dense schools, resulting in a patchy spatial distribution throughout the CCS (Thorson & Wetzel, 2015). Canary rockfish are a long-lived species, recorded as old as 84 years (Thorson & Wetzel, 2015). They mature at 7-9 years and are highly fecund upon maturation (Kendall & Lenarz, 1986; Love et al., 2002). Males are commonly the only individuals found to be above the age of 50 and females are rarely observed above the age of 30 (Thorson & Wetzel, 2015), suggesting mortality rates are higher for females than males. Thus, Canary rockfish are an ideal species for a dietary study as they display sexual, ontogenetic, and habitual differences in behavior throughout their life history.

Environmentally, intraspecific trophic variation is commonly associated with gradients of temperature, productivity, and habitat (Flaherty & Ben-David, 2010; Gårdmark & Huss, 2020; Yurkowski, Ferguson, Choy, et al., 2016). Productivity and temperature are also closely related to changes in latitude, which can be important environmental drivers of diet variability (Conover & Present, 1990; Yurkowski, Ferguson, Semeniuk, et al., 2016). Bergmann's (1847) rule states higher latitudes are generally associated with colder and more productive waters, but shorter growing seasons; thereby organisms living in these higher latitudes tend to attain larger sizes and grow more rapidly compared to the same organisms living in lower latitudes. However, this is a general paradigm and does not hold true for all species and areas of the global oceans (e.g., Mousseau, 1997; Partridge & Coyne, 1997). The CCS could be considered an anomaly to Bergmann's rule since temperature and productivity do not follow a strict latitudinal gradient due to upwelling and other oceanographic processes (Chelton et al., 1982; McGowan et al., 1998). Dietary variation can also be determined by depth and the location where individuals forage in the water column, as prey composition and availability respond to those factors (Basnett, 2021; Chiu, 2018; Pethybridge et al., 2018). Additionally, habitat relief/rugosity can influence the distribution of rockfish life stages and the composition of their prey, and therefore can be used as an indicator of trophic variation (Love et al., 2002; Rudolf & Lafferty, 2011; Tissot et al., 2007). The CCS nearshore marine environment consists of a conglomeration of kelp forests, rocky reefs, sandy bottoms, muddy bottoms, etc. making it a great system to test the effects of habitat variation on trophic ecology.

Intraspecific trophic variation and the resulting trophic niche can be evaluated through techniques such as stable isotope analysis and stomach content analysis. The synthesis of these two methods is required to understand the short-term and long-term dietary habits of a species. Stomach contents are indicators of daily trophic habits and provide accurate information on the types of prey consumed at a taxon-specific level. Although stomach contents can reveal fairly specific prey item information, it must be incorporated with another analysis method, as stomach contents can only provide a brief snapshot of the diet of an individual. Prey contents can remain within a stomach for hours to days (Hyslop, 1980), and may be dependent on an individual's location or the types of prey that are abundant at the time of consumption. Prey items consumed by an individual can fluctuate on a daily basis based on prey availability and foraging method, thus only analyzing stomach contents as a way of characterizing diet could create a temporal bias in understanding the full dietary niche.

Stable isotopes are useful for describing dietary habits over a longer period of time (i.e., days to years depending on turnover rate of tissue analyzed), but often provide less accurate information as to specific prey items, unless they possess a distinct isotopic composition. Stable isotope analysis uses the $\boldsymbol{\delta}$ notation to reflect the ratio between the lighter (i.e., ^{12}C and ^{14}N) and heavier isotopes (^{13}C and ^{15}N). $\boldsymbol{\delta}$ represents isotopic fractionation: kinetic and chemical processes that change the ratio of heavy to light isotopes. $\boldsymbol{\delta}^{13}C$ is a proxy for the source of primary production in a food web as carbon isotopes change little with TL (~0.5%

increase in $\delta^{13}C$ with each TL), but vary among primary producers that utilize different photosynthetic pathways (Fry, 1988; Minagawa & Wada, 1984; Post, 2002). $\delta^{15}N$ is often used as a proxy for TL as it fractionates, resulting in a relatively uniform 3-4% increase in $\delta^{15}N$ with a singular increase in TL (Post, 2002). Not only can isotopes and stomach contents reveal information about trophic interactions and the degree of individual specialization, but they can also be important indicators of inorganic pollutant pathways and concentrations in food webs (e.g., mercury). Certain prey preferences and $\delta^{15}N$ values can reflect the transfer of pollutants from prey to predator, and how determinantal substances enter and spread throughout a food web.

Bioaccumulation and Biomagnification of Mercury in Marine Food Webs

Mercury pollution research has exponentially increased in the last 40 years due to the heightened awareness of the presence of organic mercury in the natural environment from anthropogenic emissions and its resultant neurotoxic effects on humans (Hudson et al., 1995). Natural sources of mercury sourced into the environment include volcanic emissions, hydrothermal activity, mantle degassing, and natural weathering; prior to anthropogenic emissions, mercury was assumed to be in global equilibrium (Driscoll et al., 2013; Hudson et al., 1995; Pirrone et al., 1996). Anthropogenic sources of mercury into the atmosphere and ocean include: fossil fuel combustion, biomass burning, industrial uses, and mining (Driscoll et al., 2013; Hudson et al., 1995; Lamborg et al., 1999; Pirrone et al., 1996). These sources emit elemental and ionic mercury into the atmosphere, or deposit as non-gaseous forms into watersheds where it can enter the surface ocean via wet or dry deposition in its elemental or ionic form through air-sea interactions or transportation from rivers (Driscoll et al., 2013;

Lamborg et al., 1999; Mason & Sheu, 2002). Anaerobic microbes methylate (i.e., add a methyl group to) elemental or ionic mercury which allows for the compound to be biologically assimilated by other organisms, typically marine plankton (Fitzgerald et al., 1991; Kim & Fitzgerald, 1986). Thus, the types of mercury found within global oceans can be in the form of elemental (Hg^0), ionic (Hg^1 and Hg^2), methylated/organic ($HgCH_3$), and total (summation of elemental, ionic, and organic mercury). Given this is an anoxic process carried out by anaerobes, methylated mercury concentrations are highest in low oxygen environments such as highly productive areas, zones of upwelling, areas of higher temperatures, or after spring phytoplankton blooms. Inorganic mercury is largely not metabolized by organisms due to differential cell partitioning of organic and inorganic mercury (Mason et al., 1995; Riisgård & Hansen, 1990). Inorganic mercury is stored within cell membranes which are excreted by biological organisms, whereas methylmercury is deposited within the easily assimilated cytoplasm (Mason et al., 1995). Therefore, methylmercury is readily biomagnified through food webs (Driscoll et al., 2013; Mason et al., 1995; Zhang et al., 2020).

Marine phytoplankton assimilate methylmercury from the water column, and when they are consumed by higher TLs, mercury accumulates throughout all levels of the food web (Mason et al., 1995; Riisgård & Hansen, 1990; Watras & Bloom, 1992; Zhang et al., 2020). This phenomenon is referred to as biomagnification, which is an increase or build up in a compound's concentration with increasing TL, due to biological assimilation of prey tissue. (Chen et al., 2008; Lavoie et al., 2013; Mason et al., 1995; Riisgård & Hansen, 1990). Bioaccumulation concerns substances that amass within a single organism because they are unable to be digested or excreted due to their chemical properties, thus accumulating within cells and tissues. Degrees of bioaccumulation and biomagnification are largely attributed to zooplankton composition and oceanographic conditions and tend to be greatest in higher TL and longer-lived organisms (Zhang et al., 2020). This makes species such as the long-lived rockfish an optimal study species for understanding how bioaccumulation and biomagnification of methylmercury can vary biotically and abiotically. This study will measure the total wet weight mercury concentrations of fish tissue, which will amount to both the inorganic and organic forms of mercury in the measurement. However, it is assumed that a vast majority of the mercury in this total wet weight measurement (>95%) will be methylmercury (organic mercury) (Bloom, 1992), and is an accurate but cheaper and quicker way of measuring methylmercury directly. Thus, total mercury content will be used as a proxy for methylmercury in this study and will be referred to as total mercury concentrations or [Hg] ppm.

Rockfish live for decades, allowing for a prolonged period of time for bioaccumulation and biomagnification of pollutants (Power et al., 2002). As rockfish grow and mature, they tend to eat higher on the food chain to satisfy their increasing metabolic demands (Love et al., 2002). Larger size and more finely tuned foraging strategies can expand the trophic niche, amounting to higher degrees of biomagnification throughout ontogenetic development (Love et al., 2002; Power et al., 2002). There is a dearth of studies regarding total mercury concentrations of mid-trophic level species similar to rockfish. Total mercury refers to the amount of elemental, ionic, and organic mercury found within fish tissues. A majority of mercury studies analyze apex predators such as marine mammals (Loseto et al., 2008;

Pinzone et al., 2019), birds (Braune, 1987), sharks (McMeans et al., 2015), or large fish (Beckett & Freeman, 1974; C. L. Peterson et al., 1973), or alternatively the plankton at the base of the food chain (Watras & Bloom, 1992). Investigating levels of organic mercury pollution in rockfish, especially how it varies based on biological or environmental characteristics, could provide valuable health and safety information to fisheries managers and seafood consumers. This study aims to improve the understanding of spatial and ontogenetic variation in methylmercury levels and provide information concerning methylmercury pollution within mid-trophic level organisms of the nearshore marine food web in the CCS. Given the fluctuating history of fish stock stability and the economic value of fisheries in this region, anthropogenic pollution could be another potential source of fishery collapse and a human health concern.

Given the paradigms of bioaccumulation and biomagnification, TL is predicted to have a positive association with total mercury concentrations (Kidd et al., 1995; Lavoie et al., 2013; McMeans et al., 2015). This would suggest larger and older organisms contain elevated total mercury levels, which are the fish typically caught, sold, and consumed, due to size selective fishing practices. Marine food webs are complex, suggesting certain foraging types may be more conducive to bioaccumulation of toxicants (Power et al., 2002). Past studies have evaluated generalist and specialist predators to indicate whether prey preferences, or foraging habitat are useful indicators of mercury pollution within specific organisms. Pinzone et al. (2019) studied multiple whale species in the Mediterranean and found food web complexity, trophic position, hunting distribution, and habitat use were not significant indicators of total mercury concentrations. However, the authors identified prey type and foraging strategy as significant factors of mercury concentrations, with generalist piscivore species bioaccumulating mercury more than cephalopod specialists (Pinzone et al., 2019). Contrastingly, McMeans et al. (2015), found total mercury concentrations increasing with TL at a faster rate in pelagic rather than benthic food webs, but with benthic primary consumers having elevated total mercury concentrations compared to their pelagic counterparts. Nevertheless, both studies concluded total mercury concentrations are associated with the types of prey consumed or foraging strategy utilized, furthering the connection between diet and mercury studies.

Along with biotic factors, abiotic conditions such as: geographic location (Lavoie et al., 2013; Zhang et al., 2020), temperature (Lavoie et al., 2013; Zhang et al., 2020), productivity (Lavoie et al., 2013; Zhang et al., 2020), pH (Mason & Sheu, 2002), and topography (Zhang et al., 2020) can be primary drivers of total mercury concentrations. Organic mercury concentrations are positively correlated to areas of high production, high apparent oxygen utilization, and low oxygen due to elevated microbial activity and methylation (Zhang et al., 2020). These conditions are typical of the CCS since it is an eastern boundary current characterized with seasonal upwelling and high productivity (Zhang et al., 2020). The northern Pacific Ocean is also located at the end of global oceanic thermohaline circulation and therefore possesses oceanographic factors at depth of low oxygen concentrations, saturated nutrients, and hypoxia. Despite this, there is a competing hypothesis that high levels of productivity and biodiversity at the base of the food chain can cause biodilution of total mercury, thus lessening the degree of mercury trophic transfer in highly productive areas (Lavoie et al., 2013). Biodilution can be defined as the same mass of methylmercury in a water column fluctuating in concentration as a result of increased or decreased primary productivity resulting in the decrease of methylmercury consumption by an organism. Biodilution can also occur as a function of growth rate, in which an organism decreases the concentration of mercury in their tissues by sustaining a higher growth rate and accumulating more organic tissue to dilute the total concentration of mercury per unit body mass. High temperatures induce higher metabolic rates, which can consequently decrease organic mercury per unit body mass, due to the higher rates of excretion from an increased metabolic rate (Lavoie et al., 2013). Given the large geographic range, my study will evaluate whether certain environmental factors, including temperature, are correlated with total mercury concentrations in Canary rockfish.

Given the contrasting results of these various studies, there is a high degree of variability in the factors that contribute to mercury bioaccumulation. The identification of these driving forces could help predict where and what types of fish contain elevated total mercury concentrations that could pose a health hazard. This information could be utilized by managers for more efficient and safe fisheries management, especially given the effects of elevated temperatures and lower oxygen saturations caused by climate change (Alava et al., 2017). However, there is only a single study that encapsulates the entire U.S. West Coast regarding coastal fish mercury concentrations (Davis et al., 2016). There are also smaller scale studies of mercury concentrations within smaller spatial scales along the CCS such as the California State Water Board's decadal mercury measurements in multiple species of fish. However, these studies have not sampled a single targeted species over a large spatial range and this study aims to fill that gap. Davis et al. (2016) indicates the need for further research into specific indicators of mercury pollution for coastal fishes in the CCS to predict harmful mercury pollution and ensure healthy seafood.

Canary Rockfish (*Sebastes pinniger*) in the California Current System

The rockfish fishery in the Northeastern Pacific Ocean developed in the late 19th century using commercial trawling vessels. This fishery became particularly important during World War II due to the provisioning of red meat for soldiers which transitioned society into a larger demand for non-red meats (Alverson et al., 1964). Shortly after the war, catches dropped to meet demand and remained relatively constant until the implementation of the Magnuson-Stevens Act (MSA) in 1978. The MSA implemented stricter management restrictions, thereby decreasing overall landings throughout the remainder of the 20th century (Thorson & Wetzel, 2015). Despite these management actions, the groundfish fishery on the U.S West Coast was deemed a federal disaster in 2000 with many of the fisheries placed on the U.S endangered species list, resulting in the implementation of Rockfish Conservation Areas (RCAs) and Marine Protected Areas (MPAs) (Andrews et al., 2018; Parker et al., 2000). At this time, Canary rockfish were deemed to be at an all-time population low, which precipitated a fishery closure, as this species was identified as a limiting catch species in many other fisheries throughout the CCS (Thorson & Wetzel, 2015). Once a species is characterized as a limiting catch, other fisheries can be shut down if a certain threshold of the limited species is caught as bycatch. The fisheries management recovery plan was predicted to take 30 years to recover the groundfish fishery, but after only 15 years, the Pacific Fishery Management Council's stock assessment determined the stock to be healthy enough for reopening in 2015 (Keller et al., 2018). The Canary rockfish fishery on the U.S. west coast is considered to be healthy in 2023 as the population is above target levels, fishing is occurring at a sustainable rate, and regulations are in place to minimize any destruction due to bycatch. Despite this, there is minimal information on the stock structure of Canary rockfish along the West Coast. Deciphering their spawning stock could provide critical information for a more efficient management of this fishery. A dietary and mercury study can indicate if there are dietary preferences that may delineate stocks in this region as well as provide information about the ecosystem in which these populations reside.

The first genetic study of *S. pinniger* in the CCS found reduced gene flow and lack of a specific gene variant between fish collected from Northern California and Southern Oregon compared to those in Northern Oregon and Southern Washington (Wishard et al., 1980). This same study also suggested slight isolation between deep and shallow samples based on different frequencies of the PGM gene, suggesting a possible stock delimitation. National Oceanographic and Atmospheric Administration (NOAA) trawl surveys reported spatiotemporal discrepancies in weight, length, and age ratios indicating distinct population assemblages along the CCS at similar biogeographic breaks (Keller et al., 2018). They found larger and more sexually mature adults North of Point Mendocino, California and at depths greater than 115 m. Further, with analysis of catch-per-unit-effort, distribution, and life history data, combined with the presence of smaller and sexually immature organisms South of Cape Mendocino, the authors suggest the possible existence of distinct biological stocks along the U.S. West Coast (Keller et al., 2018). Cape Mendocino is a highly dynamic barrier with strong upwelling and converging currents that limit the amount of nearshore rocky reef habitat patches for rockfish (Gertseva et al., 2017). This information suggests a paucity of habitat utilization by rockfish in this area, causing a lack of gene flow and partitioning the stock at this biogeographic barrier. Another study analyzed *S. pinniger* $\boldsymbol{\delta}^{18}$O and $\boldsymbol{\delta}^{13}$C isotopes along Washington and Oregon, suggesting Canary rockfish may belong to a single spawning stock in Oregon or Washington (Gao et al., 2013). However, these authors did not sample *S. pinniger* from California, and therefore it is difficult to discern if there are spawning stock differences between Oregon, Washington, and California. This presents a dilemma for managers as to whether *S. pinniger* belongs to a single or multiple stocks and how to most effectively manage this species. My thesis, which spans from Washington to Southern California, will help decipher how to manage this economically important fishery as it may reveal discrepancies in trophic position, foraging strategy, and prey preference, which all contribute to the delineation of stocks.

The samples for this study were collected in 2017 and 2018, which were deemed to be normal years in the ENSO cycle. However, it is important to note that this time period immediately followed the marine heat wave anomalies of 2014-2016, and therefore rockfish may continue to experience the effects of these events. Studying this period of acclimation and recovery after the heat wave will provide a reference to evaluate climate change effects in the future. Therefore, this study has four main objectives:

1. Characterize the diet and associated factors controlling gut contents through prey item identification of *S. pinniger* within the CCS.
2. Use stable isotope analysis of $\boldsymbol{\delta}^{13}$C and $\boldsymbol{\delta}^{15}$N to determine trophic position and the dietary niche of *S. pinniger* within the CCS and how it may be influenced by environmental conditions and ontogenetic shifts.

3. Determine how total wet weight mercury concentrations may vary based on biological or environmental gradients.
4. Determine if there are associations between prey preferences/stomach contents, isotope values/TL, and total wet weight mercury concentrations of *S. pinniger* in the CCS.

Management of *S. pinniger* and other rockfish species will be greatly enhanced via an understanding of their place, role, and variability in the nearshore marine food web. In addition, understanding associations between trophic position and pollution accumulation is essential to properly manage the fishery for safe human consumption.

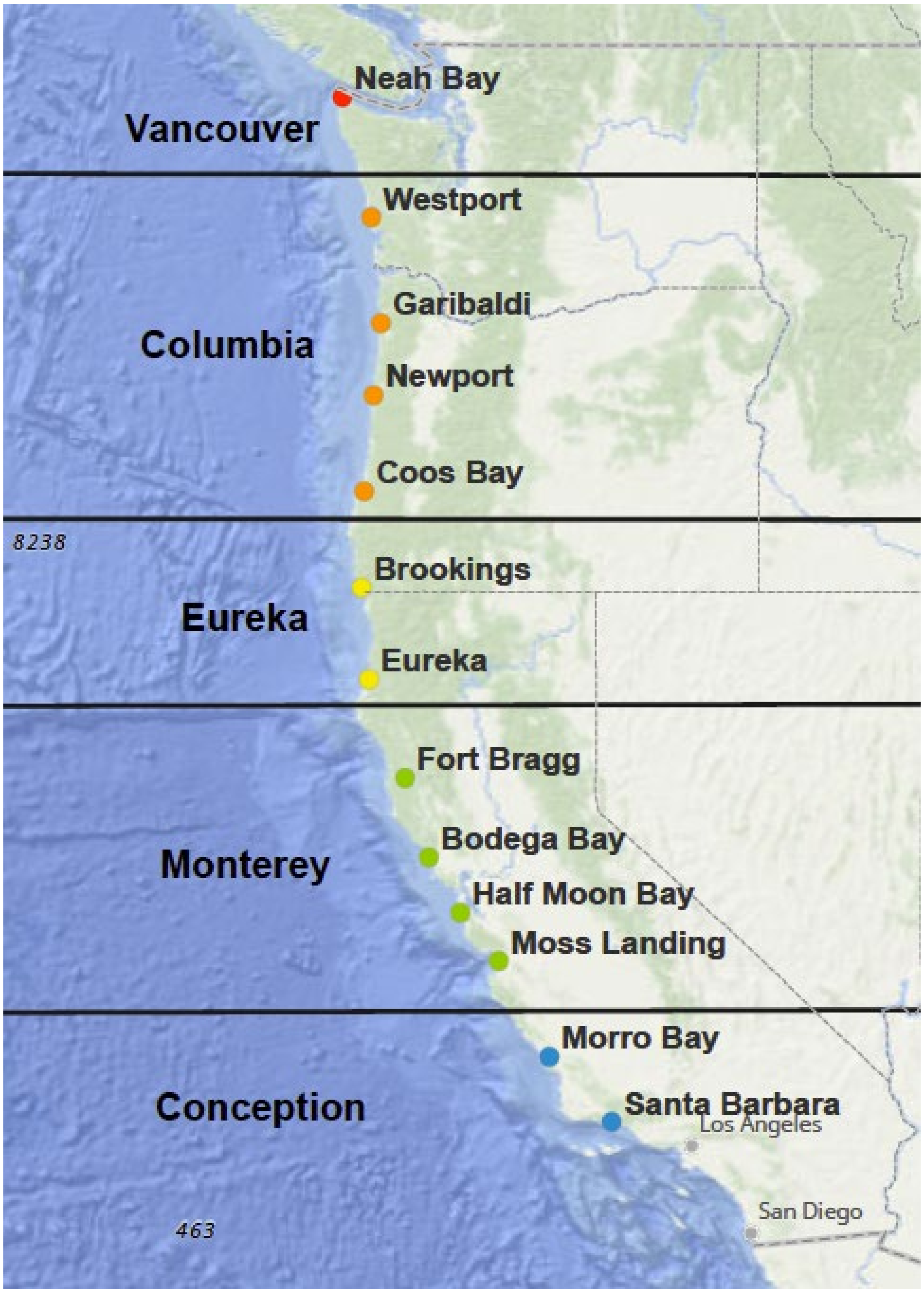
Materials and Methodology

Fish Sampling and Storage

Canary Rockfish specimens were collected in the Summer of 2017 and 2018 at 13 locations from Washington to California: Westport, Neah Bay, Coos Bay, Garibaldi, Newport, Brookings, Bodega Bay, Fort Bragg, Eureka, Moss Landing, Half Moon Bay, Morro Bay, and Santa Barbara (Figure 1). These 13 ports also lie within five fisheries management regions utilized by the Pacific Fishery Management Council to manage fisheries with regards to spatial differences and biogeographical barriers. These five fisheries management regions encompass the U.S. West Coast from Washington to California: Vancouver, Columbia, Eureka, Monterey, and Conception. In this study, individuals will typically be grouped by these fisheries management regions to test for spatial variability amongst the samples. These collections were conducted under the San Jose State University Institutional Animal Care and Use Committee protocol (#964) in addition to federal (SRP #31-2017 [2017], LOA #02-2018 [2018]), and state (California: #6477, Oregon: #21047 [2017], and Washington #17-024) permits. Canary rockfish individuals were collected via volunteer recreational anglers on chartered commercial passenger fishing vessels using baited and unbaited shrimp flies. Starting depth, latitude, longitude, and benthic relief (1-3 scale) were collected for each fishing drift. Benthic relief is a measurement of the rugosity of the seafloor and can be used to assess habitat complexity. In this study, a measurement of 1 on the relief scale would indicate a relatively flat seafloor surface, and a measurement of 3 would indicate a complex seafloor surface containing many peaks and valleys along the

Figure 1

Map of the 13 Sampling Ports Where Samples Were Collected Represented by the Colored Dots. The Dots Are Colored by the Five Fishery Management Regions the Ports Are Located Within, and Are Also Labeled by the Black Lines



seafloor immediately underneath the boat. A total of 1562 samples were collected statewide (Table 1), including 351 fish with intact stomachs for gut content analysis (barotrauma effects from angling caused inversion of stomachs and their contents in many samples). Of the samples collected, 496 were used for stable isotope analysis, and 288 samples were utilized for mercury analysis (Table 1) across the different regions sampled. Each fish collected was euthanized via cranial concussion and stored on ice until dissection which occurred immediately upon returning to port. Prior to dissection, fish were measured for total, fork, and standard length (nearest 0.1 cm), and weighed (nearest 0.01 kg, Using Berkley Digital Fish Scale). These measurements also determined Fulton's K which indicates the relative condition of a fish since it is a ratio of length to weight in a fish ($\frac{100* Weight}{Length^3}$), and can also be indicative of energy reserves, similar to a body mass index of a fish. Two vials of dorsal muscle tissues were collected per fish and stored in 1.5 ml cryovial tubes, which were then frozen. The stomachs were preserved in 10% buffered formalin and transferred to 70% ethanol to be stored at Moss Landing Marine Laboratories (MLML). Gonad and liver weights (nearest 0.1g, using Ohaus Scout SPX2201) were recorded for each fish to assist with determination of reproductive status and condition (gonadosomatic index [GSI] and hepatosomatic index [HSI]). Maturity status and sex were determined through visual inspection of the gonads.

Environmental Data

Average temperature and average productivity for each geographic region were calculated through NASA's GIOVANNI satellite database using their MODIS datasets for sea surface temperature (SST) in °C and chlorophyll-a concentrations in mg/m^3. These

Table 1

Total Number of Canary Rockfish Samples Collected, Used for Stomach Content Analysis, Used for Isotope Analysis, and Used for Mercury Analysis Sorted by Management Region and Summarized by their Totals

Management Region	Number of stomachs	Number of stomachs with contents	Number of samples for isotope analysis	Number of samples for mercury analysis
Vancouver	170	38	48	26
Columbia	548	119	172	114
Eureka	240	63	84	66
Monterey	402	85	109	63
Conception	202	46	83	19
Total	1562	351	496	288

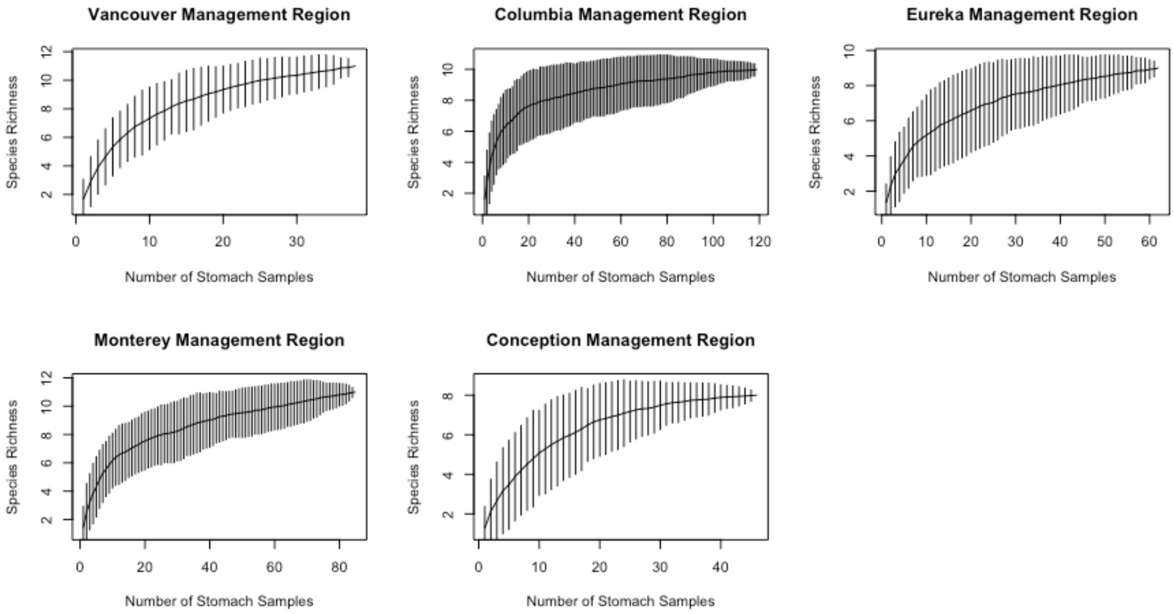
datasets took 8 measurements a day in 4X4 km boxes for both SST and chlorophyll-a. The coordinates of all the fish caught at each fishing port were used to extract data by drawing boxes that included the coordinates of each fish at each port. Each of the measurements within each coordinate box at each fishing port were averaged for a mean SST and chlorophyll-a value over a 10-year time period to account for decadal variability (2008-2018). This 10-year time period allowed for natural variation in the ENSO cycle to occur within the dataset, with the goal of averaging environmental conditions over the long life span of Canary rockfish. Additionally, a majority of the samples were collected in the summer months, therefore incorporating average data over the entire year, and not just a single season, will help to eliminate some of the seasonal bias in environmental conditions.

Stomach Content Analysis

To determine if there were sufficient stomach sample sizes in each fisheries management region to describe *S. pinniger* diets along the CCS, prey accumulation curves were created. Eleven higher taxonomic prey groups were generated from the 27 total prey items observed in the diet. These were then plotted as a function of the number of stomachs analyzed in each management region, using the vegan community ecology package in R (Figure 2). As sample

Figure 2

Prey Accumulation Curves for Canary Rockfish Prey Items Sorted by Fisheries Management Region. The Curved Horizontal Line Represents the Mean Number of Prey Items While the Surrounding Vertical Lines Represent 95% Confidence Intervals. The X-Axis Represents the Number of Stomachs Sampled Within the Region and the Y-Axis Represents the Mean Number of Prey Items Found Within Stomachs in that Region



size increases, the variation in diet should plateau because new prey items are introduced into the diet less frequently as there is a greater encapsulation of diet with increasing stomach samples. Once this curve reaches an asymptote, it is assumed the sample size is sufficient for describing the diet of sampled specimens by the number of higher taxonomic prey groupings. To determine if an asymptote had been reached, a linear regression was run on the last 5 points of the line to determine a slope ≤ 0.05.

Stomach content analysis was performed to determine specific prey items and how prey composition varies. Each stomach was sliced open, contents were scooped into jars, and preserved in 70% ethanol. Later, each jar was poured over a 500 µm sieve, waiting 5 minutes for the contents to properly settle out and filter through the sieve. Every item retained on the sieve was visually inspected with a dissecting microscope to identify items to the nearest taxonomic level. When otoliths and krill eyes were found, they were counted and the count was halved, to account for the abundance of each paired item. Otoliths were inspected again under a microscope to determine the specimen down to the species level if possible. Each identified item was counted for abundance and measured to the nearest milligram to calculate a variety of dietary indices: percent by abundance and weight (%N, %W), prey-specific abundance for both number and weight (%PN, %PW), frequency of occurrence (%FO), and prey-specific index of relative importance (%PSIRI). The equations used to calculate these dietary indices used in this study are listed below.

$$\text{(\%N, \%W) Percent Abundance/Weight} = \left(\frac{A\ or\ W_i}{Total\ A\ or\ W}\right) * 100$$

where A=Abundance and W=Weight.

Percent abundance and weight provide a comparison of the proportionality of certain prey items to the overall diet of all individuals in the dataset.

$$\text{(\%PN, \%PW) Prey-specific Abundance}_i = \left(\frac{\sum_{j=1}^{n} \quad Aij}{Ni}\right) * 100$$

where A= proportional abundance by number or weight of each prey category, i= prey category, j=stomach sample, and N_i= number of stomachs that contain the prey category.

Prey-specific abundance or prey specific weight was used to indicate the relevance of specific prey items to the dataset at large.

$$\text{(\%FO) Frequency of occurrence} = \left(\frac{Ni}{n}\right) *100$$

where N_i = number of stomachs that contain prey category j, n = number of stomachs sampled.

FO indicated how common certain prey items are with respect to individuals or subsets of diets as well as *S. pinniger* diets as a whole. Further, this was used to evaluate prey items significantly contributing to total wet weight mercury concentrations and TL variability.

Prey-specific index of relative importance:

$$\%\mathrm{PSIRI}_i = \left(\frac{\%FO_i \times (\%PN_i + \%PW_i)}{2}\right) * 100$$

Where %FO = percentage frequency of occurrence, $\%PN_i$ = percent by number of stomachs that contain that prey item, and $\%PW_i$ = percent by weight of prey items in stomachs.

PSIRI uses FO, number, and weight data to indicate the importance of specific prey items/prey groups. This normalizes the distribution of prey items and helps to pinpoint the most significant prey items found within the stomachs.

The following equation will be used to calculate TL.

$$\mathrm{TL} = 1 + \left(\sum_{j=1}^{n} P_j \times TL_j\right)\text{(Cortés, 1999)}$$

where P_j = proportion of prey category, j, TL_j = trophic level of prey category j, and Generalized prey categories by Ebert and Bizzarro (2007).

Mean and standard deviations of TL were calculated following Cortés (1999) and using values found in Ebert and Bizzarro (2007). Ebert and Bizzarro determined the mean TL of common taxonomic prey items in the Northeastern Pacific Ocean and therefore TL can be calculated using the formula given in Cortés (1999) and the proportions of prey items found in the *S. pinniger* stomachs.

In addition to the calculated dietary metrics above, the R Individual Specialization (RInSp) package in R was used to calculate an Individual Specialization (IS) score and corresponding p-value based on Bolnick et al. (2003). This IS value measures the proportional similarity between the resource distribution of the individual and the distribution of the population as a whole, varying from 1 (complete overlap between the individual and the population) towards 0, with smaller values representing a higher degree of IS in resource use.

$$PS_i = 1 - 0.5 \sum_j \left| p_{ij} - q_j \right|$$

where p_{ij} = frequency of category j in the individual's, i, diet, q_j = frequency of category j in the population as a whole.

$$IS = \frac{\sum (PS_i)}{N}$$

where N = sample size.

A permutational multivariate analysis of variance (PERMANOVA) was run in RStudio to analyze differences in prey composition amongst the individual Canary rockfish stomachs. %N and %W of the 11 higher taxonomic prey groups were run in the PERMANOVA to differentiate which categorical variables: sex, maturity, management region, or port explain significant variability of diets, and which of the models (abundance or weight) is a better descriptor of diet overall. Additionally, a fourth root transformation (and other numerical transformations) was used on both %W and %N to determine if a transformed dataset resulted in a better overall model. The fourth root transformed %W data created the best overall model for the dataset and was used as the basis for the remainder of the univariate and multivariate statistics unless otherwise stated. A Bray-Curtis similarity matrix was derived from the %W transformed data and ran through the PERMANOVA to test each categorical variable on the prey data matrix. The PERMANOVA produced r^2 and pseudo-F values for each variable that indicate the amount of variance the particular variables represent within the dataset and the ratio of between and within level variation. To visually represent these results, plots were created in Non-metric Multidimensional Scaling (NMDS) space with ellipses representing significant variables from the PERMANOVA and vectors representing the prey groups to evaluate which prey taxon groups contribute to dietary differences and how prey groups vary in relationship to the categorical variables. The direction in which the prey vectors point with respect to the ellipses boundaries indicates those prey categories have higher weight values within those particular subsets of the dataset. Similarly, if these gray vectors point in the opposite direction of the ellipses boundaries, this would suggest those prey items have lower weight values as a function of those variables. For the NMDS plots, the amphipod prey category was dropped because its values were outliers that did not accurately represent the values of the other prey categories. Tukey Honest Significant Difference post-hoc tests were run on the significant variables from the PERMANOVA to test differences between individual levels of each variable.

A distance-based redundancy analysis (dbRDA) was performed to assess the significance of the continuous variables: standard length, weight, depth, relief, SST, chlorophyll-a, GSI, HSI, Fulton's K, latitude, and longitude contributions to dietary differences. The dbRDA was run on the same %W fourth-root transformed Bray-Curtis prey matrix data using the vegan package in R. The model then determined the significant continuous variables via their contribution to explaining the variance in the prey data matrix and were visually represented in a similar ordination plot. Permutation tests were also run on the continuous variables of the dbRDA to test if average values of taxon prey group %W values were significantly different. The dbRDA was visually represented in capscale space which is a constrained version of metric scaling of non-Euclidean dissimilarity indices based on Bray-Curtis distance. Therefore, variables or prey items that orient themselves in similar directions are likely correlated with one another and those that orient in opposite directions are negatively associated. Since the dbRDA is an extension of multilinear regression analysis, a Variance Inflation Factor (VIF) was run to test for multicollinearity. SST and weight contained VIF values greater than 10 (values > 10 are deemed to be collinear with other variables and should be excluded from the model) and were therefore excluded from the dbRDA and resulting permutation analysis due to multicollinearity. A permutation test was run to determine the significance of the remaining continuous variables: standard length, depth, relief, chlorophyll-a, latitude, longitude, Fulton's K, GSI, and HSI on the dbRDA model.

A similarities percentages (SIMPER) function in the vegan package in R performed pairwise comparisons on the raw prey weight data between different variable subsets and identified average dissimilarity percentages between the two groups and the prey items contributing most to the witnessed dissimilarity. When using SIMPER, the most prolific species found within the diet usually have the highest variances, therefore displaying high contribution values despite not significantly differing among groups. This model was run with and without 999 permutations to account for this bias and the results were within 0.01% of each other, therefore deemed not biased within this dataset. In addition to the SIMPER analysis, diversity of the diet was analyzed using the Shannon-Weiner diversity index and the degree of IS was measured using the RInSp package in R and the PSicalc function based on

Bolnick et al. (2003). The Shannon-Weiner diversity indices were calculated based on raw abundance data, then summarized by means and standard deviations based on specific subsets of the dataset. A Shannon-Weiner diversity value was calculated for each individual sample and was then averaged to compare among different subsets of variables. The higher the Shannon-Weiner diversity value indicates an increase in diversity, and lower values represent a lower degree of diversity. The IS value and corresponding p-value given in Table 7 (p. 51) measures IS based on the average pairwise overlap of the niche distribution of individuals and the population.

Stable Isotope Analysis

Stable isotope values were calculated by rinsing dorsal muscle tissues in HCl solution to remove inorganic carbon, freeze-drying the products, and grinding samples into a fine powder. This powder was run through the Thermo Scientific Delta V mass spectrometer which outputs isotope values, compared against standard carbon and nitrogen values, to achieve isotopic ratios indicated as $\boldsymbol{\delta}^{13}$C and $\boldsymbol{\delta}^{15}$N. $\boldsymbol{\delta}^{13}$C represents whether a sample is enriched or depleted in ^{13}C relative to the standard (V-PDB), and is utilized to trace the variability in dietary carbon sources. $\boldsymbol{\delta}^{15}$N represents whether the sample is enriched or depleted in ^{15}N relative to the standard (atmospheric air) and serves as a proxy for TL. The standard used for ^{13}C is Pee Dee Belemnite (V-PDB, an extinct squid with a calcium carbonate skeleton) and the standard used for ^{15}N is nitrogen found in atmospheric air (B. J. Peterson & Fry, 1987).

$$\square^{13}\mathrm{C} = \left[\frac{\left(\frac{13C}{12C}\right) sample}{\left(\frac{13C}{12C}\right) standard} - 1\right] \times 1000$$

$$\square^{15}\mathrm{N} = \left[\frac{\left(\frac{15N}{14N}\right) sample}{\left(\frac{15N}{14N}\right) standard} - 1\right] \times 1000$$

The Stable Isotope Bayesian Ellipses (SIBER) package in R was used to fit bivariate ellipses depicting the size of the isotopic niche, to assess factors associated with niche variation, and to display the degree of trophic niche overlap among various groups in the data (Jackson et al., 2011; Madigan et al., 2012; Syväranta et al., 2013). Each individual was plotted in bivariate stable isotope space with an ellipse area calculated for each response variable such as: sex, length, maturity, weight, latitude, longitude, average chlorophyll-a, average SST, GSI, HSI, Fulton's K, depth, and relief. Each ellipse and their respective overlap or lack of overlap indicates the degree to which isotopic niches differ (higher area overlap representing more similar trophic niches). The respective size of each ellipse indicates isotopic diversity in the diet, with larger ellipses indicating greater diversity and smaller ellipses indicating less diversity in the diet of that group.

SIBER was used in R to calculate spatial isotopic metrics: nitrogen range (NR), carbon range (CR), total area of convex hull (TA), mean distance to centroid (CD), mean nearest neighbor distance (NND), and standard deviation of nearest neighbor distance (SDNND) based on the plotted ellipses (Layman et al., 2007). NR represents trophic diversity by calculating the differences between the highest and lowest $\boldsymbol{\delta}^{15}$N values (larger values indicate greater diversity). Similarly, CR is calculated by the difference of the highest and lowest $\boldsymbol{\delta}^{13}$C values and is used to differentiate between the basal resources consumed in each subset (larger values represents a multitude of basal resources encapsulated by the diet). Total area of the convex hull represents trophic diversity within a group by calculating the total area of the δ^{13}C and δ^{15}N bivariate space (larger values indicate greater trophic diversity). CD is calculated by the Euclidean distance from the mean δ^{13}C and δ^{15}N value and represents the average trophic diversity within a group. NND is measured by the Euclidean distance between two individuals and can distinguish how similar (smaller values) or dissimilar (larger values) their trophic niches are. Finally, standard deviation of the mean nearest neighbor determines the evenness of the trophic spread among all samples.

Generalized linear models (GLMs) were conducted to test the effects of all the biological and environmental variables on δ^{13}C and δ^{15}N. An Akaike Information Criterion (AIC) stepwise regression was performed for each GLM to indicate which collection of predictor variables produced the best fitting model for each isotopic variable with the fewest number of variables possible. An AIC is a mathematical method for evaluating how well a model fits the data relative to the number of parameters the model requires to reach that level of precision. A frontwards and backwards stepwise regression was performed for each individual isotope and TL value to determine the best model for each isotope. Each AIC considered all the variables, including depth, latitude, longitude, chlorophyll-a, SST, relief, weight, length, GSI, HSI, sex, maturity, and Fulton's K and selected the best combination to describe the variance in the select isotope.

Mercury Concentration Analysis

Total wet weight mercury (sum of all organic and inorganic mercury species) concentrations were measured in the Marine Pollution Studies Lab at MLML via thermal decomposition, amalgamation, and atomic absorption spectrometry of dorsal muscle tissue using a Milestone DMA-80 direct mercury analyzer following EPA method 7473 (US

Environmental Protection Agency [USEPA], 2007). Controlled heating in an oxygenated decomposition furnace liberates solid and aqueous forms of mercury in the tissue samples inside the instrument (USEPA, 2007). These samples are then dried and thermochemically decomposed inside a decomposition furnace (USEPA, 2007). The products formed from this process are then transported by flowing oxygen to the catalytic section of the furnace where oxidation traps the excess halogens and oxides (USEPA, 2007). The remaining products are processed in an amalgamator which selectively traps mercury, and more oxygen is flushed through the system to remove remaining undesired products (USEPA, 2007). This amalgamator is then rapidly heated to release mercury in its vapor form which is carried through two absorbance cells under an atomic absorption spectrophotometer (accurate to the nearest 0.01 nanogram) measuring the quantity of mercury twice at two different sensitivities (USEPA, 2007). Atomic absorbance was measured using peak height at 253.7 nanometers as a function of wet mercury concentration in parts per million (ppm or mg/kg).

For every batch of samples processed (20 total samples), 3 method blanks, a low and high check, certified reference materials, matrix spike/matrix spike duplicate, and duplicates of samples underwent the same process for quality assurance. Method blanks are responsible for indicating the presence of contamination within samples from the boats used to hold the samples and the method detection limit is 0.1 nanograms of total mercury. The method blanks consist of 3 empty sample boats (2 nickel and 1 quartz) and when run through the same process, must be less than 10% of the lowest certified sample material sample concentration in order to deem samples acceptable. The certified sample material used in this study is DORM-5 at 10.00, 1.0, and 0.1 ppm. Laboratory control samples are spiked with mercury concentrations equivalent to low or mid-range standards and are acceptable at ± 20% of spiked value after execution. Matrix spikes of 1.00 ppm and 10.00 ppm and their duplicates are processed to account for bias and precision. 20% will be the limit of maximum deviation for both percent recovery and relative percent difference of the quality assurance samples. Finally, wet weight total mercury concentrations were determined with the atomic absorbance results by constructing a calibration curve with absorbance of standards against nanograms of mercury using the 1.00 ppm and 10.00 ppm matrix spikes. Then, using the known mercury masses that constructed the calibration curve, each sample's absorbance provides a mass of mercury which is divided by the mass of the tissue analyzed to provide a concentration. This value presents the total mercury, but a vast majority of this mercury (>95%) is thought to be organic (Bloom, 1992). This value is calculated in wet weight of total mercury (mg/kg or ppm) and will be represented in the remainder of text as either total mercury concentrations or [Hg] ppm.

A GLM using AIC was run to assess how total mercury concentrations change based on the same biological and environmental factors used previously for gut content and stable isotope analyses. Variables that were either continuous or a mix of continuous and categorical were better represented by using a GLM. Another frontwards and backwards stepwise AIC was conducted to compare multiple models with different collections of variables to indicate which model is best to describe the variance in total mercury concentrations with the fewest number of variables.

Synthesizing Gut Content, Isotope, and Mercury Results

The incorporation of stable isotopes, stomach contents, and total mercury concentration datasets is important for indicating prey items that drive variability in trophic position and total mercury concentrations. A total of five GLMs and AICs were run using isotopic values, average prey concentrations, and average total mercury concentrations to determine which variables were significantly associated across the population as a whole. The five GLMs were: (a) mercury vs %W of prey groups, (b) mercury vs $\boldsymbol{\delta}^{13}$C, $\boldsymbol{\delta}^{15}$N, and TL, (c) $\boldsymbol{\delta}^{13}$C vs %W of prey category, (d) $\boldsymbol{\delta}^{15}$N vs %W of each prey category, (e) TL vs %W of each prey category. Any significant correlations identified by the model results were graphically represented. Principal component analyses (PCA) were also conducted to reduce the dimensionality of the dietary data, biological traits, and environmental factors to visualize how all of these variables are interrelated. Three PCAs were run: (a) including gut content prey items and isotopic values, (b) including biological variables: Fulton's K, HSI, GSI, weight and length, and (c) including environmental factors: chlorophyll-a, SST, latitude, relief, depth, and longitude as a means of representing variance in total mercury concentrations. Principal component scores for PC axis 1 and PC axis 2 were input into linear regressions, testing associations between new indices of diet variation, biological traits, and environmental conditions against total mercury concentrations to test which variables contribute to variances in total mercury concentrations in Canary rockfish in the CCS.

Results

Stomach Content Analysis

There were a total of 1562 fish collected from 13 different ports and 5 fisheries management regions along Washington, Oregon, and California. 351 of these samples were used for stomach content analysis, 496 were used for stable isotope analysis, and 288 for mercury analysis (Table 1). Overall, there were 272 samples containing stomach contents, stable isotope values, and mercury samples. Within the 351 stomachs there was a total of 27 prey items summarized into 11 higher taxonomic levels: teleosts, shrimp, crab, squid, krill, pyrosomes, amphipods, isopods, copepods, unknown decapods, and an other category (Tables 2 & 3). Overall, the most important and frequently occurring prey items were krill (%PSIRI = 55.96, %FO = 44.16) and teleosts (%PSIRI = 21.48, %FO = 21.08) (Table 3). However, there was a deviance from the most important prey items when looking at %N and %W with krill (83.42%) and crab (7.32%) containing the highest %N and teleosts (42.15%) and krill (28.51%) containing the highest %W (Table 3). When examining individual prey items, the most frequently occurring and most important items were krill (%FO = 44.16, %PSIRI = 55.96) and unidentified teleosts (%FO = 17.95, %PSIRI = 20.08) (Table 2). Individual prey items with the highest %N were krill (83.42%) and megalops crabs (6.02%), and the highest %W were unidentified teleosts (39.46%) and krill (28.51%).

A PERMANOVA model was used to ascertain which of the categorical variables (management region, port, sex, or maturity) contributed significantly to variance in prey items of the diet. This model was run on the variables independently as well as the

Table 2

All 27 Prey Items Found in the 351 Stomach Contents, Color-Coded by the 11 Higher Taxonomic Levels. Additional Information Includes Total Abundance, Weight in Grams, %N, %W, %PN, %PW, %FO, %PSIRI, and Total Abundance Counts and Weights of All Prey Items at the Bottom

Prey Group	**Prey Item**	**# of Stomachs**	**Total Abundance**	**%PN**	**%N**	**Total Weight (g)**	**%PW**	**%W**	**%FO**	**%PSIRI**
Teleosts	Unidentified	63	102	1.10	0.69	743.10	62.63	39.46	17.95	20.08
	Engraulidae mordax	1	1	0.68	0.01	4.06	21.53	0.22	0.28	0.11
	Sebastes rosaceus	3	4	0.91	0.03	10.53	18.64	0.56	0.85	0.29
	Sebastes goodei	1	1	0.68	0.01	5.39	28.60	0.29	0.28	0.15
	Sebastes saxicola	1	1	0.68	0.01	19.53	103.68	1.04	0.28	0.52
	Sebastes mystinus	2	3	1.02	0.02	3.18	8.45	0.17	0.57	0.09
	Sebastes jordani	2	2	0.68	0.01	5.07	13.46	0.27	0.57	0.14
	Sebastes wilsoni	1	3	2.04	0.02	2.27	12.05	0.12	0.28	0.07
	Rhinogobiops nicholsii	1	1	0.68	0.01	0.66	3.49	0.03	0.28	0.02
Shrimp	Unidentified	9	42	3.18	0.29	39.41	23.25	2.09	2.56	1.19
	Crangonidae	53	334	4.29	2.27	59.78	5.99	3.17	15.10	2.72
	Pandulus jordani	6	33	3.74	0.22	55.71	49.31	2.96	1.71	1.59
	Pandulus goniurus	1	2	1.36	0.01	6.64	35.27	0.35	0.28	0.18
Crab	Unidentified	37	188	3.46	1.28	66.09	9.49	3.51	10.54	2.39
	Megalops	57	884	10.55	6.02	32.96	3.07	1.75	16.24	3.88
	Cancer productus	3	3	0.68	0.02	2.34	4.14	0.12	0.85	0.07
Squid	Unidentified	3	3	0.68	0.02	3.91	6.92	0.21	0.85	0.11
	Doryteuthis opalescens	5	6	0.82	0.04	64.49	68.49	3.42	1.42	1.73
Krill		155	12258	53.82	83.42	536.85	18.39	28.51	44.16	55.96
Pyrosome		34	113	2.26	0.77	129.69	20.26	6.89	9.69	3.83
Amphipod		2	3	1.02	0.02	0.45	1.19	0.02	0.57	0.02
Isopod		8	10	0.85	0.07	0.34	0.23	0.02	2.28	0.04
Copepod		28	532	12.93	3.62	9.09	1.72	0.48	7.98	2.05
Decapods		14	133	6.46	0.91	11.60	4.40	0.62	3.99	0.76
Other	Unidentified Tissue	14	14	0.68	0.10	69.44	26.34	3.69	3.99	1.89
	Parasite	13	18	0.94	0.12	0.14	0.06	0.01	3.70	0.06
	Cystoseira expansa	1	1	0.68	0.01	0.52	2.76	0.03	0.28	0.02
Total:		351	14695			1883.23				

Table 3

Prey Item Table Sorted by the 11 Higher Taxonomic Groups with Summarized Abundance and Weight Counts from the 27 Total Items. Includes Dietary Metrics such as %N, %W, %PN, %PW, %FO, and %PSIRI in Addition to Total Abundance Counts and Weight in Grams in Total at the Bottom

Prey Group	**# of Stomachs**	**Total Abundance**	**%PN**	**%N**	**Total Weight (g)**	**%PW**	**%W**	**%FO**	**%PSIRI**	**Niche Breadth**	**Standardized Niche Breadth**
Teleost	74	118	1.09	0.80	793.78	56.96	42.15	21.08	21.48	22.50	2.15
Shrimp	69	411	4.05	2.80	161.54	12.43	8.58	19.66	5.69	25.88	2.49
Crab	97	1075	7.54	7.32	101.39	5.55	5.38	27.64	6.35	13.09	1.21
Squid	8	9	0.77	0.06	68.40	45.40	3.63	2.28	1.85	1925.02	192.40
Krill	155	12258	53.82	83.42	536.85	18.39	28.51	44.16	55.96	5.13	0.41
Pyrosome	34	113	2.26	0.77	129.69	20.26	6.89	9.69	3.83	106.58	10.56
Amphipod	2	3	1.02	0.02	0.45	1.19	0.02	0.57	0.02	30800.25	3079.93
Isopod	8	10	0.85	0.07	0.34	0.23	0.02	2.28	0.04	1925.02	192.40
Copepod	28	532	12.93	3.62	9.09	1.72	0.48	7.98	2.05	157.14	15.61
Decapod	14	133	6.46	0.91	11.60	4.40	0.62	3.99	0.76	628.58	62.76
Other	28	33	0.80	0.22	70.10	13.29	3.72	7.98	1.97	157.14	15.61
Totals	351	14695			1883.23						

interactions amongst the variables which is denoted in Table 4 by the * symbol. After running both the raw weight and abundance data in addition to other transformations of the data through the model (square-root, fourth-root, and log-transformed), ultimately, the %W transformation was determined to be the best overall model for the PERMANOVA and the dbRDA. Therefore, this dataset was chosen to describe the variation in diet and determine which of the variables were significant for the remainder of analysis, unless otherwise stated. In the final model, the individual variables of management region (p = 0.0001) and port (p = 0.0001) were significant and sex (p = 0.1791) and maturity (p = 0.3636) were not significant factors in describing variance in *S. pinniger* diets (Table 4). In terms of interactions, management region*sex (p = 0.0133) was significant, with none of the other interactions being significant. Management region had the largest Pseudo-F value (6.266), and therefore is the most explanatory variable of the model followed by port and maturity status. The significant interaction of management region and sex is represented in Figure 3, and indicates the diets of males and females differed across management regions. Figure 3 displays the differences in the proportion of prey items partitioned by sex within the different management regions. Thus, the sexes are consuming prey items in different proportions based on the location in which they reside. Given that management region and port were the only significant individual factors, the variance observed in *S. pinniger* diets can be attributed mostly to spatial and environmental differences, but with sex contributing slightly to the variance as well.

Table 4

PERMANOVA Model Results with Significant Differences in Prey Item %W Data Represented in Bold. Pseudo-F is a Ratio of Between-Level Variation and Within-Level Variation. Smaller Values Represent Either Within Level Variance Decreasing or Between Level Variance Increasing. Higher Pseudo-F Values Indicate Variables that Are More Explanatory of the Variance in the Model

Variable	DF	Sum of Squares	F	R^2	P-value
Management Region	4	8.821	6.266	0.06513	**0.0001**
Port	8	6.246	2.218	0.04611	**0.0001**
Maturity	2	0.376	1.068	0.00278	0.3626
Sex	2	0.955	1.356	0.00705	0.1791
Management Region*Maturity	4	1.468	1.043	0.01084	0.4026
Port*Maturity	8	3.357	1.192	0.02478	0.1838
Management Region*Sex	5	3.070	1.744	0.02266	**0.0133**
Port*Sex	8	3.554	1.262	0.02624	0.1167
Maturity*Sex	1	0.374	1.063	0.00276	0.3663
Management Region*Maturity*Sex	4	1.075	0.738	0.00794	0.755
Port*Maturity*Sex	5	0.914	0.519	0.00675	0.9799
Residuals	298	88.594		0.68533	
Total	349	129.272		1	

The PERMANOVA model with the individual variables was also represented in NMDS space with ellipses generated for management region (Figure 4A), maturity status (Figure 4B), and sex (Figure 4C). In these visual representations, the prey category amphipod was excluded due to its extreme outlier values. In all of the models, the NMDS1 axis accounted for 19.9% and NMDS2 axis 11.7% of the dataset variance, totaling 31.6% of the variance in the dataset being represented. This is a fairly low amount of the total variance being represented, but this is likely because this model was based only on the categorical variables and because the prey item dataset is quite large and contains many zero values. All of the fisheries management regions, sexual maturity, and sex ellipses share large areas of overlap in NMDS space indicating the relative similarities of diets among these variables. However, there are differences in ellipses size as well as orientation in NMDS space that suggest some distinction between regions. The NMDS1 axis correlates with teleosts, krill, crab, shrimp,

Figure 3

Average %W of the Eleven Prey Items Separated by Management Region (Top X Axis) and Divided by Sex (Bottom X Axis)

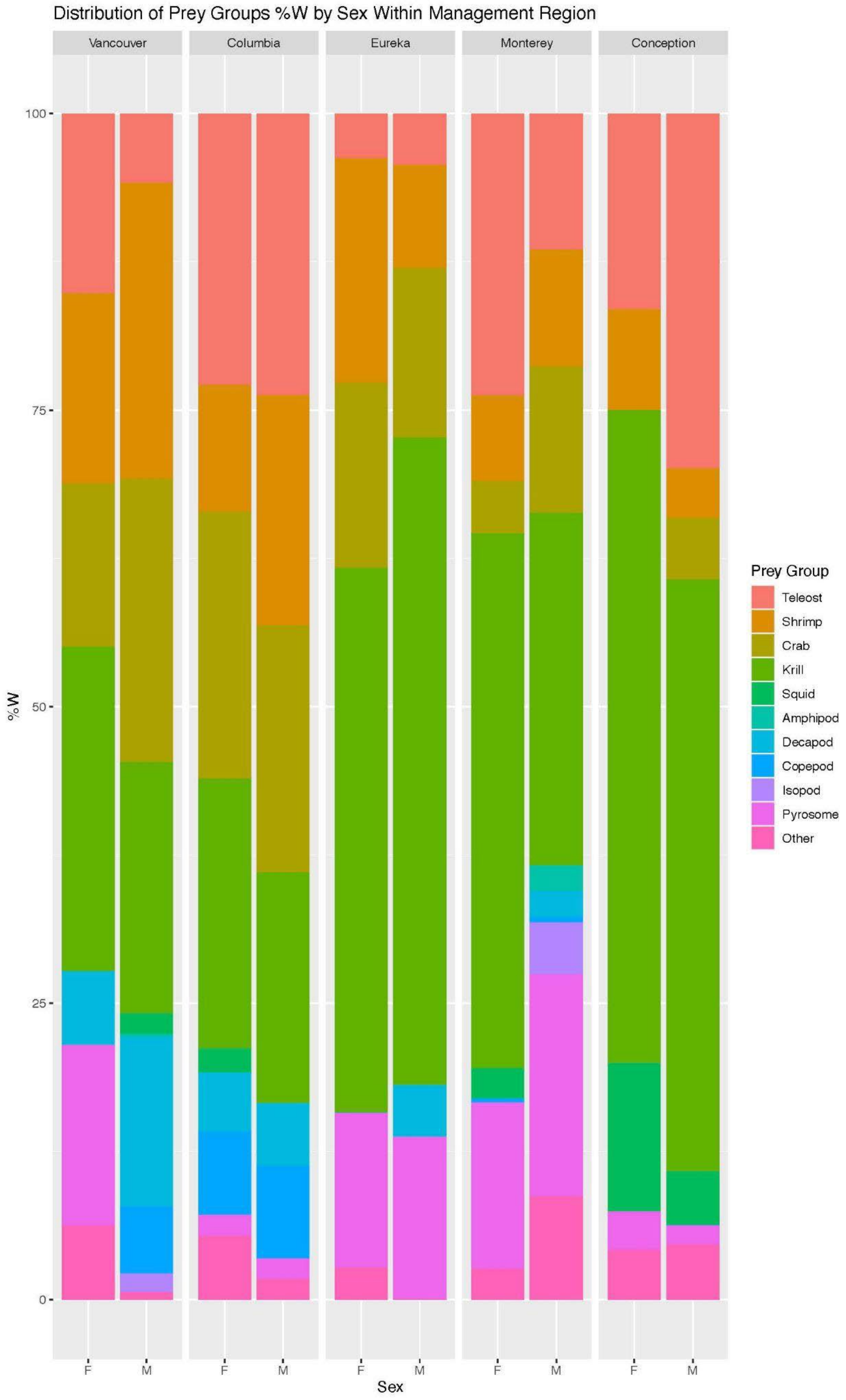
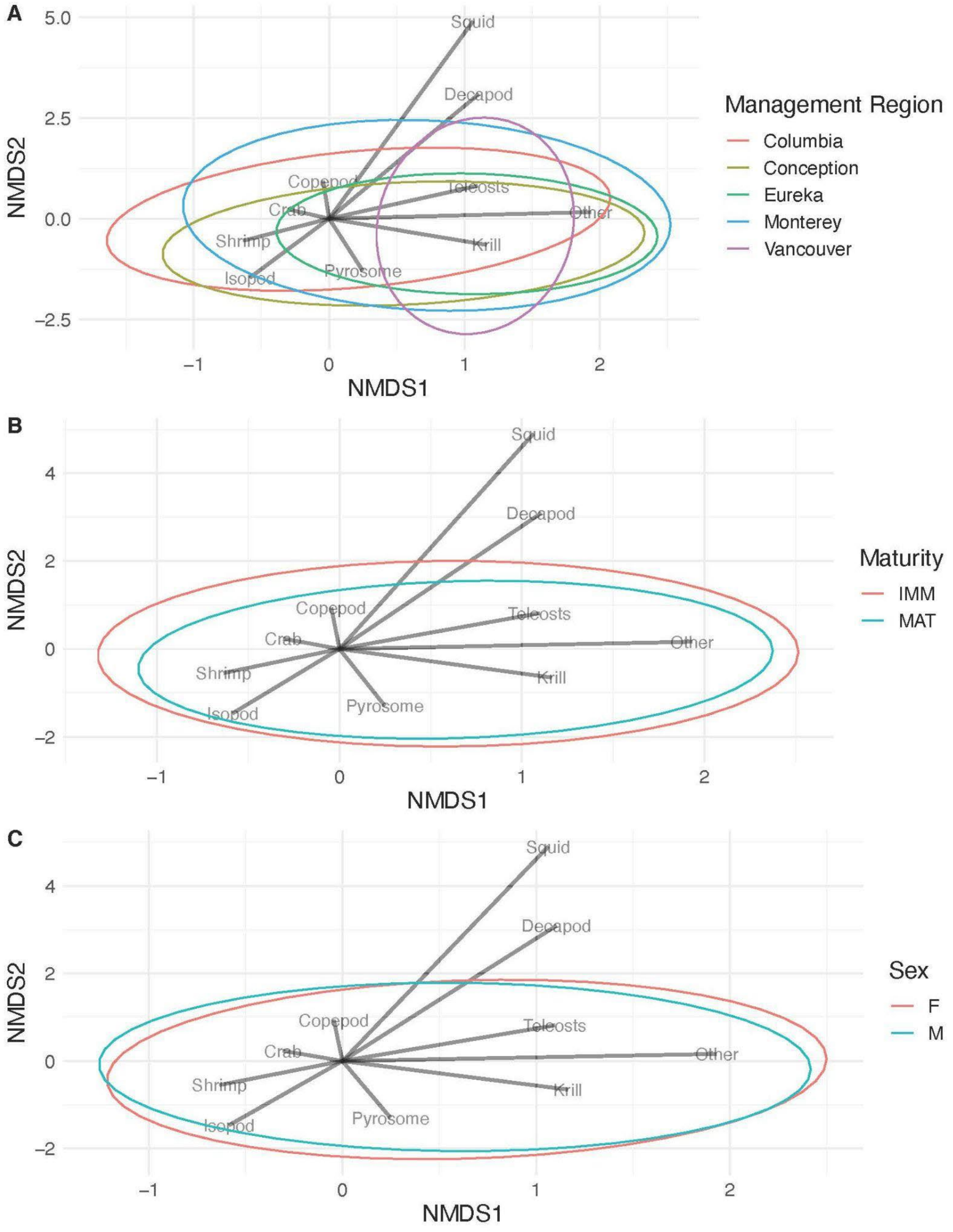


Figure 4

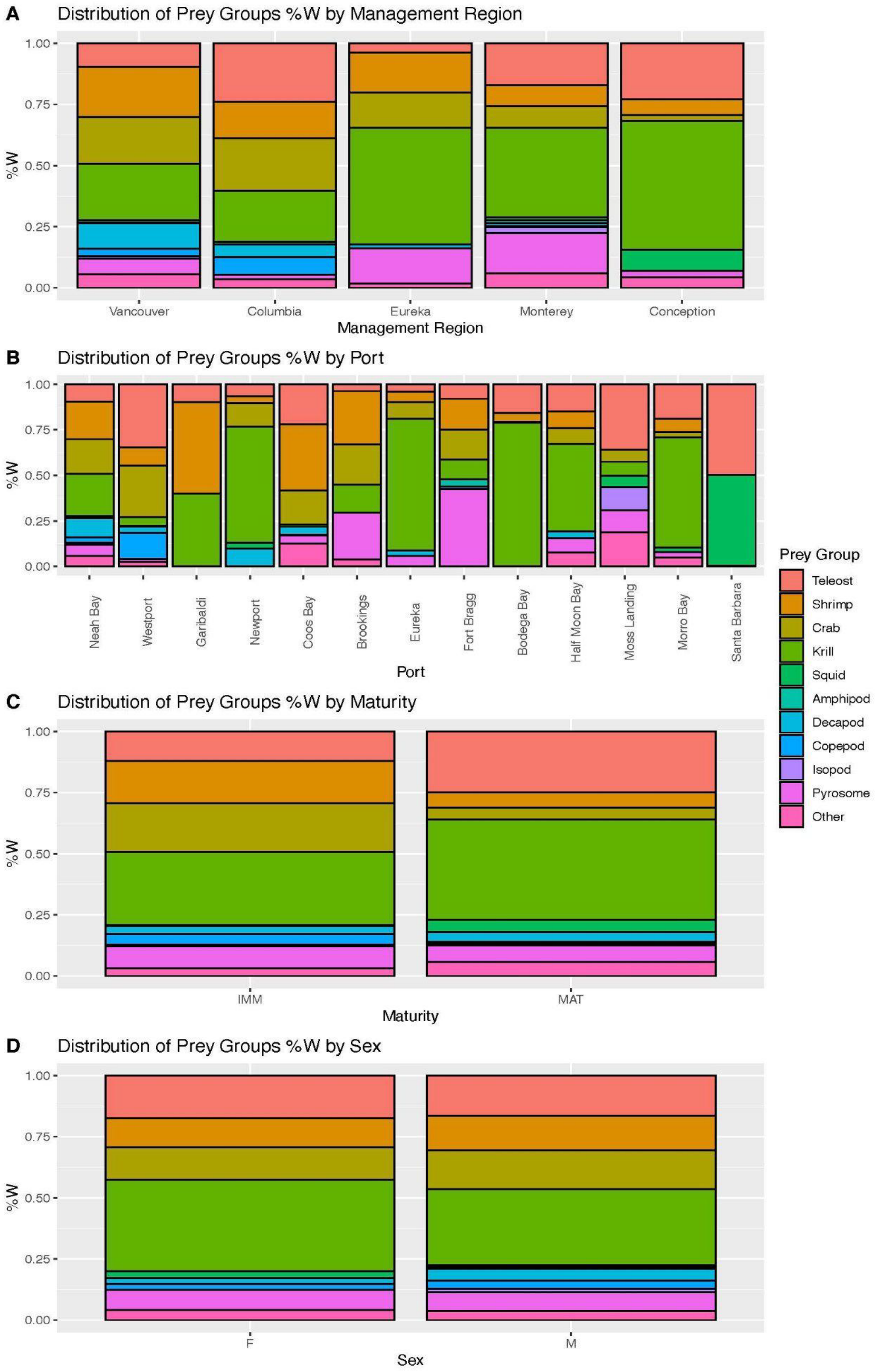
NMDS Ordination Plots for Significant PERMANOVA Variables and Prey Items. (A) Management Region; (B) Sexual Maturity; and (C) by Sex. The X- and Y-Axes Represent the Non-Metric Multidimensional Scales, NMDS1 and NMDS2 which Account for the Majority of Variance (NMDS1=19.9%, NMDS2=11.7%) within the Dataset. The Ellipses Display 95% Confidence Intervals Representing the Fish Within Each Subsetted Variable and the Gray Arrows Represent 10 Prey Groups (Amphipod Is Dropped Here as too Extreme of an Outlier) and How They Vary with Respect to the Individual Points/Fish



and other prey groups. The NMDS2 axis varies with squid, unknown decapods, copepods, and pyrosome. The isopod prey group appears to be equally represented by both NMDS1 and NMDS2. The Vancouver ellipse orients itself in the opposite direction of the other management regions and associates more so with the NMDS2 axis than NMDS1 (Figure 4A). Vancouver also appears to have the largest variance in NMDS2 values and lowest in NMDS1, which is the opposite of all of the other management regions (Figure 4A). Therefore, individuals within the Vancouver ellipse are more likely to consume squids, pyrosomes, and unknown decapods than the other regions, and likely have overall different diets in comparison to individuals from the other management regions. This is confirmed when comparing these results to Figure 5A as the Vancouver region contains the largest proportion of unknown decapods and squid. Pyrosomes, on the other hand, are more dominant in proportion in the Monterey and Eureka regions compared to the Vancouver region. Similarly, the isopod vector points towards the end of the Monterey ellipse, and in Figure 5A, isopods are the largest in proportion in the Monterey region. In terms of maturity, the mature ellipse is slightly more confined in NMDS space than the immature ellipse (Figure 4B). There is still a large amount of overlap between the two ellipses suggesting that both sexually mature and immature fish consume similar diets. Mature individuals likely have a bit more of a specialist diet, and immature individuals a more generalist diet, causing a slight narrowing of prey niche space upon maturation (Figure 4B). In terms of sex, females and males have the greatest amount of overlap, suggesting that sex likely does not have much of an effect on Canary rockfish diets. Although, given that management region*sex is

Figure 5

Stacked Bar Plots Exhibiting %W of Prey Groups Distributed Among Management Region (A), Port (B), Maturity (C), and Sex (D). The Legend Displays the 11 Higher Taxonomic Prey Groupings and Are the Same for Each Subsection of the Figure



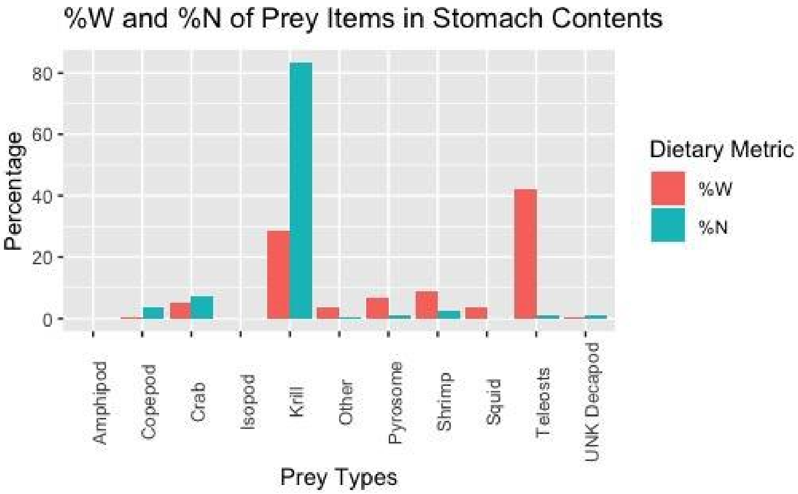
significant there may be slight differences in male and female diets when comparing across management regions.

Stacked bar plots were created for all of the individual PERMANOVA variables: management region, port, sexual maturity, and sex to display how %W of the 11 prey item groups change proportionally within these variables (Figure 5). Canary rockfish exhibit relative consistency in prey proportion across the five management regions, with some distinct changes. Eureka and Conception appear to have the largest proportions of krill among all regions (Figure 5A). Columbia and Conception also have the largest proportion of teleosts, with Eureka having the least. Individuals within the Vancouver and Columbia region also consume unknown decapods and copepods, which do not appear nearly as often in the diets of individuals in Eureka, Monterey, and Conception, further south in the CCS. These overall trends do not appear to follow any sort of latitudinal gradient from higher to lower latitudes that would suggest an environmental effect on prey composition. Looking at the port level, there are many more distinct differences in prey proportions at each port in comparison to looking at the broader scale management region level (Figure 5B). This is likely due to the more localized effects of habitat variation and prey availability at the port level and more of an assimilated conglomeration at the management region level, again with no clear latitudinal gradients displayed. The only two prey groups that appear at every single port are teleosts and krill, indicating their dominance and importance in Canary rockfish diets within the CCS. When looking at the shift in diets from immature to mature fish, there is a higher reliance on teleosts and krill in the diet of mature fish (Figure 5C). Immature fish recorded larger proportions of shrimp and crabs, with all of the other prey groups remaining relatively consistent between immature and mature fish. It appears that immature fish eat a more balanced and generalistic diet in comparison to mature adults, who may specialize a bit more on specific prey items as they reach maturation. This coincides with the narrower ellipse of the mature individuals compared to the immature individuals in Figure 4B. When looking at prey compositions between genders, there is very little difference between %W of prey items, further supporting the fact that sex does not have an effect on diet (Figure 5D).

Since teleosts and krill have the highest %N and %W values (krill %N = 83.42%, teleosts %W = 42.15%, Table 3) and are found within every sampling site, they are optimal prey items to analyze for major differences in diet. %N and %W also represent differing levels of importance among the diet. Figure 6 displays both the %N and %W of each of the 11 prey groups. Teleosts and krill are both important items within the diet but have dramatically different values. Krill by far has the highest %N, while teleosts are the most important by %W.

Figure 6

Grouped Bar Plot with the 11 Prey Groups on the X Axis and %W (Red) and %N (Blue) Plotted on the Y Axis for Each of the Prey Items



A dbRDA was run on the %W data and is represented in Capscale space (Figure 7). The permutation test concluded chlorophyll-a (p = 0.001), depth (p = 0.002), longitude (p = 0.004), GSI (p = 0.003), and relief (p = 0.017) were significant variables contributing to the observed variance in the diet (Table 5). Chlorophyll-a (4.607), depth (3.863), and longitude (3.256) contained the largest F-values, therefore contributing the most to the variance in diet. This would indicate that environmental factors such as productivity, latitudinal location, and depth in the water column are more capable of describing variance in the diet compared to biological factors, given that 4/5 significant variables were environmental. Although it is important to note that depth and relief factors can be argued to have some sort of biological influence when it comes to Canary rockfish life histories. Considering this, and the results of the PERMANOVA, diets of Canary rockfish appear to be more affected by environmental variables than biological traits.

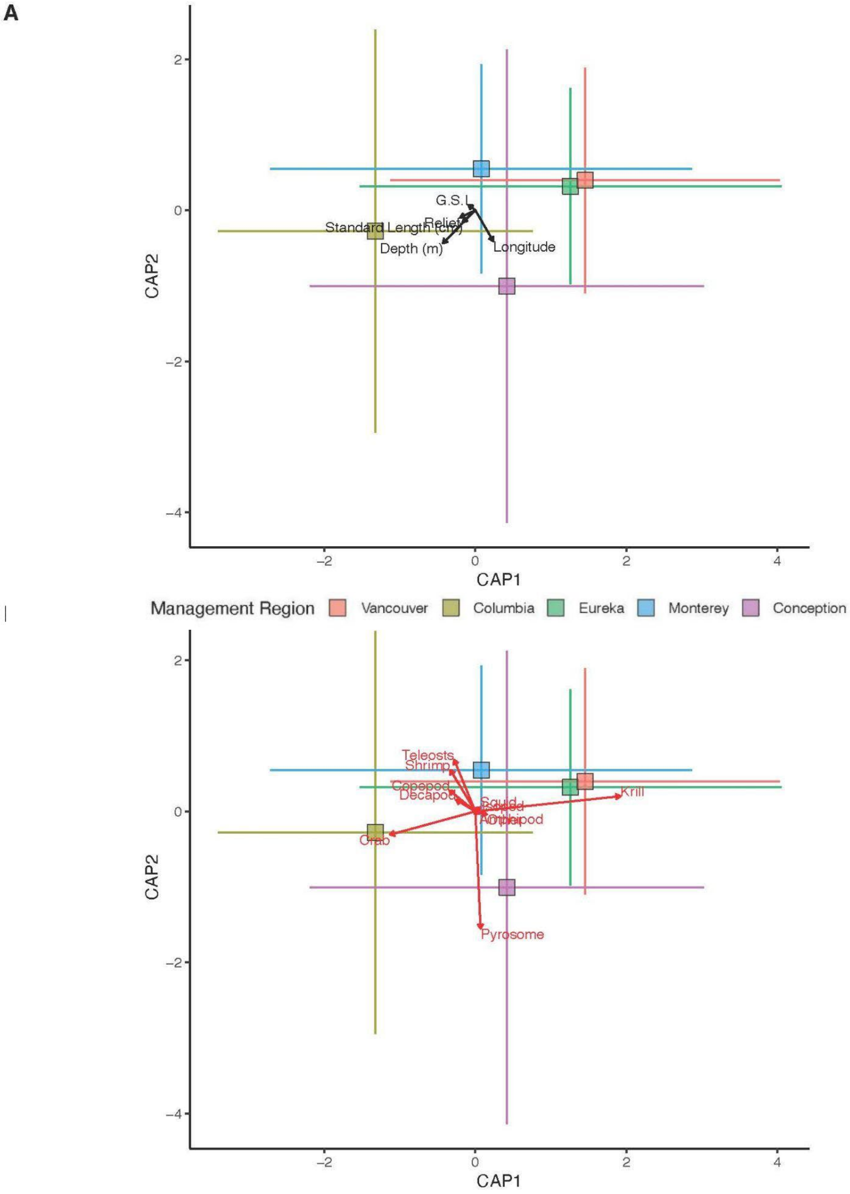
Table 5

Results of the Permutation Tests Ran on the %W dbRDA Data Matrix. The Second Column Contains Pseudo-F values for Each of the Variables. Significant Variables Contributing to Variance in the Diet Contain Bolded P-Values and Are Bolded Themselves

Variable	**F**	**p-value**
Chlorophyll-a	4.607	**0.001**
Depth (m)	3.863	**0.002**
Longitude	3.256	**0.004**
G.S.I	2.822	**0.003**
Relief	2.814	**0.017**
Fulton's K	1.123	0.310
Standard Length (cm)	0.992	0.394
Latitude	0.962	0.438
H.S.I	0.187	0.995

Figure 7

dbRDA Results in Capscale Space. In Both A and B the Boxes Are Colored Coded by the Management Region with a Legend at the Bottom. The Colored Boxes Represent the Mean CAP1 and CAP2 Values Within that Management Region and the Corresponding Colored Lines Represent a Single Standard Deviation in Both CAP1 and CAP2 for that Specific Management Region. Black Arrows in (A) Represent the Significant Continuous Variables Derived from the Permutation Tests, While Red Arrows in (B) Represent the 11 Higher Taxonomic Prey Groups Used in the dbRDA



In terms of prey items, CAP1 is correlated with krill, crab, unknown decapods, copepods, squid, amphipods, isopods, and other prey categories and CAP2 is correlated with teleosts, shrimp, and pyrosomes. Therefore, teleost and shrimp presence would be negatively correlated with increases in longitude, while crab presence in the diet increases with increases in standard length, relief, and depth. Increases in krill in the diet, corresponds with decreases in overall crab weight in the diet (Figure 7B). These plots reveal the similarity in diets of individuals within the Eureka and Vancouver regions, even though they are separated from each other in the CCS. Vancouver was also the most different ellipse when looking in NDMS space (Figure 4A) and this plot (Figure 7) reveals the similarity in diet of these two regions, which is not as evident in NMDS space. This is likely because of the use of different variables within the different models therefore capturing different levels and types of variance within the dataset. Crabs appear to be associated with individuals within the Columbia management region, pyrosome presence appears to be greatest in the Conception management region, krill were most common in the diets in the Vancouver and Eureka regions, and teleosts and shrimp made up a bigger share of the diet of fish from the Monterey region. This suggests individuals residing within a specific region could be consuming generalistic diets, but with a slight specialization on a regional prey item, possibly due to higher presences in specific areas due to ambient environmental conditions. Depth was a significant factor ($p = 0.002$) in describing variance in the diets and fish were sampled from deeper depths in the Columbia and Conception regions (Table 5; Figure 7).

Table 6 displays the dissimilarity percentages and the 4 prey groups contributing the most to the dissimilarity between management region, maturity status, and sex. Krill, teleosts, shrimps, and crabs provide the greatest dissimilarities out of all the prey groups likely because these were the prey groups found with the largest weight values. All of the pairwise comparisons display an 86% or higher dissimilarity rate indicating there is high trophic variability when comparing prey item weight across both biological and environmental levels. This may not be an indication of overall differences in diet, but just changes in proportions of item weight amongst individuals within the comparisons. The management region displaying the highest degrees of dissimilarity from other regions is Columbia with each of its pairwise comparisons in the top 5 most dissimilar pairwise comparisons. This is likely because Columbia also has the most individuals compared to the other regions, even when other regions (e.g., Vancouver) appear more different in NMDS space (Figure 4A).

Table 6

SIMPER of Canary Rockfish Gut Contents Using Raw Weight of the 11 Prey Item Groups. The Second Column Represents the Average Dissimilarity Between the Pairwise Comparisons and the Third Column Represents the Top Four Prey Groups Contributing the Most to the Dissimilarity and Are Listed from Most to Least in Terms of Contribution to Dissimilarity. The Table Is Separated by Management Region, Maturity, and Sex Comparisons

Variable-Comparison	Average Dissimilarity %	Top 4 Prey Groups Contributing to Dissimilarity
Management Region		
Columbia-Monterey	93.56	Krill, Teleost, Crab, Shrimp
Monterey-Vancouver	92.73	Kril, Teleost, Shrimp, Pyrosome
Columbia-Vancouver	91.63	Krill, Teleost, Shrimp, Crab
Columbia-Eureka	91.62	Krill, Teleost, Shrimp, Crab
Columbia-Conception	91.19	Krill, Teleost, Shrimp, Crab
Conception-Vancouver	90.73	Krill, Teleost, Shrimp, Crab
Eureka-Vancouver	89.86	Krill, Shrimp, Crab, Pyrosome
Conception-Monterey	89.15	Krill, Teleost, Pyrosome, Squid
Eureka-Monterey	89.12	Krill, Pyrosome, Teleosts, Shrimp
Conception-Eureka	86.08	Krill, Teleost, Shrimp, Pyrosome
Maturity		
Maturity-Immaturity	91.57	Krill, Teleost, Shrimp, Pyrosome
Sex		
Male-Female	90.63	Krill, Teleosts, Shrimp, Crab

Table 7 displays mean dissimilarity percentages for individuals as a function of management region, maturity status, and the dataset as a whole. All individuals were on average 78.92% dissimilar from each other, with a mean Shannon diversity value = 0.189, and a significant IS score of 0.229 (p = 0.001), indicating that individuals eat diverse and distinct diets in comparison to each other. These results suggest individuals within the Vancouver region (Shannon = 0.318 and IS = 0.239) display the most variance from each other and those in the Conception region (Shannon = 0.097 and IS = 0.368) the least, almost displaying a decrease in individual dissimilarity with a decrease in latitude despite the Monterey region (Shannon = 0.183 and IS = 0.245) not following that trend. This may be explained by the high proportion of immature fish caught in the Monterey region, and when looking at the immature subset (Shannon = 0.231 and IS = 0.366) of the data, they tend to eat more diverse diets than mature fish (Shannon = 0.118 and IS = 0.237). These results indicate a decrease in diet variance with an increase in age. However, the IS value for mature fish is significant (p = 0.002) indicating that mature individuals eat more distinct and diverse diets compared to one another, suggesting that mature Canary rockfish possibly have specialized but variable diets between individuals. This also coincides with the change in prey proportionality among mature and immature fish in Figure 5C and narrower niche of mature individuals in NDMS space (Figure 4B). Vancouver also appeared to be the most different from the other regions in NMDS space (Figure 4A), therefore IS of prey items may be driving these differences.

Table 7

Summary of Dissimilarity and Diversity Calculations of Samples. Values Include Mean Dissimilarity Percentage Between Individuals Within the Individual Variables, Shannon-Weiner Diversity Values and their Standard Deviations, Individual Specialization Score (IS), and a P-Value Representing the Significance of the IS Value. Shannon Diversity Values Indicate 0 Representing Highest Dietary Diversity and 1 Representing Complete Overlap and Therefore No Diversity in Diets. The IS Value Between 0-1 Is Proposed by Bolnick et al. (2003), Based on the Average Pairwise Overlap of the Niche Distribution of Individuals and the Population Where 1 Represents Complete Similarity Amongst Individuals and 0 Represents No Similarity Amongst Individuals. The P-Value in the Fifth Column Indicates if the IS Value is Significant and Therefore Has Significant Differences Between Niches Within the Individual Variable Measured and the Population as a Whole

Variables	**Mean Dissimilarity**	**Shannon Diversity**	**IS**	**p-value**
All Data	78.92%	0.189 ± 0.320	0.229	**0.001**
Management Region				
Vancouver	83.80%	0.318 ± 0.356	0.239	**0.012**
Columbia	81.60%	0.208 ± 0.337	0.220	0.070
Eureka	68.18%	0.152 ± 0.290	0.322	0.399
Monterey	78.37%	0.183 ± 0.336	0.245	0.027
Conception	62.78%	0.097 ± 0.208	0.368	0.446
Maturity				
Mature	75.55%	0.118 ± 0.258	0.237	**0.002**
Immature	80.91%	0.231 ± 0.345	0.266	0.366

Stable Isotope Analysis

The mean and standard deviations of δ^{13}C, δ^{15}N, and TL are summarized by management region in Table 8. δ^{13}C is largest on average in the Conception management region (17.50) and lowest in the Vancouver management region (16.88) displaying an increase in δ^{13}C with a decrease in latitude. δ^{15}N is the greatest on average in Conception (15.72) and lowest in Eureka (14.55) and does not display any clear latitudinal trend. TL calculated by stomach contents is highest in Eureka (3.62) and lowest in Monterey (3.42) and does not follow a latitudinal trend. TL displays variability amongst this individual species because the values are based on proportions of prey items in stomachs as opposed to isotopic signatures.

Table 8

Summary of the Mean Isotope Values: $\delta^{13}C$, $\delta^{15}N$, and Calculated TL Separated by Management Region. This Table Displays the Number of Samples Used for Isotopic Analysis, the Mean and Standard Deviation of $\delta^{13}C$, $\delta^{15}N$, and TL as Calculated Based on Values and Equations Outlined in Cortés, 1999 and Ebert and Bizzarro, (2007)

Region	# tissues	Mean δ^{13}C ± SD	Mean δ^{15}N ± SD	Mean TL ± SD
Vancouver	49	16.88 ± 0.33	15.02 ± 0.41	3.46 ± 0.64
Columbia	173	17.07 ± 0.62	15.52 ± 0.57	3.60 ± 0.62
Eureka	85	17.21 ± 0.45	14.55 ± 0.47	3.62 ± 0.62
Monterey	110	17.21 ± 0.55	15.17 ± 0.52	3.42 ± 0.72
Conception	84	17.50 ± 0.32	15.72 ± 0.32	3.54 ± 0.41
Total	501	17.18 ± 0.54	15.26 ± 0.63	3.52 ± 0.64

GLMs were conducted to test whether any of the environmental or biological variables were significantly associated with δ^{13}C, δ^{15}N, or calculated TL. Depth ($p = <0.0001$), relief ($p = 0.0137$), chlorophyll-a ($p = 0.0002$), SST ($p < 0.0001$), maturity ($p = 0.0351$), latitude ($p < 0.0001$), and HSI (p-value = 0.0313) were significantly correlated with δ^{13}C (Table 9). Depth and HSI were negatively correlated with δ^{13}C indicating that increases in depth and energy storage in the liver correspond with more consumption of prey items from offshore sources of primary production (Figure 8). Fish from deeper depths were more likely to feed on prey composed of offshore sources of primary production (Figure 8A). Similarly, mature fish tend to have on average more negative δ^{13}C values than immature individuals (Figure 8B), likely due to ontogenetic movements to deeper depths. Weight also displayed a negative relationship with δ^{13}C ($R^2 = 0.075$), with heavier fish typically possessing more negative δ^{13}C values, indicating consumption of prey characterized by offshore sources of primary production. Relief, chlorophyll-a, SST, and latitude were positively correlated with δ^{13}C, indicating that increases in these values correspond with higher consumption of prey with nearshore sources of primary production. These include both environmental and biological

Table 9

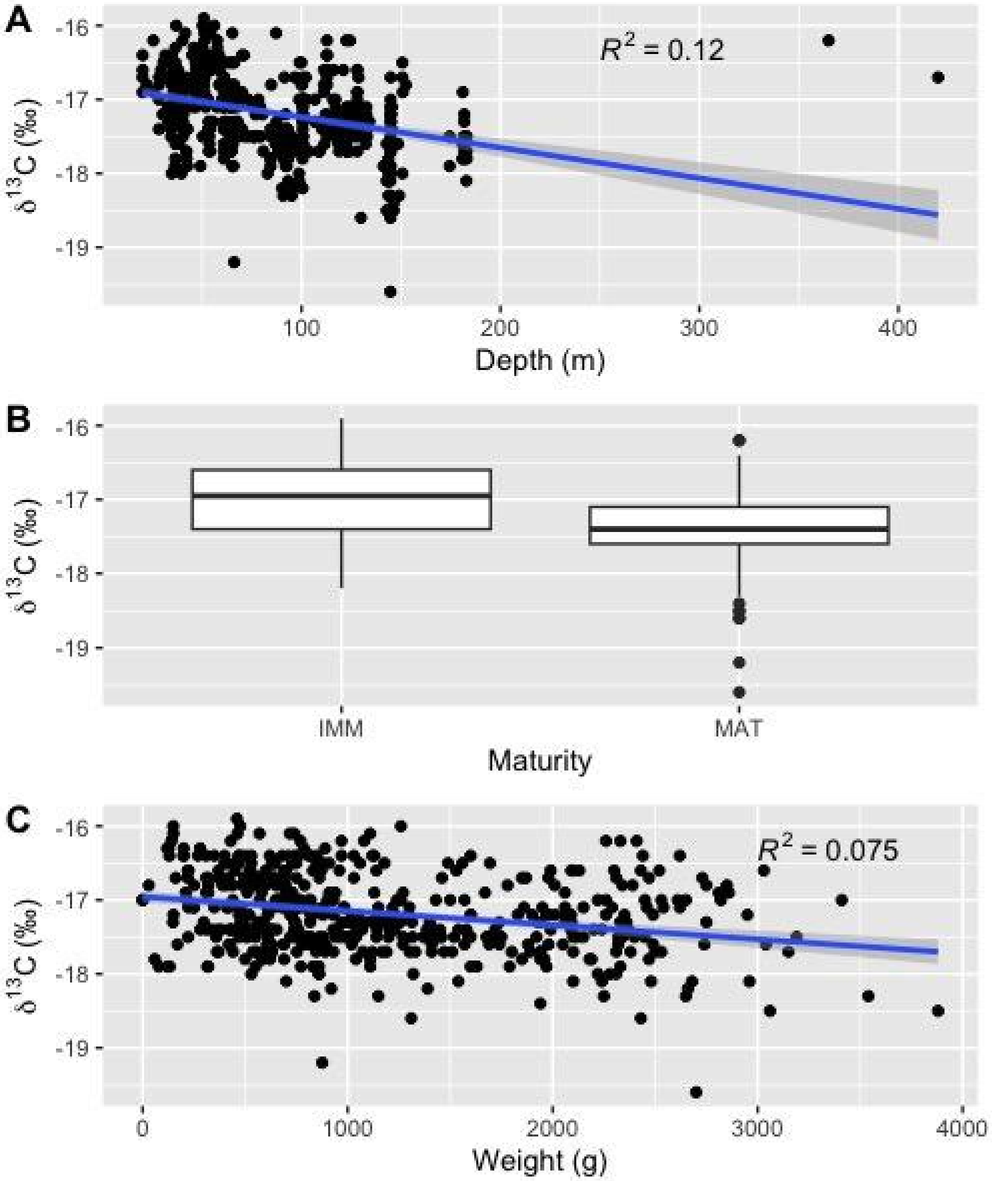
Results of the GLMs Ran Testing Which Factors Are Significantly Associated with δ^{13}C, δ^{15}N, and TL. The Table Displays Both the Independent and Dependent Variables, the Model Estimate for Each Dependent Variable, the Standard Error of Those Estimates, the T-Value, and the P-Value

Isotope	Variable	Estimate	Standard Error	t-value	p-value
δ^{13}C	**Depth**	-0.0032	0.0006	-4.959	**<0.0001**
	Relief	0.0719	0.0291	2.473	**0.0137**
	Chlorophyll-a	0.1049	0.0280	3.747	**0.0002**
	Temperature	0.2278	0.0454	5.020	**<0.0001**
	Maturity	-0.1330	0.0630	-2.113	**0.0351**
	Weight (g)	-0.0001	0.0001	-1.449	0.1480
	Latitude	0.0851	0.0095	8.967	**<0.0001**
	H.S.I	-0.0679	0.0315	-2.159	**0.0313**
δ^{15}N	Depth	0.0015	0.0008	1.852	0.0646
	Chlorophyll-a	0.2764	0.0334	8.276	**<0.0001**
	Temperature	0.4801	0.0558	8.603	**<0.0001**
	Weight (g)	0.0001	0.0001	1.491	0.1365
	Latitude	0.0676	0.0116	5.825	**<0.0001**
	H.S.I	-0.0742	0.0392	-1.894	0.0588
	G.S.I	-0.0597	0.0384	-1.557	0.1202
TL	**Relief**	0.0527	0.0238	2.212	**0.0277**
	Chlorophyll-a	-0.0440	0.0294	-1.498	0.1350
	Temperature	-0.0758	0.0280	-2.712	**0.0070**
	Maturity	-0.0964	0.0578	-1.666	0.0966
	Length (cm)	0.0116	0.0036	3.187	**0.0016**
	Fulton's K	0.1470	0.0819	1.796	0.0734

variables which emphasizes that both individual fish traits and the ambient environment can alter where individuals are sourcing carbon from the marine system. Chlorophyll-a ($p < 0.0001$), SST ($p < 0.0001$), and latitude ($p < 0.0001$) were significantly associated with δ^{15}N (Table 9). Chlorophyll-a, SST, and latitude were all positively correlated with δ^{15}N, indicating that TL of Canary rockfish is greater in locations that are warmer, more productive, and/or further north. Since most latitudes are assumed to have higher productivity and lower temperatures, the positive correlations between temperature, latitude, and δ^{15}N may be impacted at the distinctive port level than the management region level. All of these are factors indicating that the environment has a greater influence on TL than biological

Figure 8

Plots Depict Associations Between $\boldsymbol{\delta}^{13}$*C and (A) Depth, (B) Maturity Status, and (C) Weight. Linear Regressions Were Run in A and C Represented by the Blue Lines and the Gray Shading Surrounding Representing the 95% Confidence Interval of That Best Fit Line. The* R^2 *Values Are Also Included on the Scatterplots for A and C*



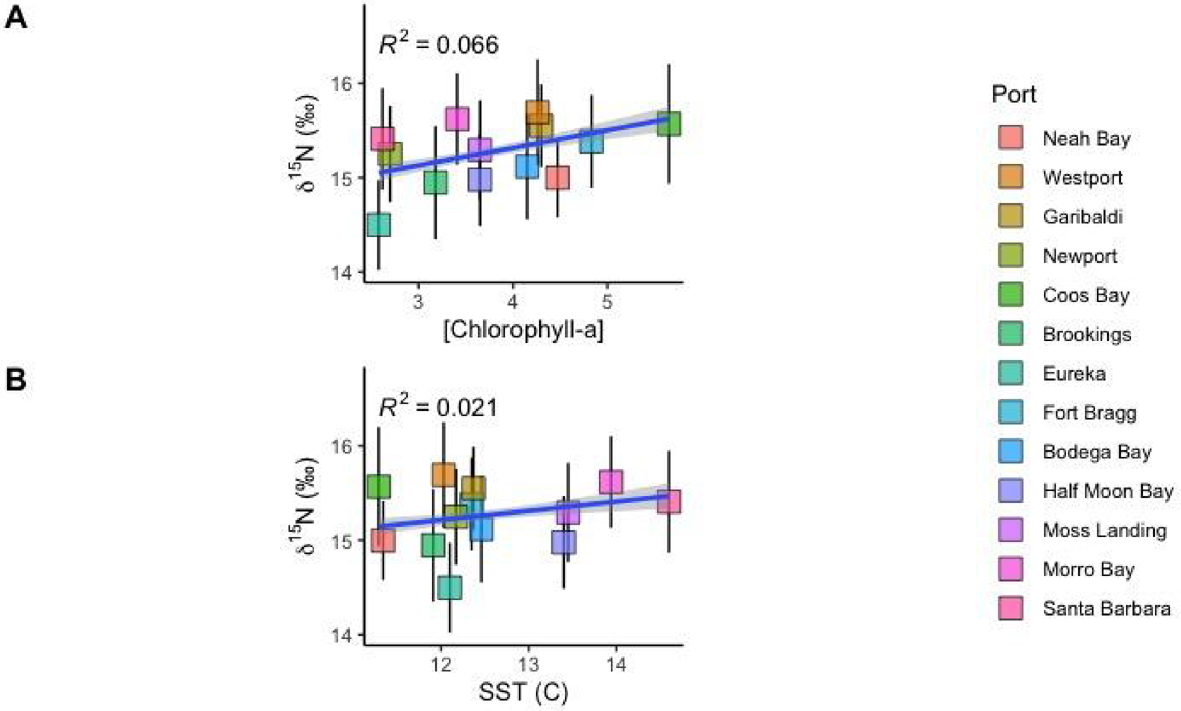
factors. In terms of depth, there is a positive relationship between increasing depth and δ^{15}N, suggesting individuals caught at deeper depths are foraging at higher TLs (Table 9). Relief ($p = 0.0277$), SST ($p = 0.0070$), and length ($p = 0.0016$) were significantly associated with calculated TL (Table 9). Relief and length were positively correlated with TL, therefore increases in relief and length are associated with increases in TL. However, temperature was negatively associated with TL which is the opposite relationship of δ^{15}N and temperature. Therefore, given the positive associations with productivity and latitude with δ^{15}N, it is assumed that temperature is negatively correlated with TL and δ^{15}N despite the results of the GLM. These biases are the reason that both TL and δ^{15}N were used in this study. Thus, it is likely colder environments are conducive to higher TL organisms. TL is affected by both abiotic and biotic factors, further emphasizing that both the ambient environment and individual traits affect TLs in Canary rockfish.

Figure 9 displays a positive relationship between δ^{15}N with SST and chlorophyll-a. Despite these being positive correlations with latitude, they do not follow North to South or South to North trends. This is likely a function of the spatial variability at the port level, where latitude does make a difference to SST and chlorophyll-a concentrations, but do not follow North to South or South to North linear trends.

Figure 10A represents the average isotopic values within each management region in bivariate isotopic space. There is a general increasing trend in δ^{13}C values from South to North likely reflecting productivity gradients where productivity in the North is higher than in the South (Figure 10B). This is also confirmed by the mean δ^{13}C values provided in Table 8. Despite this, analyzing Figure 9 at the port level, displays regional differences where

Figure 9

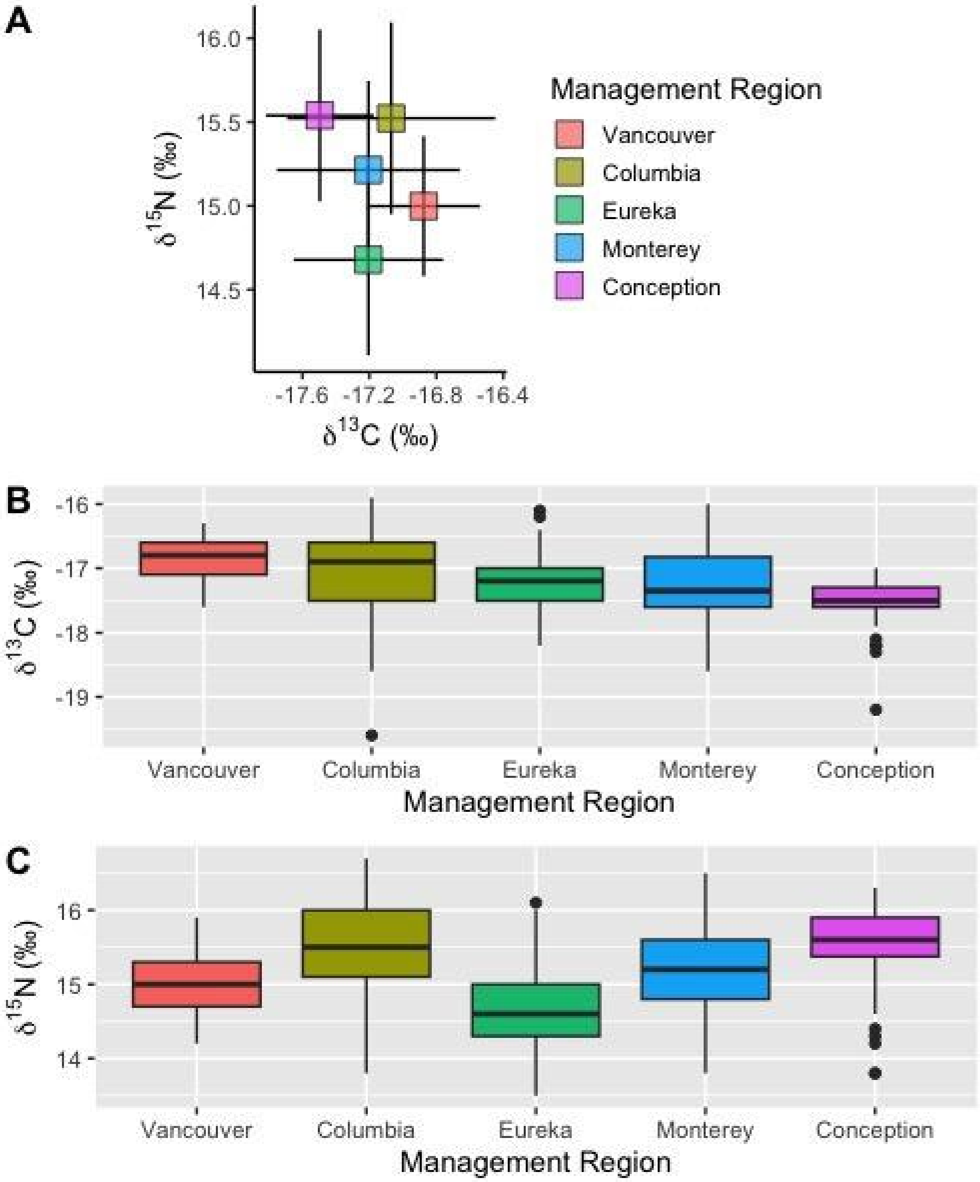
Average Canary Rockfish δ^{15}N Muscle Tissue Isotope Values at Each Port As a Function of (A) 10-Year Average Sea Surface Temperature (SST) Values and (B) 10-Year Average Chlorophyll-A Values. Error Bars Are ± 1 SE. The Port Legend Lists the Ports from Northernmost to Southernmost and the Blue Line Represents the Best-Fit Linear Regression Line and the Gray Shading Surrounding the Line Represents the 95% Confidence Interval of the Regression



not all northern ports have higher chlorophyll-a concentrations than southern ports. There is variability within the regions at the port level, but at the larger scale regional level both chlorophyll-a concentrations and δ^{13}C values follow an increasing trend from South to North. There is no apparent latitudinal trend when examining δ^{15}N values (Figure 10C). Individuals within the Eureka and Monterey regions do not have similar δ^{15}N values and are situated next to each other within the CCS, while Colombia and Conception have similar δ^{15}N values

Figure 10

(A) Bivariate Isotopic Plot of $\boldsymbol{\delta}^{13}$*C and* $\boldsymbol{\delta}^{15}$*N. Mean Values for Each Isotopic Value Are Plotted as Colored Boxes for Each Management Region with the Black Bars Representing One Standard Deviation. Box Plots of (B)* $\boldsymbol{\delta}^{13}$*C Values and (C)* $\boldsymbol{\delta}^{15}$*N Values Colored Coded by Region and Organized from North to South. The Horizontal Line inside the Boxes Represents the Median Value, the Colored Boxes Represent the Interquartile Range (IQR), the Horizontal Bars above and below the Box are ± 1.5 * IQR, and the Black Dots Represent Outliers*



and are not close to each other. Therefore, it appears that common oceanographic patterns shared by region that are close to each other do not affect $\boldsymbol{\delta}^{15}$N. However, given that TL was only significantly associated with environmental factors.

Vancouver has the smallest CR (CR = 1.30) and therefore the smallest diversity in basal resources at the base of the food web, whereas Columbia has the largest CR (CR = 3.70) and therefore the greatest diversity of carbon sources in the diet (Figure 11, Table 10). The Vancouver region also exhibited the smallest NR (NR = 1.70), while the Columbia region had the largest (NR = 2.90) and therefore the most diversity of TL of individuals within each region (Figure 11, Table 10). Finally, the same trend is true for the total area of the ellipses (Vancouver TA = 1.76, Columbia TA = 6.46) and the mean distance to the centroid (Vancouver CD = 0.48, Columbia CD = 0.75), corresponding to very small or very large isotopic niches respectively (Figure 11; Table 10). NND is largest for Monterey (NND = 0.12) and smallest for Conception (NND = 0.09) and Columbia (NND = 0.09), which indicates very dissimilar or similar trophic niches within each region, respectively (Table 10). Standard deviation of the mean nearest neighbor represents evenness of the trophic spread with Eureka being the smallest (SDNND = 0.09) and Columbia the largest (SDNND = 0.12) (Table 10).

Table 10 and Figure 11 display the isotopic ellipses by management region as well as present quantitative values for each ellipse, including total area. Total area is an important metric as it describes the total amount of variance between individuals within each

Figure 11

Canary Rockfish Dorsal Muscle Tissue Stable Isotope Biplots for (A) All Management Regions Combined and (B) Each Management Region Individually. The Dotted Lines Represent that Region's Convex Hull. The Bold Ellipses Are That Region's Standard Ellipse. Larger Standard Ellipse Areas Indicate a Larger Dietary Niche in the X or Y Direction, and Smaller Standard Ellipse Areas Indicate a Smaller Dietary Niche

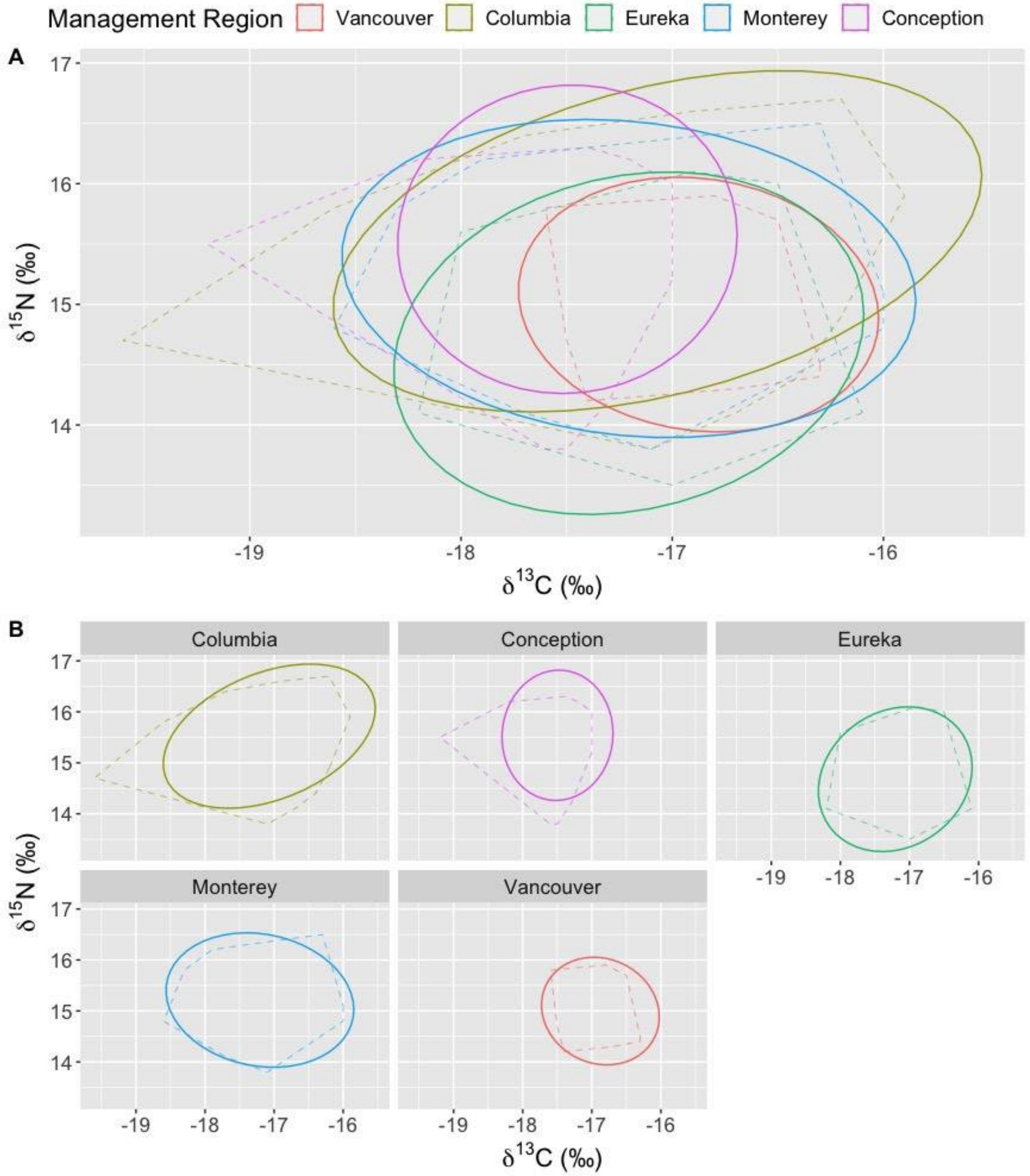


Table 10

Isotopic Niche Metrics Calculated from Canary Rockfish $\boldsymbol{\delta}^{15}$*N and* $\boldsymbol{\delta}^{13}$*C Values as a Function of Management Region and Sexual Maturity Status. NR = Nitrogen Range, CR = Carbon Range, TA = Total Area of Convex Hull, CD = Mean Distance to Centroid, NND = Mean Nearest Neighbor Distance, SDNND = Standard Deviation of NND*

Variable		NR	CR	TA	CD	NND	SDNND
Management Region	Vancouver	1.70	1.30	1.76	0.48	0.11	0.10
	Columbia	2.90	3.70	6.46	0.75	0.09	0.12
	Eureka	2.60	2.10	3.87	0.64	0.12	0.09
	Monterey	2.70	2.60	4.79	0.69	0.12	0.11
	Conception	2.50	2.20	3.29	0.48	0.09	0.11
Maturity	Mature	3.20	3.40	6.72	0.69	0.07	0.10
	Immature	2.7	2.3	4.92	0.74	0.06	0.06

management region. Figure 12 displays the total standard ellipse area (SEA) for each management region. SEA is lowest for Conception, indicating that individuals in this region have relatively low variability for isotopic values. Monterey has the highest median SEA indicating that the Monterey region also likely has large diversity in carbon and nitrogen values, similar to Columbia. This also corresponds with what is shown in Figure 11, as both Columbia and the Monterey regions appear to have the largest ellipse size and isotopic niche metrics in Table 10. Most of the variability in the SEAs appear to be driven by larger ranges in $\boldsymbol{\delta}^{15}$N as opposed to $\boldsymbol{\delta}^{13}$C.

Mercury Analysis

288 dorsal muscle tissues were analyzed for total mercury as a proxy for methylmercury (Table 11). It is important to note that Table 11 lists the average total mercury concentrations and the black lines representing the boxes in Figure 13 display the median total mercury concentrations, therefore comparisons between Table 11 and Figure 13 may appear slightly different. Vancouver (mean = 0.169 [Hg] ppm), Columbia (mean = 0.163 [Hg] ppm), and Monterey (mean = 0.168 [Hg] ppm) management region fish contained the highest average

Figure 12

Standard Ellipse Area Boxplots by Management Region. Gray Boxes Represent the 50%, 75%, and 95% Credible Intervals. Black Dots Represent the Mode

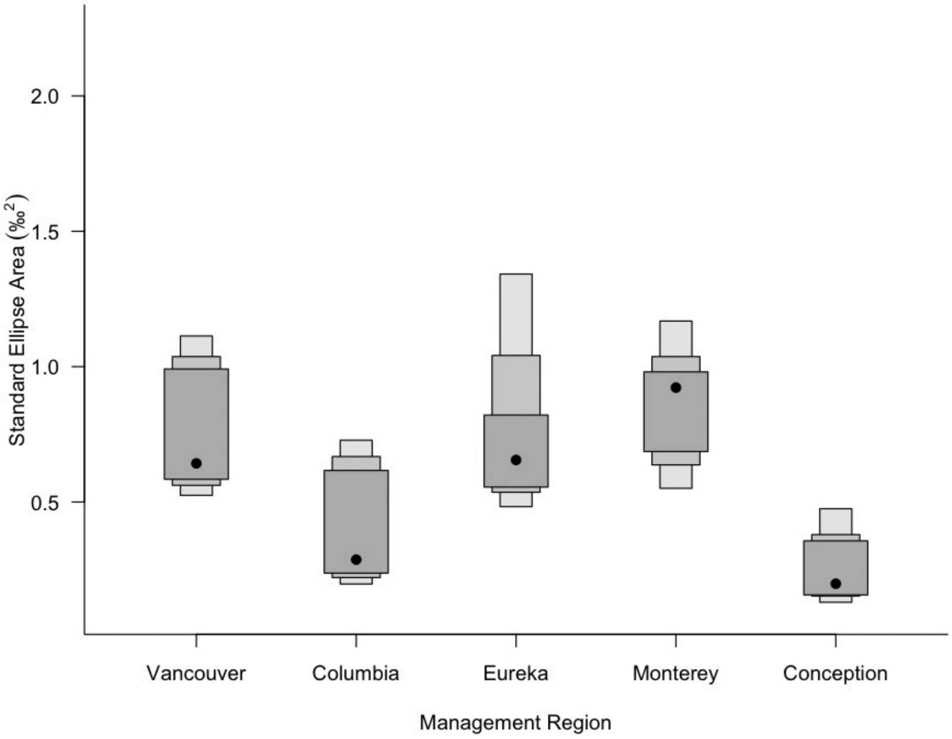


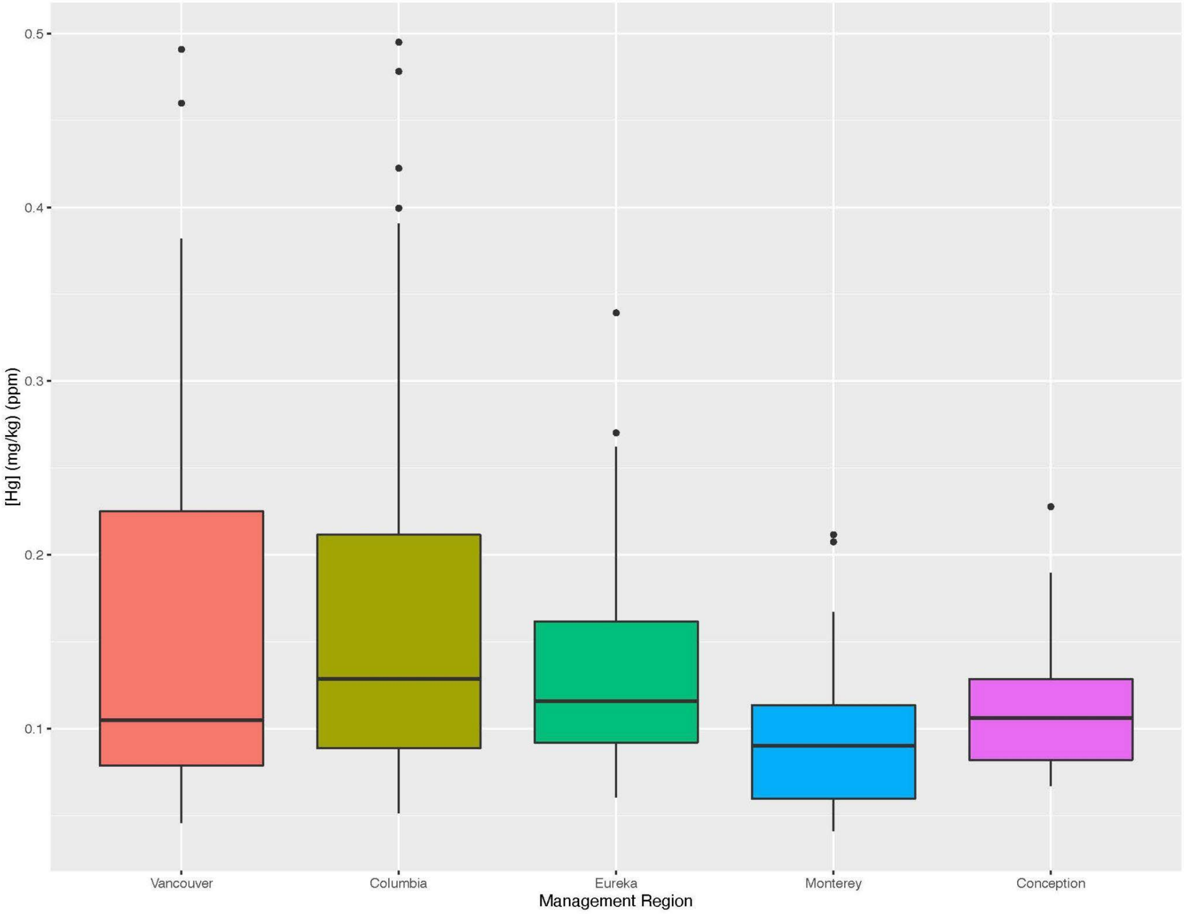
Table 11

Summary of the Number of Dorsal Muscle Tissues Utilized in Total Mercury Concentration Analysis Sorted by Fisheries Management Region, Sex, and Sexual Maturity Status (n=288). The Third Column Represents the Average Total Mercury Concentrations in Parts Per Million ± 1 SD

Variable	Number of Samples	Mean [Hg] ppm ± SD
Management Region		
Vancouver	26	0.169 ± 0.124
Columbia	114	0.163 ± 0.097
Eureka	66	0.130 ± 0.054
Monterey	63	0.168 ± 0.037
Conception	19	0.114 ± 0.042
Sex		
Female	147	0.138 ± 0.081
Male	139	0.137 ± 0.087
Maturity		
Immature	185	0.102 ± 0.039
Mature	103	0.201 ± 0.102

Figure 13

*Boxplots of Total [Hg] ppm Separated by Fisheries Management Region from North to South. The Black Horizontal Line Within Each Box Represents the Median Value, the Colored Box Represents the Interquartile Range, and the Horizontal Bars Confining the Boxes are =±1.5*IQR, and the Black Dots Represent Outliers*



total mercury concentrations, although total mercury concentrations were most variable in the Vancouver region. Management region was not a significant factor overall, but longitude was, insinuating a significant difference among regions with different longitudinal values. Eureka (mean = 0.130 [Hg] ppm) was more similar to Conception despite not sharing a latitudinal border with each other. The Conception region had the lowest total mercury concentrations (mean = 0.114 [Hg] ppm), but there was no clear latitudinal trend observed with total mercury concentrations. Sex, was statistically significant however, there is minimal difference in average total mercury concentrations with females averaging 0.138 [Hg] ppm and males averaging 0.137 [Hg] ppm. Mature fish (0.201 [Hg] ppm) had double the mercury in their tissues on average compared to immature fish (0.102 [Hg] ppm).

A GLM was conducted to test whether the environmental and biological variables were significantly associated with total mercury concentration. The model selection procedure eliminated the variables: relief, chlorophyll-a, length, latitude, HSI, and GSI and retained the variables: depth, SST, sex, sexual maturity, weight, Fulton's K, and longitude within the model. Sex ($p = 0.0126$), weight ($p < 0.0001$), Fulton's K ($p < 0.0001$), and longitude ($p < 0.0001$) were deemed to be significant variables in explaining total mercury concentrations. Weight and longitude were positively associated with total mercury concentrations in their tissues. Longitude could be used as a distance to shore variable, but given the dynamic West Coast of the United States it is unfair to use that as a descriptor of distance from shore across the sample area. Thus, here longitude is used as a proxy for management regions with Vancouver, Columbia, and Eureka having the largest longitude values and Monterey and Conception having the smallest longitude values. Region does have a negative latitudinal trend with total mercury concentrations, however there is still significant overlap of their IQRs thus this is not a statistically significant trend (Figure 13). This trend could be indicative that methylmercury, therefore inter-organismal total mercury concentrations are elevated in areas of high productivity. Additionally, there is increased variability of the total mercury concentration values with increases in latitude, with more northern regions possessing more variable total mercury concentrations (Figure 13). There is more of a noticeable difference and less overlap of the IQR boxes when looking at total [Hg] ppm between sexual maturity statuses (Figure 14). Despite maturity not being a significant factor in the GLM, a Welch's two-sample t-test was conducted and determined the mean total mercury concentrations between the immature and mature groups was significant ($t = -9.5594$, $p < 0.0001$). Sexually mature fish on average have twice the total [Hg] ppm compared to immature fish (Figure 14). Despite the doubling in total mercury concentrations between mature and immature fish, the model identified this factor as being marginally non-significant, potentially due to multicollinearity with the predictor of weight. Fulton's K, temperature, and depth are negatively associated with mercury, therefore individuals in poorer body condition (less energy reserves), and those residing in cooler temperatures and at deeper depths tend to possess higher total mercury concentrations. A majority of these are biological variables, indicating that total mercury concentrations within Canary rockfish are more dependent upon individual fish traits rather than ambient environmental conditions.

Fulton's K and weight were two significant variables ($p < 0.0001$, Table 12) describing variance in total [Hg] ppm in the GLM model. Fulton's K is a function of both length and weight of the individual fish with values > 1 indicating a fattier fish and values < 1 indicating a skinnier fish. There are strong positive correlations (weight $R^2 = 0.53$, length $R^2 = 0.51$) with both length and weight with total [Hg] ppm (Figure 15). These, in addition to sexual maturity, appear to represent the strongest correlating variables with total mercury concentrations in Canary rockfish in the CCS. Therefore larger, heavier, and sexually mature

Figure 14

*Boxplots of Total [Hg] ppm Separated by Sexual Maturity Status. The Black Horizontal Line Within Each Box Represents the Median Value, the Colored Box Represents the Interquartile Range, and the Horizontal Bars Confining the Boxes are =±1.5*IQR, and the Black Dots Represent Outliers*

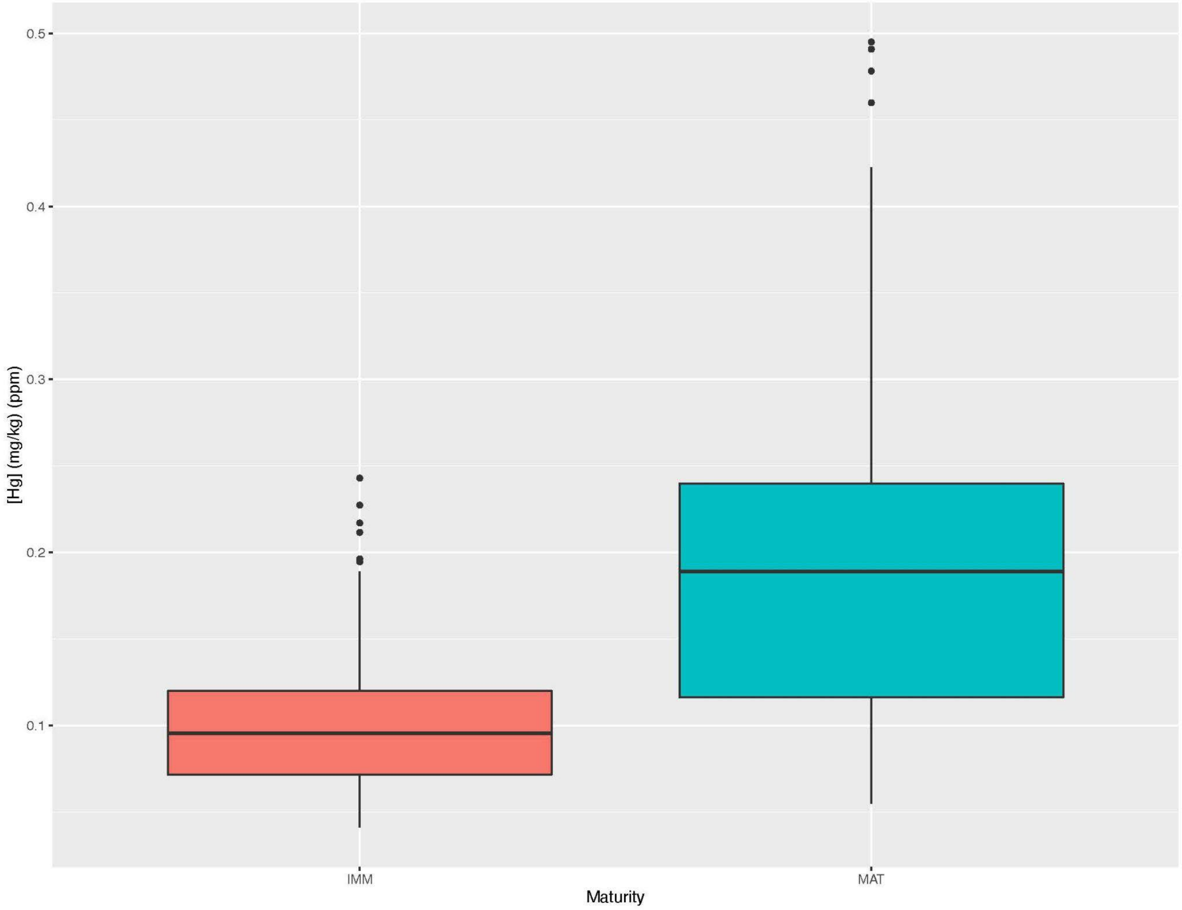


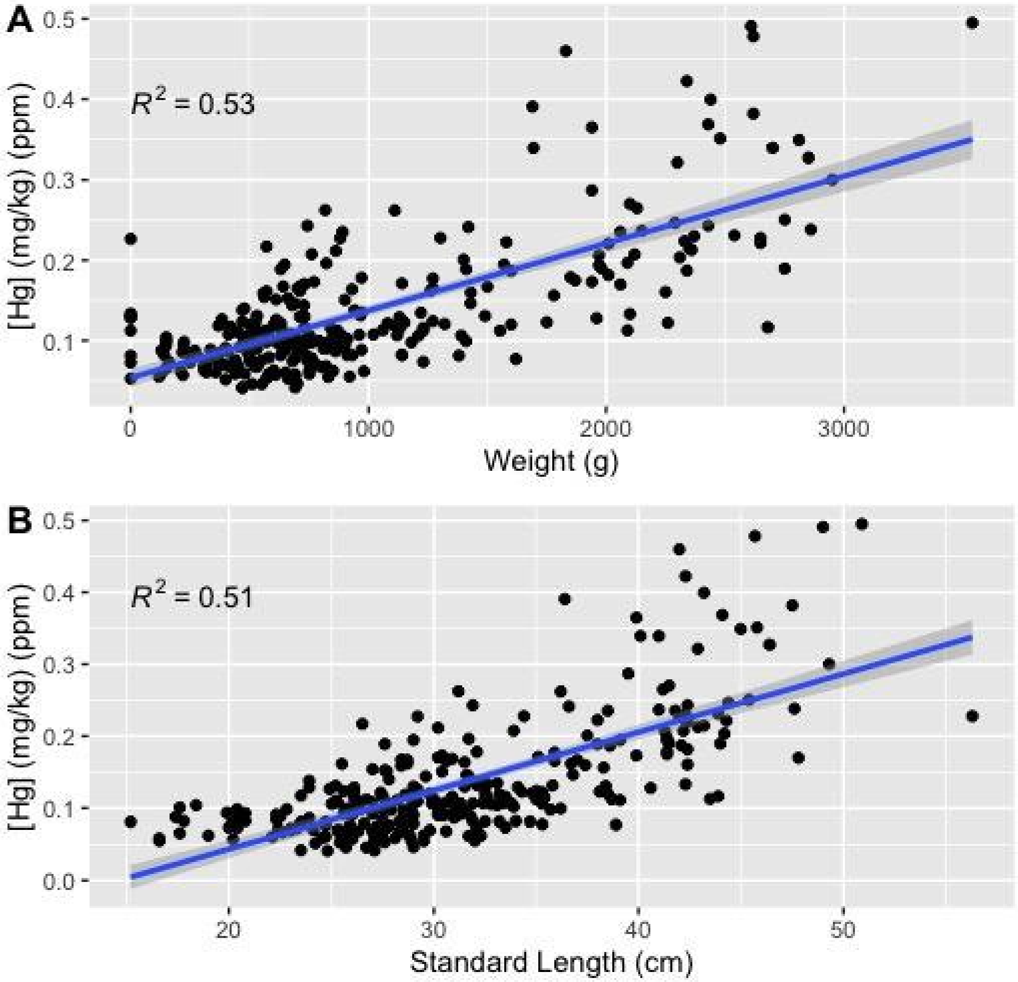
Table 12

GLM for Total [Hg] ppm on Both the Continuous and Categorical Variables Within the Dataset. The Significant P-Values Are Bolded

Variable	Estimate	Standard Error	t-value	p-value
Depth	-2.05E-04	1.23E-04	-1.675	0.0951
Temperature	-5.45E-03	3.58E-03	-1.52	0.1296
Sex	1.57E-02	6.26E-03	2.512	**0.0126**
Maturity	1.94E-02	1.08E-02	1.789	0.0748
Weight	8.87E-05	9.13E-06	9.707	**<0.0001**
Fulton's K	-4.39E-02	1.37E-02	-4.231	**<0.0001**
Longitude	1.42E-02	3.23E-03	-4.386	**<0.0001**

Figure 15

Scatter Plots Depicted Associations Between Total [Hg] ppm and (A) Weight and (B) Standard Length of Canary Rockfish. The Blue Lines Represent the Linear Relationship and Regression Between the Variables and the Gray Shading Surrounding the Line is Representative of a 95% Confidence Interval of that Regression



Canary rockfish tend to on average possess higher concentrations of mercury within their dorsal tissues. There appears to be more variance in weight and length values when analyzing higher total mercury concentrations, but this is likely because fish plateau in growth as they age, but can still accumulate higher concentrations of mercury without growing larger in size.

Stomach Contents, Stable Isotopes, and Mercury Concentration Analysis

Five statistical models were analyzed to evaluate correlations between mercury, prey items, and isotopic values. The first GLM (n=272) tested whether total mercury concentrations were associated with %W of the 11 prey items. %W of teleosts ($p < 0.0001$) and krill ($p = 0.0018$) were significant prey items explaining [Hg] ppm in Canary rockfish, with tissue mercury increasing with increasing %W of teleosts in the diet (Table 13). Krill and teleost prey groups were the two most important prey groups in terms of number (%N krill = 83.42%, Table 3), and weight (%W teleosts = 42.15%, Table 3), and explained the overall dissimilarity in diets among individuals (Table 6). There is a clear increase in total mercury concentrations in individuals that have a higher proportion of teleosts in their diet (Figure 16). The second GLM (n=204) tested associations between [Hg] ppm and the isotopic and TL calculations. $\boldsymbol{\delta}^{13}C$ ($p < 0.0001$) and $\boldsymbol{\delta}^{15}N$ ($p = 0.0003$) were significant factors in explaining [Hg] ppm in Canary rockfish, with mercury levels being higher in fish with more negative $\boldsymbol{\delta}^{13}C$ levels (i.e., offshore sources of production) and those feeding at a higher TL (i.e., higher $\boldsymbol{\delta}^{15}N$) (Table 13). The third GLM (n=272) tested what prey items predicted $\boldsymbol{\delta}^{13}C$ levels, retaining shrimp, crab, krill, squid, and pyrosomes during AIC model selection. Shrimp ($p = 0.0442$), crab ($p = 0.0059$), and krill ($p = 0.0032$) were significant predictors of $\boldsymbol{\delta}^{13}C$ values, which is indicative of where individuals source their primary producers within the food web (Table 13). $\boldsymbol{\delta}^{13}C$ values peak in the moderate category for each shrimp, crab, and teleost prey categories (Figure 17). The low and high categories for each prey item's %W are relatively similar in $\boldsymbol{\delta}^{13}C$ values, indicating that $\boldsymbol{\delta}^{13}C$ does not follow any sort of trend when analyzing %W of prey items in the stomachs. The fourth GLM

Table 13

Results of the 5 AICs and GLMs Ran on the Entire Dataset. The 5 GLMs/AICs Were 1) [Hg] ppm ~ Prey Items, 2) [Hg] ppm ~ Isotope and TL Calculations, 3) $\delta^{13}C$ *~ Prey Items, 4)* $\delta^{15}N$ *~ Prey Items, 5) TL ~ Prey Items. Any Significant Prey Variables Are Represented in Bold*

Dependent Variable	Independent Variables	Estimate	Standard Error	t-value	p-value
[Hg] ppm	**Teleosts**	0.0006	0.0001	4.477	**<0.0001**
	Krill	0.0004	0.0001	3.150	**0.0018**
	Squid	0.0007	0.0004	1.713	0.0879
	Copepods	-0.0005	0.0003	-1.460	0.1455
[Hg] ppm	**δ^{13}C**	-0.0468	0.0115	-4.068	**<0.0001**
	δ^{15}N	0.0370	0.0101	3.675	**0.0003**
	TL	0.0271	0.0169	1.602	0.1107
δ^{13}C	**Shrimp**	0.0021	0.0011	2.022	**0.0442**
	Crab	0.0028	0.0010	2.773	**0.0059**
	Krill	-0.0024	0.0008	-2.973	**0.0032**
	Squid	-0.0042	0.0025	-1.702	0.0899
	Pyrosome	-0.0024	0.0014	-1.776	0.0769
δ^{15}N	**Teleosts**	0.0028	0.0011	2.692	**0.0076**
	Krill	-0.0024	0.0009	-2.661	**0.0083**
TL	**Teleosts**	0.0013	0.0007	2.021	**0.0447**
	Copepods	-0.0027	0.0014	-1.949	0.0526

Figure 16

Grouped Bar Plot Displaying Significant Prey Items for Describing Variance in Total [Hg] ppm. Krill is Represented by the Red Bars and Teleosts by Blue Bars. %W of the Prey Items Were Binned into Low, Moderate, and High Categories with the Mean [Hg] ppm Within Each Bin Represented by the Bars. The Black Error Bars Represent a Single Standard Error in Each Direction of the Mean

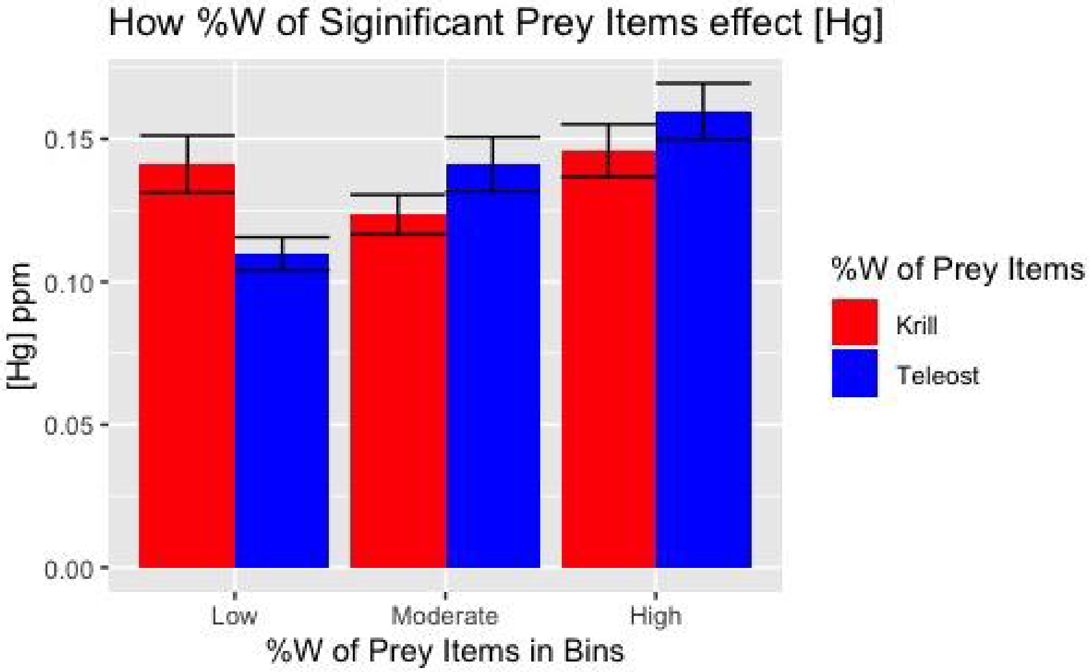
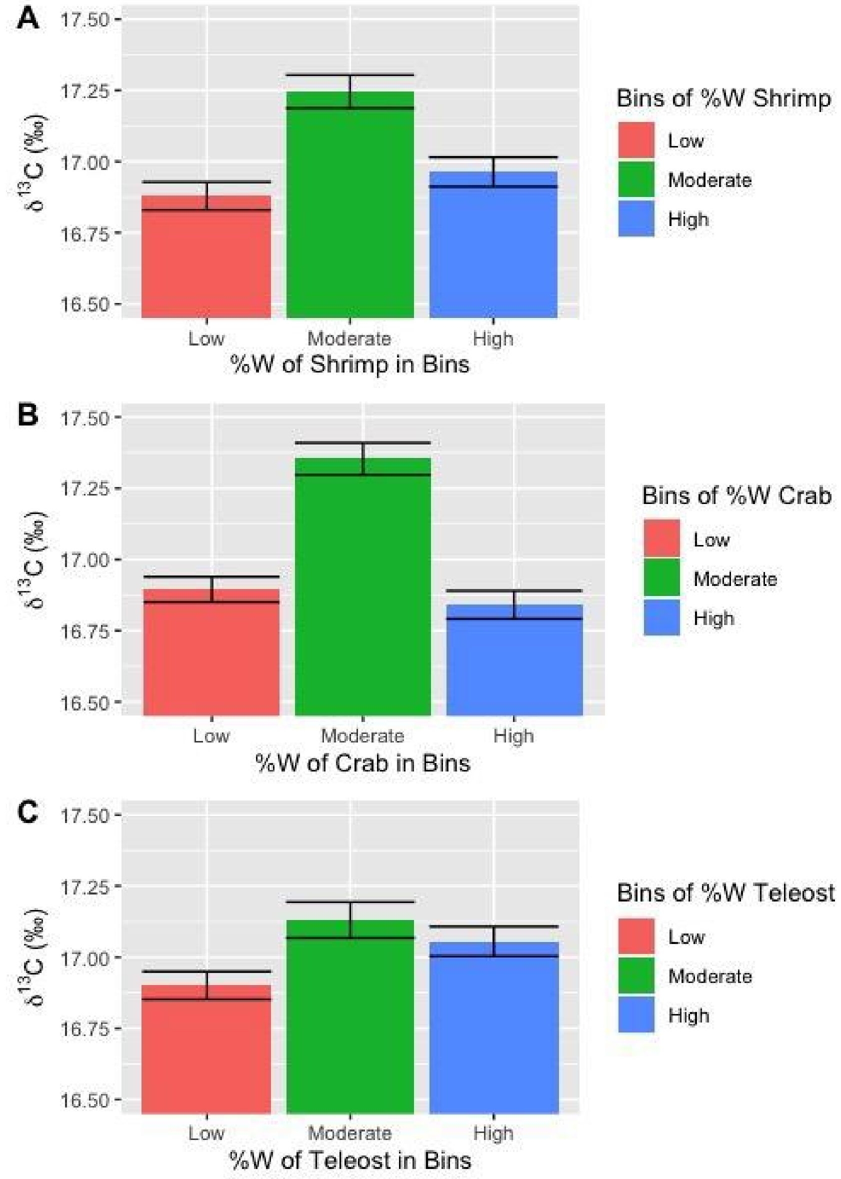


Figure 17

Grouped Bar Plots Displaying Significant Prey Items for Describing Variance in $\boldsymbol{\delta}^{13}$*C Values for (A) Shrimp, (B) Crabs, and (C) Teleosts. %W of Each Prey Item Were Binned into Low (Pink), Moderate (Green), and High (Blue) Categories and Plotted the Mean* $\boldsymbol{\delta}^{13}$*C Within Each of Those Bins. The Black Error Bars Represent A Single Standard Error in Each Direction of the Mean*



(n=272) tested δ^{15}N against prey items and the model selection procedure retained %W of teleosts (p = 0.0076) and krill (p = 0.0083) as significant predictors (Table 13). There is a strong negative relationship between krill and δ^{15}N with Canary rockfish feeding at lower TLs with a higher proportion of krill in the diet (Figure 18A). δ^{15}N values were lowest in fish that consumed a moderate amount of teleosts in the diet, but δ^{15}N values were relatively similar between individuals of both low and high %W of teleosts in their diet (Figure 18B). Thus, krill has a stronger and clearer relationship in describing δ^{15}N values compared to teleosts. The fifth GLM (n=204) tested TL against %W of prey items and the AIC model selection included teleosts and copepods. Teleosts (p = 0.0447) were the only prey group capable of describing variance in TL (Table 13). TL decreased with increasing %W of krill in the diets which is similar to the negative trend witnessed between δ^{15}N and krill (Figures 18 & 19). TL was highest in fish that consumed the greatest proportion of teleosts in the diet, but TL values fluctuated amongst the low, moderate, and high groups, without displaying a clear correlation (Figure 19). Teleosts and krill were included and/or significant in each of the GLMs ran on prey items.

Overall, as total [Hg] ppm increases, δ^{13}C decreases (Figure 20A), and δ^{15}N increases (Figure 20B). High values of [Hg] ppm are generally more variable when it comes to isotopic values compared to low and moderate [Hg] ppm values as shown by the increasing range of the confidence intervals towards the ends of each regression line (Figure 20). The scatterplots possess relatively low R^2 values (A = 0.05 and B = 0.02), suggesting isotopic values are too variable to be accurate predictors of [Hg] ppm, and is likely informed by other factors such as prey items, biological traits, and/or environmental conditions.

Figure 18

Bar Plots Representing Significant Prey Items Contributing to Variance in $\boldsymbol{\delta}^{15}N$ *for (A) Krill and (B) Teleosts. %W of Each Prey Item Were Binned into Low (Red), Moderate (Green), and High (Blue) Values for Each Prey Item and the Mean* $\boldsymbol{\delta}^{15}N$ *for Each Bin Represented by the Colored Bars. The Black Error Bars Represent a Single Standard Error in Each Direction of the Mean*

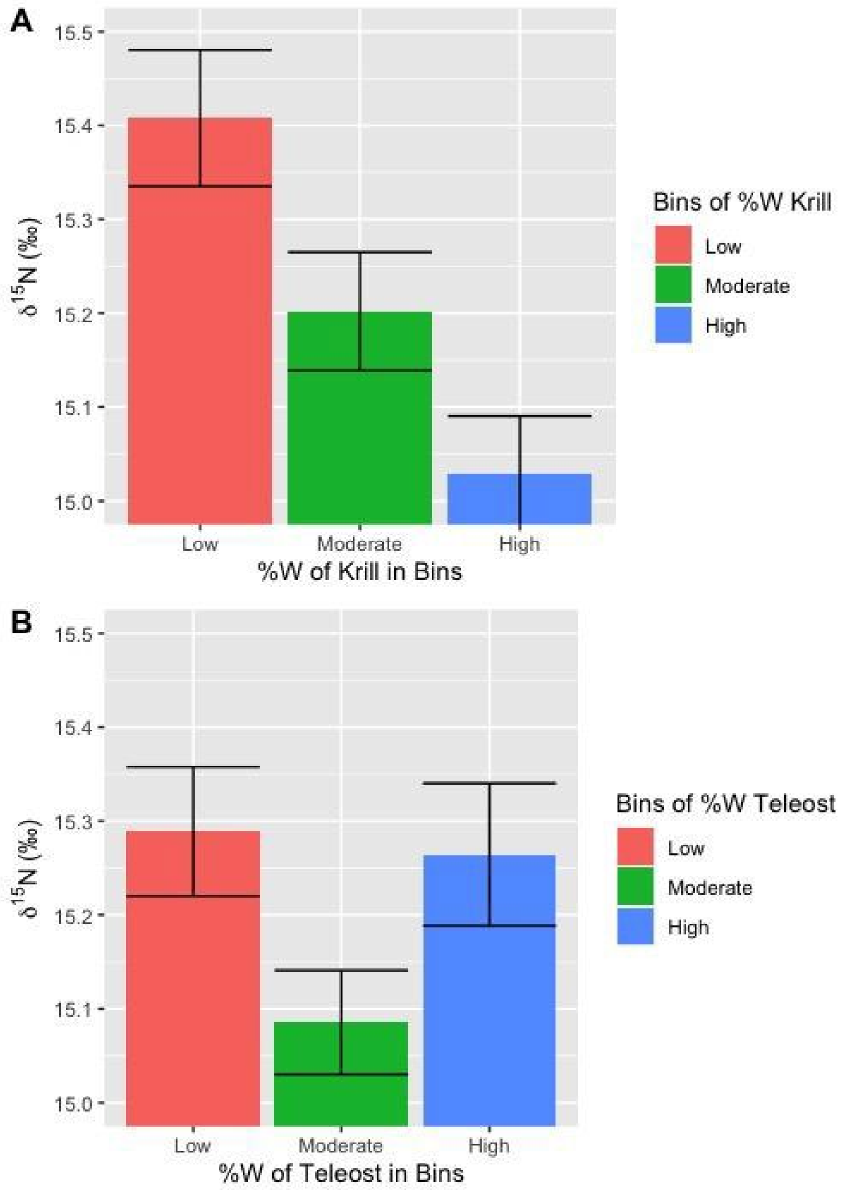


Figure 19

Bar Plots Displaying Prey Items Contributing to Variance in TL for (A) Krill and (B) Teleosts. %W of Each Prey Item Was Binned into Low (Red), Moderate (Green), and High (Blue) Values for Each Prey Item and the Mean TL for Each Bin Represented by the Colored Bars. The Black Error Bars Represent a Single Standard Error In Each Direction of the Mean

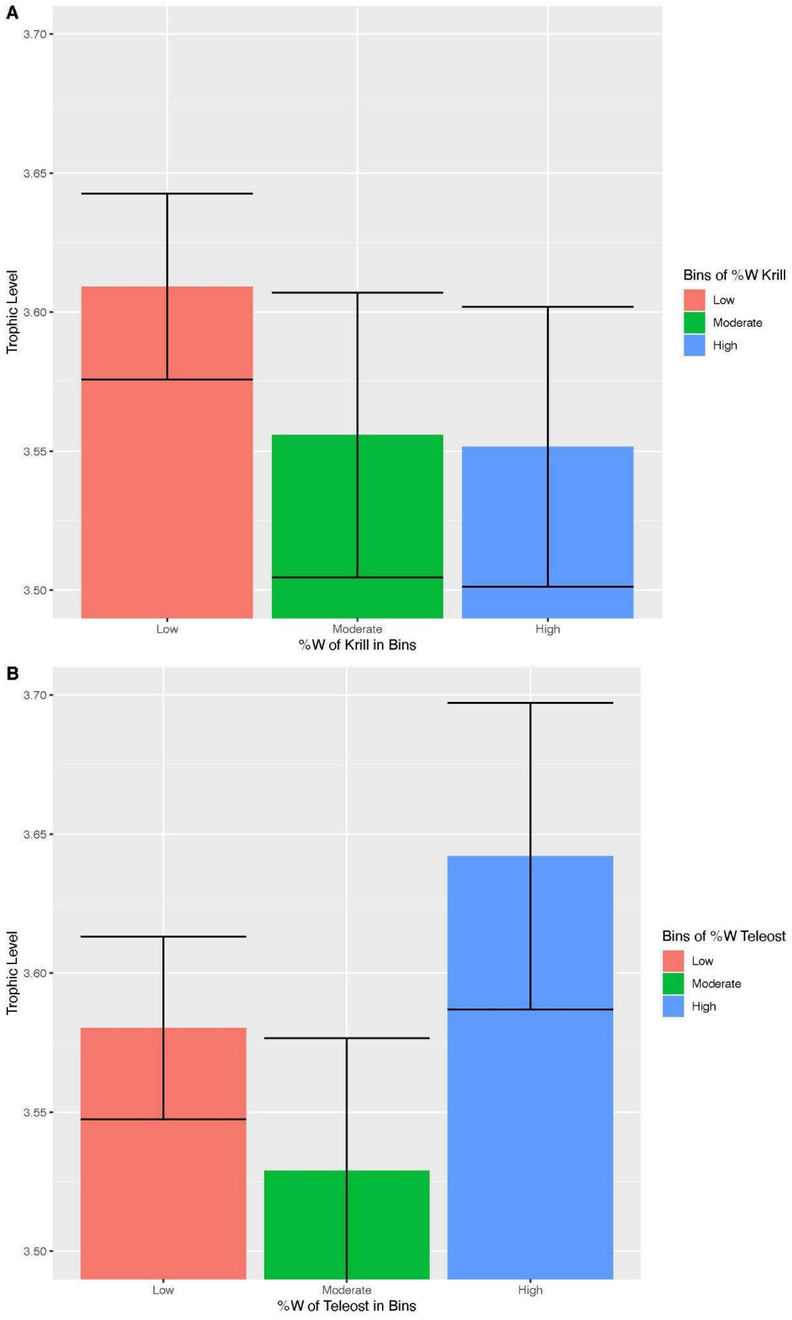
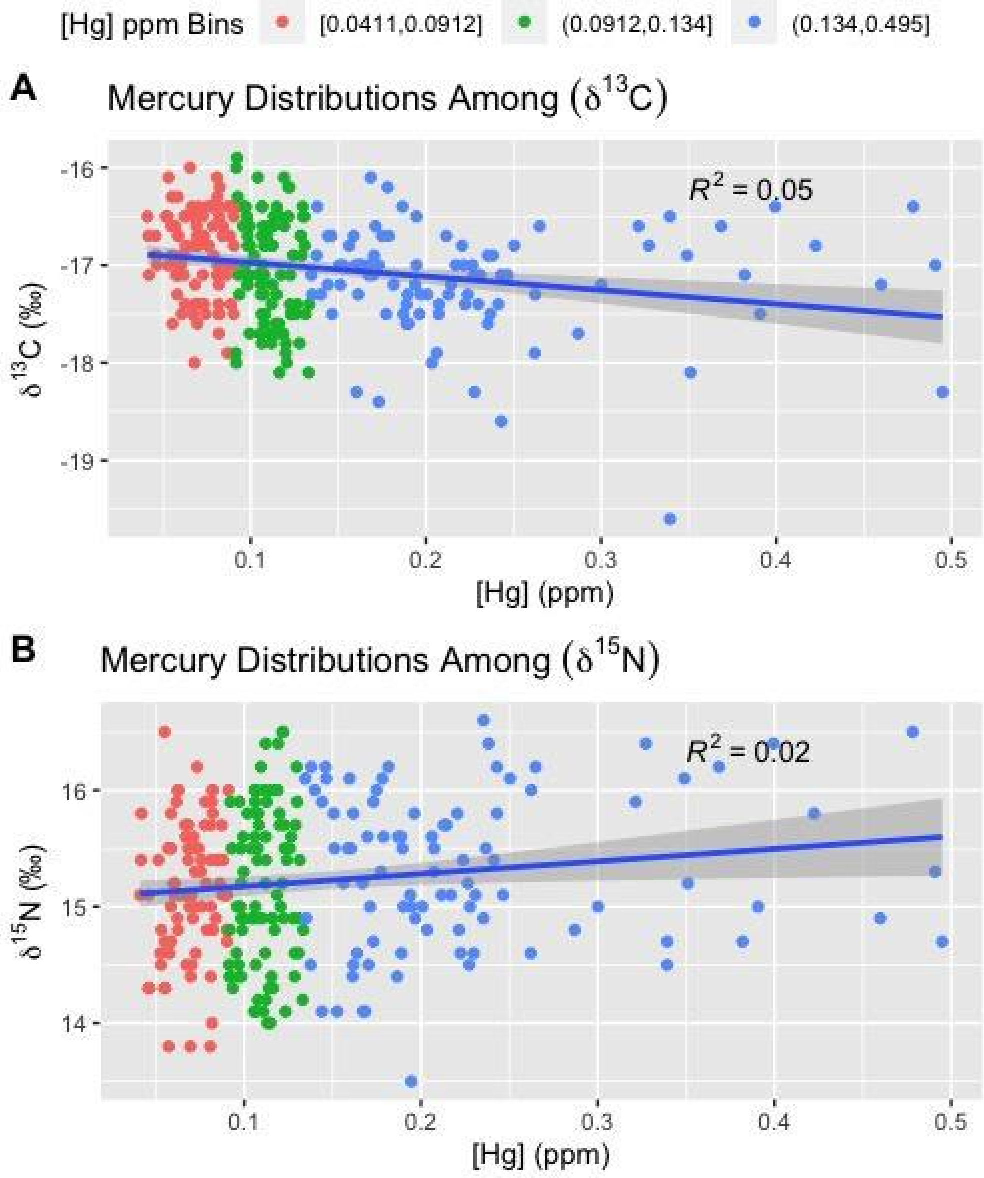


Figure 20

Scatter Plots of $\boldsymbol{\delta}^{13}$*C (A) and* $\boldsymbol{\delta}^{15}$*N (B) Values for Canary Rockfish Grouped into Low, Medium, and High Total [Hg] ppm Values. Type II Regressions Were Conducted and a Best Fit Line Was Plotted (Blue Line) and the Gray Shading Surrounding the Line Represents the 95% Confidence Interval of the Regression Line*



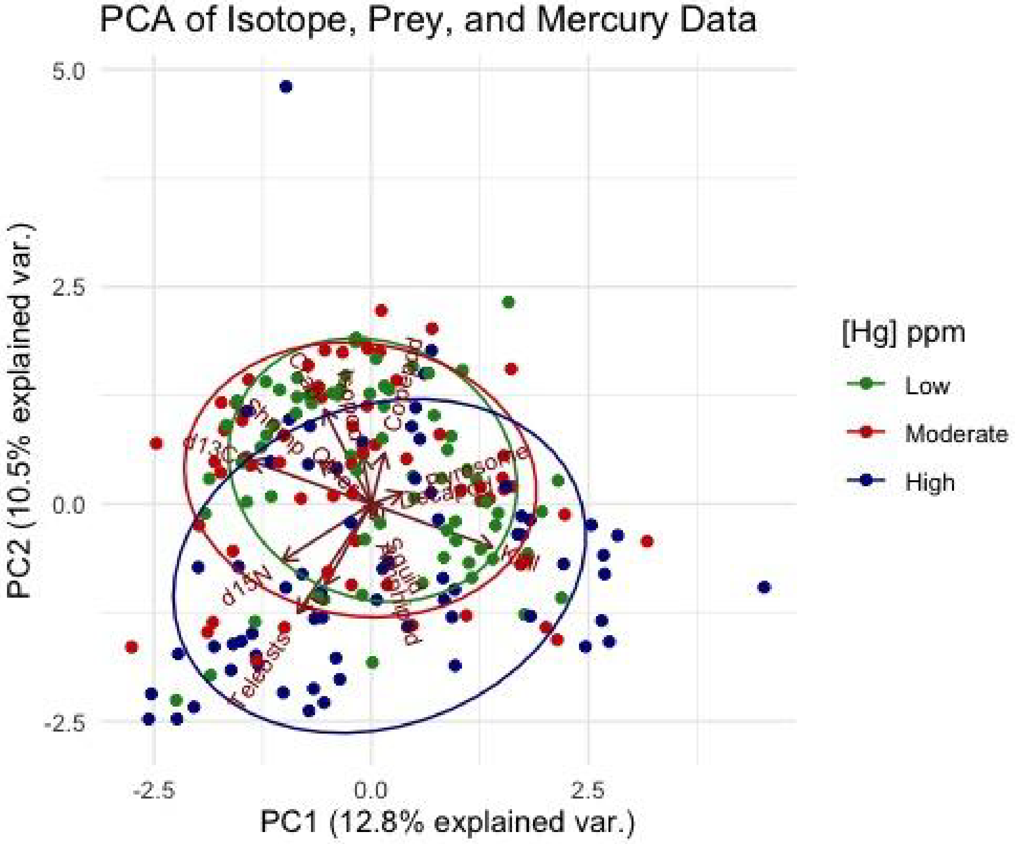
The first PCA included the %W of all 11 prey categories, stable isotope values, and estimates of TL data (Figure 21). PC1 is represented positively by pyrosomes, decapods, and krill, and negatively by δ^{13}C, explaining 12.8% of the variance. PC2 is represented positively by Copepods, crabs, and isopods and negatively by squid and amphipods explaining 10.5% of the variance. PC1 and PC2 are equally represented by shrimp, δ^{15}N, teleosts, and TL, totaling 23.3% of the variance. Fish with high total mercury concentrations tended to consume a higher proportion of teleosts and krill (similar to the GLM results) and had elevated δ^{15}N (Figure 21). In contrast, fish with lower total mercury concentrations consumed more crab, shrimp, isopods, and copepods in the diet. The low and moderate total mercury concentration ellipses contain a lot of overlap whereas the high mercury ellipse is a bit more separated in PC space. The results of this PCA indicate stomach contents and stable isotope values are both associated with tissue total mercury concentrations.

PC2 (Figure 22B, $R^2 = 0.17$) appears to have a negative relationship with Canary rockfish mercury content, suggesting fish with higher total mercury concentrations consume fewer crustaceans and more teleosts which could be related to δ^{13}C values as well and tend to possess higher TLs and δ^{15}N values. PC1 does not appear to have a linear relationship with total mercury concentrations.

The second PCA was composed of biological variables: Fulton's K, HSI, GSI, weight, and length (Figure 23). PC1 is represented positively by GSI, weight, and length and explains 48.9% of the variance in biological variables. PC2 is represented positively by Fulton's K and explains 21.2% of the variance. HSI positively represents both PC1 and PC2, which combined explain 70.1% of the variance. Total mercury concentrations appear to increase in

Figure 21

PCA Visualization of Isotope and Prey Groups as a Function of Total Mercury Concentrations. PC1 Explains 12.8% and PC2 Describes 10.5% of Overall Dataset Variance Totaling 23.3% of Variance Represented. Ellipses Represent 95% Confidence Intervals for Total [Hg] ppm. Each of the Red Arrows Represents the Eigenvector for all of the Individual Variables Tested



individuals that are larger in size, weigh more, and possess higher GSI values (Figure 23). Similar to the prior PCA, there is overlap between the low and moderate [Hg] ppm ellipse with the high [Hg] ppm ellipse exhibiting overlap with the others. However, there is more of a distinction between the low and moderate ellipses, suggesting biological variables are better able to distinguish the differences between individuals of low and moderate total mercury concentrations.

Figure 22
Linear Regressions Testing the Association Between PC1 and PC2 with Total Mercury Concentrations in Canary Rockfish. The Best Fit Line Was Plotted (Blue Line) with the Gray Shading Surrounding the Line Representing the 95% Confidence Interval of the Regression Line

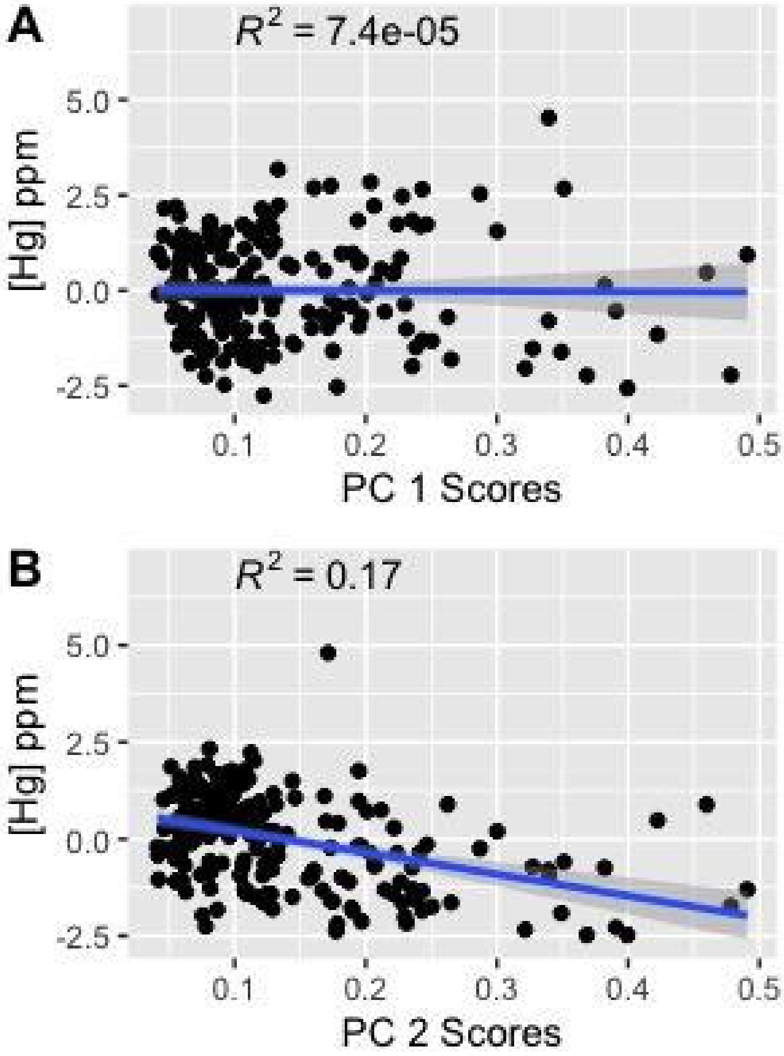
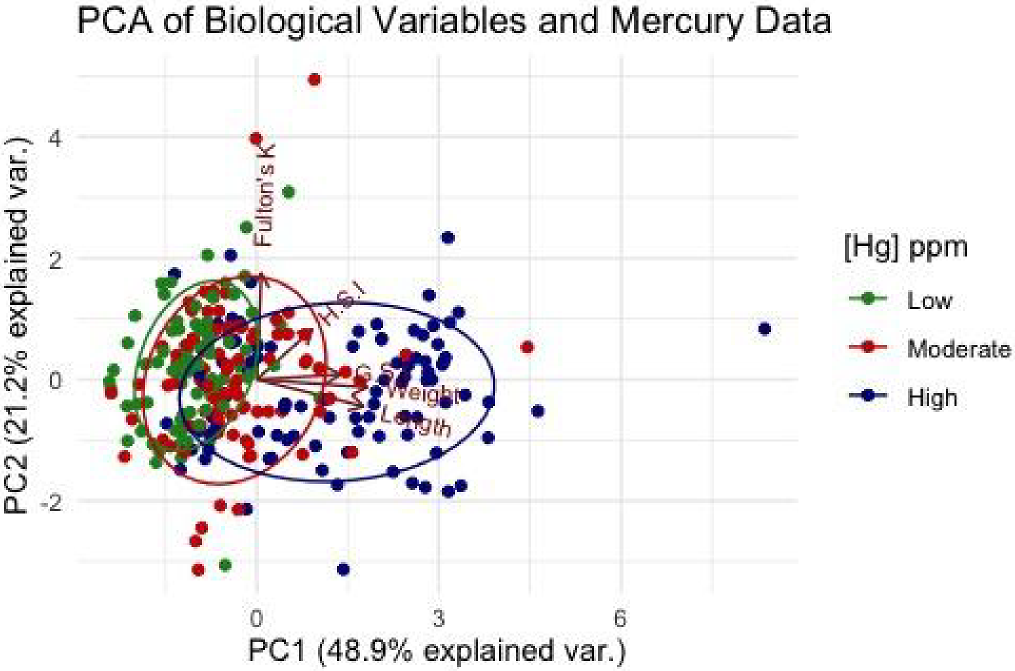


Figure 23

PCA Visualization of Biological Variables: Length, Weight, HSI, GSI, and Fulton's K Grouped by Total Mercury Concentrations. PC1 Explains 48.9% and PC2 Describes 21.2% of Overall Dataset Variance Combined to Represent 70.1% of Dataset Variance. The Ellipses Represent 95% Confidence Intervals for Total [Hg] ppm. Each of the Red Arrows Represents the Eigenvector for all of the Individual Variables Tested

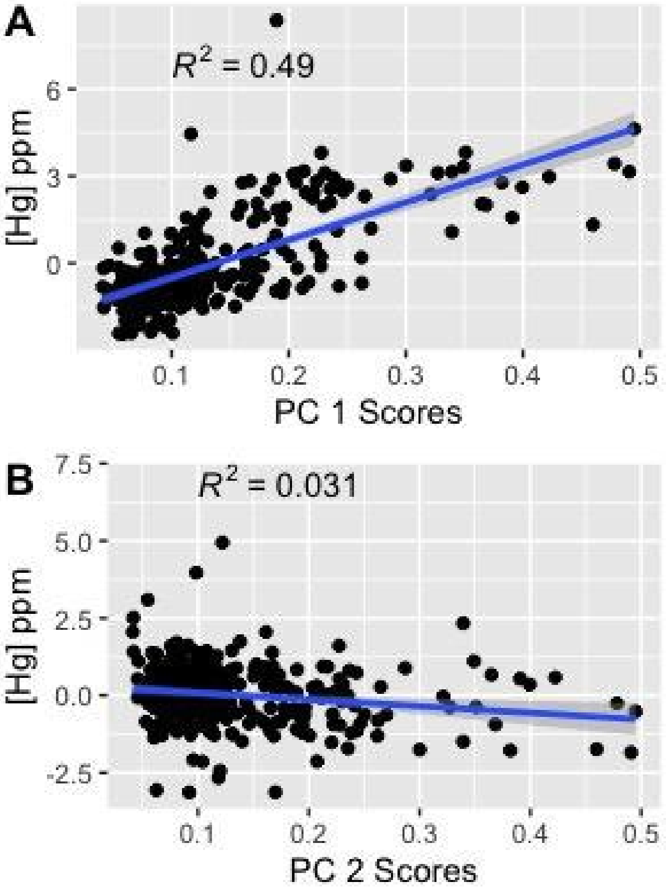


PC1 (Figure 24A) and PC2 (Figure 24B) were significantly associated with mercury content in Canary rockfish. PC1 is positively correlated with GSI, length, and weight, indicating that larger and heavier individuals tend to have higher [Hg] ppm values. PC1 also has a $R^2 = 0.49$ which is a moderately strong positive correlation, indicating PC1 scores from this PCA may be able to estimate total mercury concentrations in Canary rockfish in the CCS.

The last PCA comprises environmental variables: relief, SST, longitude, depth, chlorophyll-a, and latitude (Figure 25). PC1 is represented positively by SST and longitude, and negatively by latitude, explaining 48.0% of the variance. PC2 is represented positively

Figure 24

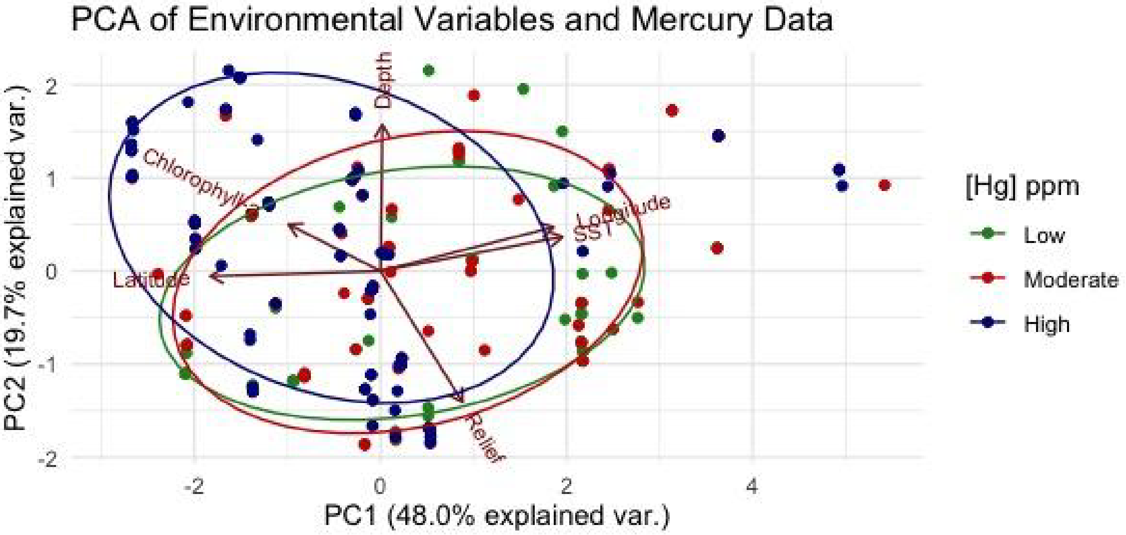
Linear Regressions of (A) PC1 and (B) PC2 Based on the Canary rockfish Biological Variables. There is a Best Fit Line (Blue Line) with Gray Shading Surrounding the Line Representing the 95% Confidence Interval of the Regression Line



by depth and negatively by relief displaying 19.7% of dataset variance. PC1 and PC2 are equally represented by chlorophyll-a, and overall the first two PC axes explain 67.7% of the variance in the environmental variables. There is a large degree of overlap between the low, moderate, and high ellipses of [Hg] ppm suggesting environmental variables do the poorest job at differentiating total mercury concentrations amongst individuals.

Figure 25

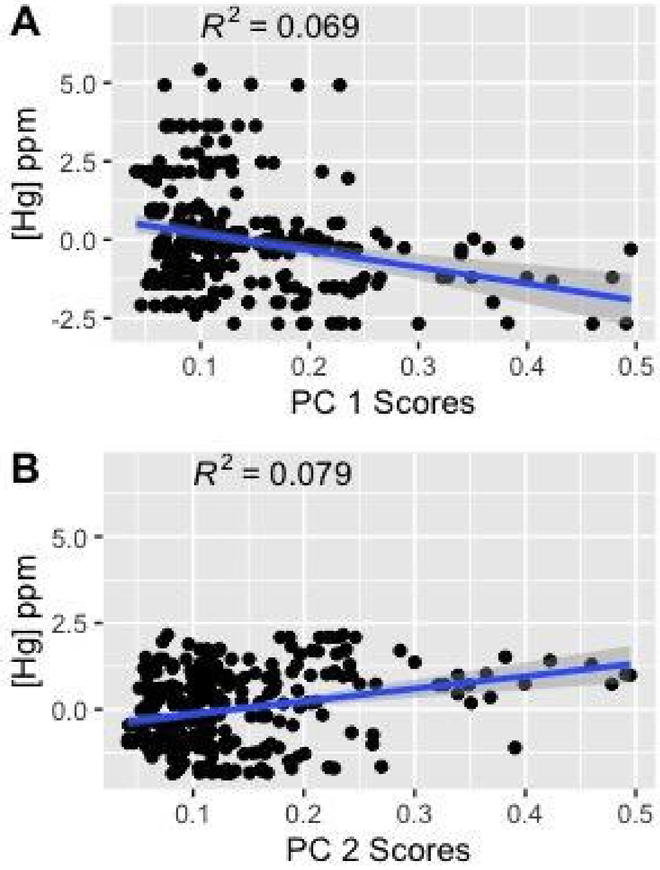
PCA Visualization of Environmental Variables: Relief, SST, Longitude, Depth, Chlorophyll-a, and Latitude Grouped by Total Mercury Concentrations. PC1 Explains 48.0% and PC2 Describes 19.7% of the Variance. Ellipses Represent 95% Confidence Intervals for Total [Hg] ppm. Each of the Red Arrows Represents the Eigenvector for all of the Individual Variables Tested



Both PC1 (Figure 26A) and PC2 (Figure 26B) were significantly associated with mercury levels. However, both of the R^2 values (PC1 = 0.069, PC2 = 0.079) are fairly weak and suggest, despite being significant, the PC axes are not great estimators of [Hg] ppm. PC1 is correlated positively with longitude and SST and negatively with latitude, suggesting individuals in warmer areas and lower latitudes typically have lower [Hg] ppm values. This is consistent with the latitudinal trends witnessed in Figure 13. PC2 is positively correlated with depth and negatively with relief, therefore individuals caught at deeper depths and higher relief tended to have higher total mercury concentrations.

Figure 26

Linear Regressions of PC1 and PC2 Values for Each Individual Based on the Environmental Variables. The Best Fit Line Was Plotted (Blue Line) with Gray Shading Surrounding the Line Representing the 95% Confidence Interval of the Regression Line



Discussion

Stomach Contents

This study aimed to describe the environmental and biological factors contributing to variability in the trophic ecology and total mercury concentrations of Canary rockfish within the CCS. This was accomplished through stomach content, stable isotope, and mercury concentration analyses. The combination of stomach content and stable isotope analyses helped to eliminate spatiotemporal biases that appear when only utilizing one of these strategies. When analyzing stomach contents, both abundance and weight were used to eliminate any bias brought about by numerical analysis. Prey items with high %N are typically smaller organisms that are capable of fitting more individuals within a stomach without weighing too much in total. Whereas prey items with high %W are typically larger organisms that take up more room within stomachs, but cannot fit many individuals. These are both great indicators of dietary preferences and neither one should be used individually to characterize a diet. For example, a larger teleost can satiate an individual likely for longer than hundreds of krill, but these have drastically different numbers when it comes to abundance. This is likely why %W was the best choice for determining variance with the multivariate statistical models because it normalizes the contributions of individuals within a diet based on overall weight in a stomach. There were 27 prey items found within the stomach contents, which, at a first glance, would indicate that Canary rockfish consume a generalistic diet (Table 2). However, the extremely high reliance on krill (by number) and teleost fishes (by weight) would suggest Canary rockfish are specialists at the individual level, but appear to be generalists at the population level (Table 3 and Figure 6). The specialization on specific prey items amongst individuals was particularly influenced by location, including spatial factors such as latitude, longitude, chlorophyll-a, depth, and relief.

Gerking (2013) defines individuals who specialize on specific prey items as a function of their environmental and spatial location as opportunists. However, given the extremely high reliance on krill and teleosts amongst all individuals and locations (Figure 5), Canary rockfish appear to be specialists. Prior research contains conflicting results with Brodeur et al. (1987) characterizing rockfish as specialists and Love et al. (2002) characterizing them as both generalists and opportunists. Generally, specialists are more common when the base of the food web is diverse and with abundant prey resources, while generalists are more common when resources are scarce. Given the productive nature of the CCS, it is therefore assumed, based on this study, that Canary rockfish are generalists. Both Brodeur et al. (1987) and Love et al. (2002) indicate similar important prey items for Canary rockfish, including: teleosts, krill, crabs, amphipods, and copepods, as found in this study, confirming the similarity in diets despite difference in proportions. The proportion at which stomach contents were found in this study, indicates variability depending on the location sampled.

Canary rockfish diets were more influenced by environmental variables such as regional location, and the differences associated with changes in latitude (Table 4). Changes in latitude can alter the habitat type, or partition individuals of a specific life history stage towards a particular region. For example, a study of ringed seals in the Arctic reported more adults consuming more forage fish and having higher TLs than juveniles and subadults at lower latitudes (Yurkowski, Ferguson, Choy, et al., 2016). Species such as California Sheephead exhibit geographic variation in their diet due to intraspecific competition and proximity to MPAs (Hamilton et al., 2011). Similarly, Gopher rockfish also display dietary differences due to competition, latitude, and depth, causing shifts in the abundance of key prey items (Loury, 2011). Gerking (2013) relates changes in dietary specialization and prey abundance to periods of increased prey competition caused by environmental changes that impact prey item abundance.

This study detected different prey proportions in Canary rockfish across ports spanning 937 km along the West Coast of the United States. Squid and unknown decapod prey groups appeared to drive the most dissimilarity among individuals (Figure 4), while differences in proportions of the common prey groups, like krill and teleosts, fluctuated along the coast (Figure 5B). Specifically, the diets of fish from the northern Vancouver and Columbia regions contained higher proportions of shrimp, crabs, and other decapod crustaceans (Figure 5A). Therefore, individuals in these northern regions are consuming higher proportions of benthic prey items which may be a function of the biodiverse food web in the regions, or the increased presence of these prey items in these areas. Squid were found in the highest proportion in the southernmost Conception region and were not a common prey item in the remainder of the regions (Figure 5A). This is likely because the squid fishery is largest in Southern California, with the commercial fishery being established in Monterey Bay 130 years ago, and expanding to the South (Vojkovich, 1998). Fort Bragg had a very large proportion of pyrosomes which are only found, if at all, in small amounts amongst the other ports (Figure 5B). Similarly, isopods were found in a large proportion in diets of fish near Moss Landing, but not at other ports (Figure 5B). Copepods were only found in notable proportions at Westport (Figure 5B), further highlighting the idea that specific prey items appear to be regionally important, but not to the diet of the Canary rockfish as a whole. Lastly, krill was also the most common and teleosts the least common in the Eureka region (Figure 5A), suggesting that krill were easily and highly accessible in this region. The degree of competition is outside the scope of this study but could be another possible explanation in the patterns of prey in the stomach contents. More likely, the higher abundances of prey items at a specific region or port, is likely a function of their increased abundances in those areas.

The Conception region encompasses the Southern California Bight which is known to have differing oceanic conditions relative to the rest of the CCS due to the northerly flowing Southern California Countercurrent (Hickey, 1979). Brodeur et al. (1987) identified the importance of certain prey items in diets of rockfish changed throughout the years sampled, depending on ENSO cycles in the CCS and the seasons in which individuals were sampled. Higher temperatures have consistently been found to increase the metabolic requirements of fish and influence prey acquisition within a species across broad geographical distributions (Behrens & Lafferty, 2012; Bethea et al., 2007). This is usually caused by higher temperatures influencing the types of animals that can reside within those temperatures, and therefore shift the proportion of prey items found within predator stomachs. Alternatively, this could also be represented as a predatory behavioral change in which predators consume more nutrient dense prey items to satiate their increased metabolic rates as a result of the change in temperature.

In this study, the Conception region has the highest density of krill in the diet (Figure 5A), and the highest overall SST (Figure 9B), compared to the other regions. Therefore, this most southern region that is characteristic of higher temperatures due to the Southern California Countercurrent could be better able to support krill larvae, resulting in higher proportions found in the Canary rockfish diets. Brodeur et al. (1987) also observed regional differences in the diets of rockfish along the CCS where environmental factors such as proximity to rivers, like the Columbia River in Washington, influenced a higher presence of euphausiids and decapod larvae in stomach contents. In this study, there were higher proportions of crustaceans (i.e., shrimps, crabs, and decapods) found in the Vancouver and Columbia regions (Figure 5A). These two regions house major river runoffs such as the Puget Sound and Columbia River, thus decapods may be able to flourish in larger abundances in the nearshore waters of these regions, causing the increased presence in the diets of Canary rockfish. Therefore, proximity to juvenile rearing or birthing areas can influence the types and proportions of prey found within predator stomachs.

Depth has also been shown to influence trophic ecology as prey availability and composition change with depth as different depths can alter the productivity, temperature, nutrient concentrations, light availability, and habitat type suitable for different types of organisms (Basnett, 2021; Bulman & Koslow, 1992). Depth was a driving difference witnessed in the diets of individuals residing in the Columbia and Conception regions (Figure 7A). A majority of the individuals caught at the deepest depths were caught within the Columbia region which could be driving this pattern. Whether that be because the depth of the continental shelf and rocky reefs in this area are deeper compared to the others, or that individuals actually reside deeper in this region is outside the scope of this study. Individuals within the Columbia region outweigh individuals in the Conception region in terms of the amount of samples found at deeper depths. However, Conception has a much smaller sample size than Columbia (Table 1) and although not as many individuals are found at depth compared to the Columbia region, a larger majority of those in Conception were found at depth. Columbia and Conception contain the highest proportion of teleosts (Figure 5A), thus individuals within these regions are residing in deeper depths and consuming higher weights of teleosts. Rockfish tend to aggregate in deeper depths as they mature, grow, and get older, therefore this life history change, and changes to dietary preferences as a function of depth, could be a function of ontogenetic development (Love et al., 2002). This could explain the increased presence of teleosts, higher TL, and harder to forage for prey items in their diet and would suggest that more mature or older rockfish are living in these deeper depths, and even perhaps in higher densities in the Columbia and Conception management regions. This is similar to the findings of Yurkowski, Ferguson, Choy, et al. (2016) which found that adults and subadults of ringed seals occupied different spatial areas of the arctic and consequently consumed more teleosts as they matured. Brodeur et al. (1987) did not indicate differences in diet based on biological factors and instead presented evidence for the environmental impact on diet, but discusses that this can change based on the species within Sebastes. This could possibly indicate how changes in environmental conditions impact the abundance of prey items in Canary rockfish diets, leading to IS.

Male and female diets did not differ drastically in proportion, however the sexes amongst each management region differed to their counterparts in other regions. For example, females consumed greater amounts of teleosts in Columbia, Monterey, and Conception and males consumed more teleosts in Columbia and Conception (Figure 3). Further, females and males consumed higher proportions of krill in Eureka, Monterey, and Conception (Figure 3). Shrimps and crabs also appear to decrease in proportion with decreases in latitudes in the more southern regions (Figure 3). These trends witnessed between the sexes and teleosts, shrimp, crab, and krill, also follow the same trends discussed across management regions. Thus, these differences can be argued to be an environmental effect on IS between the regions, and not a biological effect of the sexes. Although not significant, there was a slight difference between immature and mature fish diets, with mature fish consuming more teleosts and krill than their immature counterparts (Figure 5C). Similar again to the findings of Yurkowski, Ferguson, Choy, et al. (2016) in which adult ringed seals consumed higher proportions of Pacific cod than the subadults. Canary rockfish diets did not differ strongly in response to body size (Table 5) or sex (Figure 5D) which is contrary to many fish trophic ecology studies. For example, Kingsford (1992) reported differences in the size of prey consumed by the Leopard coral grouper with changes in ontogenetic development; larger and older fish consumed larger prey items than that of their younger and smaller counterparts. This is a difficult claim to make in this study, as most of the stomach contents had been partially digested upon dissection, therefore it is difficult to claim a difference in prey size. Qamar et al. (2015) displayed sexual dietary preferences of the Torpedo Trevally, with males consuming higher rates of shrimp and females consuming more fish. This may not be the case here as the biological differences between male and female Canary rockfish are not distinct enough to warrant dietary changes. Length and weight were analyzed in this study to test their effect on diet, but neither of these were significant in displaying variability in Canary rockfish diets (Table 5). Considering the data presented in this study, Canary rockfish are specialists (despite a numerous amount of prey items found) with dietary differences mainly driven by spatial and temporal changes in environmental conditions.

Stable Isotopes

This study found variation in the isotopic and calculated TLs of Canary rockfish in the CCS with a 3.7‰ range in δ^{13}C, 3.2‰ range of δ^{15}N, and 0.99 range in calculated TL (Table 8 and 10). Although there was range in this study, the mean values calculated by region did display significant overlap (Table 8). Thus, at the individual level isotopes can range, but when averaged at a population level there does not appear to be significant differences. Two previous studies that have reported the isotopic signature of Canary rockfish. Bosley et al. (2014) evaluated multiple rockfish species across several years and found that interspecific variation in isotopic signatures, specifically δ^{13}C, can fluctuate yearly. The more negative or larger the values of δ^{13}C in this study are indicative of prey sources from pelagic primary production pathways, and the less negative or smaller values of δ^{13}C are indicative of prey sources from neritic or benthic primary production pathways. However, Bosley et al. (2014) reported on average smaller δ^{15}N values and larger δ^{13}C values for Canary rockfish muscle tissues in both 2002 and 2006. Thus, the samples collected in this study, taken in 2017 and 2018, were likely consuming higher TL organisms and organisms from pelagic and offshore primary production pathways (i.e., teleosts) compared to those sampled in Bosley et al. δ^{13}C variation was more influenced by environmental factors such as depth, relief, chlorophyll-a, temperature, and latitude, but also by sexual maturity and HSI (Table 9). Gao et al. (2013) similarly described variation in δ^{13}C values (-5.4‰ to - 1.4‰) and noted a clear distinction between juvenile and adult values, which was also found in this study. This would indicate a significant ontogenetic shift in resource allocation from nearshore to pelagic productivity, likely explaining why sexual maturity was significantly correlated with δ^{13}C (Table 9 and Figure 8B). Juveniles have less energy expenditure compared to adults as they have higher metabolic and growth rates than their adult counterparts, thus the significance of HSI could also be a function of sexual maturity (Table 9). Jonsson and Jonsson (1993) claim that sexual maturation of fish usually occurs as somatic growth plateaus, occurring when energetic cost of maintenance is equal to energetic intake. Thus, HSI would begin to increase towards the beginning of sexual maturity. I observed a weak negative association between body size and δ^{13}C values (Table 9), with larger fish relying more on offshore sources of primary production, such as teleosts or other pelagic prey items. Despite these relationships, the variation in δ^{13}C was also highly dependent on environmental factors. Individuals in environments characteristic of shallower depths, higher latitudes, higher relief, higher primary productivity, and higher temperatures consumed prey items indicative of pelagic and offshore production (Table 9). Similar relationships between δ^{13}C in fish tissues and temperature have been reported by Sweeting et al. (2007), who attributed this positive association to metabolic and respiration rate changes with increases in temperature. Opposingly, Hirons et al. (2001) reported a negative relationship with productivity and δ^{13}C, attributing this relationship to decreased phytoplankton growth rates, thus it is interesting to see the opposite in this study. This would suggest that individuals consuming more pelagic prey are living in environments with higher productivity (possibly at higher latitudes) and thus there is a biological effect causing these environmental relationships. Depth, in this study could be used as a proxy for distance to shore, therefore the negative relationship with

$\boldsymbol{\delta}^{13}$C (Table 9 and Figure 8A) appears counterintuitive as those that live deeper and further offshore, should be consuming more pelagic prey than benthic or nearshore prey. These results would suggest the opposite of Love et al. (2002) that mature adults that tend to consume higher rates of teleosts and pelagic prey are actually residing closer to shore. It is also possible that there is a specific prey item, such as krill, that is high in abundance yet nearshore in distribution, that could be altering the relationship between depth and $\boldsymbol{\delta}^{13}$C. Gao et al. (2013) reported different values for $\boldsymbol{\delta}^{13}$C, but they utilized otolith bones for their isotopic analysis and therefore the comparison between studies may be inaccurate as Caut et al. (2009) claims there are significant differences among tissue types for $\boldsymbol{\delta}^{13}$C and $\boldsymbol{\delta}^{15}$N values.

$\boldsymbol{\delta}^{15}$N is used as a proxy for TL as it fractionates and increases a steady 3-4% per TL thus allowing it to be used as a proxy for TL (Post, 2002). $\boldsymbol{\delta}^{15}$N values have not yet been reported for Canary rockfish in the CCS, but considering trends in the literature it was expected $\boldsymbol{\delta}^{15}$N would vary based on biological traits. In this study, only environmental factors were significant in representing the variance of $\boldsymbol{\delta}^{15}$N, with individuals feeding within higher temperatures, higher productivity, and higher latitude environments possessing higher $\boldsymbol{\delta}^{15}$N values (Table 9). The positive relationship between $\boldsymbol{\delta}^{15}$N and chlorophyll-a (Table 9) could be explained by productive areas producing a more complex food web allowing for higher abundances of prey items available at higher TLs. This could also be explained by a baseline shift in plankton $\boldsymbol{\delta}^{15}$N values, but there is no published literature during this study's time period to confirm or deny the shift in baseline plankton $\boldsymbol{\delta}^{15}$N values. However, Ohman et al. (2012) has found some spatiotemporal differences in zooplankton $\boldsymbol{\delta}^{15}$N values in the past, with elevated $\boldsymbol{\delta}^{15}$N values in southern regions of the CCS and during periods of El Niño. The authors attributed this shift to changes in the average nitrate concentration in the mixed layer, suggesting varied nitrate utilization at the base of the food web. This could also explain why this study found a positive correlation between $\boldsymbol{\delta}^{15}$N and temperature (Table 9) as El Niño is characteristic of elevated temperatures and altered nitrate concentrations in the CCS. Opposingly, Hilton et al. (2006) reported a strong relationship between long term declines in $\boldsymbol{\delta}^{15}$N values for Rockhopper penguins and rising SSTs. They attributed this to a shift in diet towards lower TL prey items over time in warmer years, but given this occurred in a different oceanic environment, it appears organisms in the CCS possess higher $\boldsymbol{\delta}^{15}$N values in warmer years. Yurkowski, Ferguson, Choy, et al. (2016) reported decreases in TL (proxy for $\boldsymbol{\delta}^{15}$N) in Arctic ringed seals with decreases in latitude, attributing this to the greater complexity in trophic structure within the zooplankton communities in more northern latitudes. Likewise, Frederiksen et al. (2006) reported changes in productivity resulted in enhanced planktonic communities which in turn increased the abundance of their fish and mammal predators (i.e., sandeel and marine birds) and further increased the size of the stocks due to the cascading effects of increased productivity into increased plankton abundance. Thus, high chlorophyll-a environments may be home to higher TL organisms due to an enhanced base of the food web. Bosley et al. (2014) reported rockfish $\boldsymbol{\delta}^{15}$N values were not significantly related to any of the prey items found within the diet, but the fluctuations followed similar isotopic trends of zooplankton witnessed in the CCS in the same time period. Therefore, the fluctuating environmental conditions such as productivity, temperature, and nutrients possessed isotopic effects on the plankton at the base of the food web which could have had a cascading bottom-up effect on the remainder of the food web, with a more minimal effect from specific dietary choices.

The CCS system does not follow common oceanographic latitudinal trends in temperature and productivity (Checkley & Barth, 2009; Chelton et al., 1982; Hickey, 1979), therefore higher latitudes are not always conducive to more productive or lower temperature environments than their lower latitudinal counterparts (Figure 9). The CCS is unique because specific locations along the coast are more susceptible to seasonal and decadal upwelling and productivity blooms. This is caused by the localized seasonal upwelling driven by the spring high pressure system off of the coast, and the larger scale upwelling suppressed by El Niño events and enhanced by El Niña events (in the CCS). In most oceanic systems, there is an increase in SST from North to South and an increase in chlorophyll-a from South to North (Bergmann, 1847). However, the CCS is located on an eastern boundary current and is susceptible to upwellings and changes in ENSO cycles. With chlorophyll-a and temperature being significantly related to many of the isotopic and TL calculations (Table 9), it is important to represent how these factors fluctuate throughout the sample system. In terms of SST, there is a significant break in between the ports of southern and more central/northern latitudes separating Half Moon Bay, Moss Landing, Morro Bay, and Santa Barbara from the other more closely grouped ports of Washington, Oregon, and Northern California (Figure 8B). This is likely because of the influence of the warmer northerly Southern California Countercurrent than the colder southerly California Current (Hickey, 1979). This is also affected by the geological structure of the coast, as Point Conception is the limit for this Southernly California Countercurrent. Thus, these ports within the Monterey and Conception regions are generally warmer, and similar to the reports of δ^{15}N in Ohman et al. (2012), these southernmost regions are home to higher δ^{15}N values. Other than that, there is no real latitudinal trend in terms of SST or chlorophyll-a as values from Neah Bay to Bodega Bay are not consistent with their latitudinal order (Figure 8). Thus, although chlorophyll-a and temperature are significantly related to δ^{13}C and δ^{15}N (Table 9), it is difficult to discern latitudinal trends with these factors. This may also be a factor of the 10-year average utilized in this study to retrieve average chlorophyll-a and SST values at each of the ports.

TL is an estimate based on a predetermined isotopic value (Ebert & Bizzarro, 2007) and the proportion of prey items found in individual stomachs (Cortés, 1999). Relief, temperature, and length were significant in describing variance in TL (Table 9). Despite this, there were no strong trends witnessed between TL and relief. Given than δ^{15}N, a proxy for TL, was also positively related to temperature (Table 9), SST appears to have both a long term effect on isotopic signatures, as reported in Ohman et al. (2012), as well as a short term influence on the prey items consumed, as reported in Hilton et al. (2006). TL increased with increasing length, which is likely associated with sexual maturity and coincides with the increase seen in pelagic prey items in sexually mature fish (Table 9 and Figure 5C), likely to sustain their higher metabolic rate. For example, Hodum and Hobson (2000) analyzed petrel birds which also consume, for a majority of their diets, krill and teleosts. They reported individuals with higher δ^{15}N and therefore TLs, tended to consume higher proportion of fish than krill, similar to what I found in Canary rockfish. Given that rockfish tend to aggregate in more complex environments as they mature (and get larger) (Love et al., 2002), these relationships suggest that larger fish living in more complex environments tend to have larger TLs, as a consequence of consuming higher proportions of teleosts or other higher TL prey.

The size of the isotopic niche changed throughout the management regions measures, generally with the largest niches belonging to regions with the greatest number of samples, and the lowest niches in regions with the least amount of samples (Figure 11 and Table 10). This could simply be a bias from the coding software used, SIBER in R, as this has been cited to be a potential problem in the past (Jackson et al., 2011). However, I ran the code with and without 999 permutations and the difference between results was minimal suggesting this is not a present bias in the study. When analyzing latitude, although it is not perfect, there is a slight decrease in variability in both nitrogen and CRs from north to south, with Vancouver being an anomaly (Table 10). Columbia appears to be the region with the most diverse stomach contents, and the most even in terms of proportionality of the eleven different prey items (Figure 5A). This could explain why both carbon and NRs are so high, as individuals within this region are consuming the most diverse diet, utilizing both offshore and nearshore primary production pathways, and consuming different TL prey. However, Vancouver as well possesses a fairly diverse diet and relatively even proportion of prey items, but contains the lowest amounts of CRs and NRs, as well as the smallest sample size. In terms of the decrease in niche ranges further South, there is more specialization of prey items in the Eureka, Monterey, and Conception regions, particularly a dominance of krill and teleosts, with less reliance on shrimp and crab (Figure 5A). Thus, possibly there may be a slight bias from the SIBER coding system, but the change in isotopic niches appears to be driven slightly by the choices in prey items as a function of latitude. However, since these are long-term (isotope) and short-term (stomach contents) measurements respectively, it is hard to draw definitive conclusions between the two, unless long term diet studies are conducted.

Mercury

In this study, total mercury concentrations were positively correlated with weight, length, longitude, and sexual maturity, and negatively correlated with Fulton's K (Table 12). Although latitude is a better proxy for region, it was not significant in this study. Longitude is relatively stable in the Vancouver, Columbia, and Eureka regions, and begins to decrease in the Monterey and Conception regions, thus also displays latitudinal/regional trends. This is because the coastline in the northern latitudes of Washington, Oregon, and even Northern California (Vancouver, Columbia, and Eureka management regions) are relatively stable and contain larger longitude values. Whereas, further down the coast in Central and Southern California (Monterey and Conception management regions), these lower latitudes have longitude values that begin to decrease due to the structure of the coast. Therefore, increase in longitude, or more northern latitudes, corresponded to higher median total mercury concentrations. Despite this, the mean values (Table 11) are not as consistent as the median values (Figure 13) as there are lower mean total mercury concentration values in the Eureka region and higher in the Monterey region. Opposingly, Davis et al. (2016) reported mercury was generally lower in mid-trophic level fish from higher latitudes than in the lower parts of the CCS, but did not display complete latitudinal correlation. Additionally, there is more variance in total mercury concentrations in these northern latitudes which decreases with decreasing latitudes (Figure 13). Davis et al. (2016) indicated specific hot spots along the coast (i.e., Northern California Coast, Puget Sound, and San Francisco Bay) that did not follow this latitudinal trend, but instead coincided with areas close to estuaries or river mouth entries, historically influenced by mining or other anthropogenic activity, and found lower concentrations along the coasts of Oregon and the outer coasts of Washington. These proximity to these fresh water sources may impact the variability in these Northern latitudes as they are home to major estuaries such as the Puget Sound and Columbia River watershed. Páez et al. (2022) documented anthropogenic effects in the nearshore environment can be a major cause contributing to variation in mercury concentrations in fish. These authors analyzed three fish species in Baja California, Mexico with different proximities to human dumping sites. They attributed the main differences in mercury concentrations was proximal location to mercury contamination with fish found closer to these sites containing elevated mercury concentrations. Proximity to a large river mouth, mining site, or factory site could be directly polluting regional waters and biomagnifying through the local food webs, allowing for fish to contain anomalous mercury concentration values regardless of their biological traits or dietary behaviors. Canary rockfish are coastally associated, and species living closer to shore typically contain higher concentrations of mercury compared to those that are more offshore (Greenfield & Jahn, 2010; Le Croizier et al., 2019). This could explain why longitude was positively correlated to total mercury concentrations (Table 12), but given the dynamic and broad coastline of this study, longitude is difficult to associate with proximity to shore. However, depth is negatively associated with total mercury concentrations (Table 12), and this combination of factors would suggest that those living closer to shore have elevated total mercury concentrations. Nearshore areas are more conducive to biological production and low oxygen which favors bacterially mediated mercury methylation (Fitzgerald et al., 1991; Kim & Fitzgerald, 1986) and the sources of mercury typically come from terrestrial weathering, erosion, mining, or volcanic activity runoff (Driscoll et al., 2013; Hudson et al., 1995; Lamborg et al., 1999; Pirrone et al., 1996). Davis et al. (2016) and Zhang et al. (2020) suggest the idea that certain areas may be upwelling mercury closer to the coast and therefore this upwelling, enhanced productivity, and lower oxygen levels could contribute to higher organic mercury concentrations. Similarly, Médieu et al. (2022) reported mercury concentration differences in Pacific Skipjack Tuna could be explained by the depth of the sweater methylmercury peak near low-oxygen zones, causing increased mercury concentrations in regions where oxygen depletion is shallow. This hypothesis contradicts other findings in the literature that detail areas of high productivity as a mechanism for biodiluting mercury concentrations that are transferred to higher TLs (Lavoie et al., 2013). My study suggests that total mercury concentrations are higher in fish living closer to shore and in northern latitudes or areas close to freshwater inputs.

Davis et al. (2016) indicated similar mercury concentration values of some *Sebastidae* species (despite not reporting specifically on Canary rockfish), and even higher values for certain species like Copper rockfish with values over 1.0 ppm. Also similar to the findings of this study, Davis et al. (2016) found larger individuals within a species tended to have higher mercury concentrations, with some of the residual variance in this measure being accounted for by TL (supplied by Fishbase.org) and growth rate. For example, they reported Blue and Gopher rockfish had similar age and sizes, but Gopher rockfish had a higher TL and larger average mercury concentrations. Similarly, Copper and Black rockfish possessed relatively the same TLs and sizes, but Copper rockfish exhibited a much slower growth rate and higher mercury concentrations. This could explain why, in this study, Fulton's K was negatively associated with total mercury concentrations (Table 12), as fish with smaller energy reserves, and thus less capacity to use energy for growth (slower growth rate), contained higher total mercury concentrations. This may be because less energy for growth and less growth overall coincides with less tissue density, and if mercury accumulates over time, mercury would accumulate in denser and thus higher proportions in fish with slower growth rates. Additionally, this could be a function of a transition to sexual maturity as somatic growth plateaus during the onset of sexual maturation (Jonsson & Jonsson, 1993). Therefore, these sexually mature fish with decreased growth rates have had more time to accumulate mercury as opposed to sexually immature individuals. Length and weight are also correlated with maturity (Table 12). In this study, longer, heavier, and sexually mature fish possessed higher total mercury concentrations. This coincides with many studies in the literature that indicated larger (Barber et al., 1972; Beckett & Freeman, 1974) and older fish (Burger & Gochfeld, 2007) possess higher concentrations of mercury in their tissues.

Larger and heavier fish containing elevated total mercury concentrations is important when thinking about human health and current fisheries management plans as Canary rockfish are only limited in catch by their size and overall tonnage based on IFQs on a yearly basis. This is a common fisheries management plan as it disallows the taking of smaller individuals as a mechanism for allowing fish to reach a reproductive age, before removing them from the stock/population. Despite this being an effective strategy in ensuring sustainability of the stock, it also promotes the selective harvesting of larger, heavier, and older fish typically containing higher concentrations of mercury. This study highlights how mid-trophic level fish have often been ignored as possessing potentially harmful mercury concentrations to human health. Samples in this study contained up to 0.5 ppm of mercury, which is high for a mid-trophic level fish and actually advised by the State of California for children and pregnant women to not consume. The FDA legal action limit related to commercial fishing is 1.0 ppm of mercury which is twice the limit of most other countries. Most of their recommended consumption parameters will be of fish much lower than 1.0 ppm. Given the findings of Davis et al. (2016) in which Copper rockfish and species in the CCS have levels of mercury approaching, or above this legal limit for mercury, something may need to be done about the management of high mercury fish in the CCS. This may be a more persistent problem in a species like rockfish given they are long-lived and can accumulate mercury for long periods of time before they are caught and consumed (Power et al., 2002). The results of this study can help determine the severity of a health threat this commercial and recreational fishery can be in this region. However, further research is necessary concerning mercury concentrations of other rockfish species in this area, and if these mercury concentrations are increasing through time and space.

Relationships Between Trophic Ecology and Mercury

This study is innovative because it synthesizes relationships between stomach contents/prey items, stable isotopes, and total mercury concentrations for a singular species over a broad geographical range. Teleosts and krill are the most important prey items (by abundance and weight) (Table 3 and Figure 6) and contribute to describing variance in total mercury concentrations and isotopic values. Within individuals, those with higher total mercury concentrations possess larger %W values of teleosts within their stomachs (Figure 16). This is likely because teleosts are the prey items with the highest average TL, therefore are conducive to accumulating higher total mercury concentrations compared to species lower in the food web. $\boldsymbol{\delta}^{15}$N also has a positive relationship with total mercury concentrations, where individuals of higher TLs contain elevated total mercury concentrations (Table 13 and Figure 20B and 21). Similarly, Kidd et al. (1995) reported log Hg as significantly positively related to $\boldsymbol{\delta}^{15}$N in yellow perch, northern pike, lake cisco, and lake trout, and found this was driven by their prey choices. Additionally, Yoshino et al. (2020) reported as significant relationship between mercury and $\boldsymbol{\delta}^{15}$N, and went further to display this was a function of feeding in food webs with lower $\boldsymbol{\delta}^{13}$C values (benthic/nearshore production). Polito et al. (2016) reported penguins consuming higher rates of mesopelagic prey (i.e., fish) as opposed to epipelagic or benthic prey (i.e., crustaceans, krill, or decapods) contained higher concentrations of mercury due the increased biomagnification of mercury in the pelagic food web. Likewise, Loseto et al. (2008) reported higher concentrations of mercury in Beluga whales that lived near epibenthic food webs and the pelagic Amundsen Gulf, and lower concentrations in those that lived in the nearshore estuarine shelf. These are similar to the findings of this study and Davis et al. (2016) which reports higher mercury concentrations in nearshore environments. Krill consumption was negatively associated with $\boldsymbol{\delta}^{15}$N (Table 13 and Figure 18A), suggesting there are lesser amounts of krill found in the stomachs of higher TL fish. Assuming individuals with a higher $\boldsymbol{\delta}^{15}$N are typically older and larger, it is likely Canary rockfish consume more teleosts and less krill as they mature, resulting in higher total mercury concentrations from consumption of higher TL prey. However, this study displayed that mature individuals eat both more teleosts and krill as they age and less shrimp and crab (Figure 5C). Thus shrimp and crab are likely driving this trend, not the krill. Dutton and Fisher (2011) have reported IS on prey items (i.e., amphipods or worms) can significantly affect the concentrations of mercury in fish, similar to what is shown in this study. Therefore, it seems as though dietary choices are a function of foraging strategy, habitat, and maturity level resulting in discrepancies in total mercury concentrations slightly dependent on both biological traits and oceanographic conditions.

Shrimp, crabs, and teleosts were significant prey items in describing variance witnessed in $\boldsymbol{\delta}^{13}$C values, with shrimp and crabs representing prey items of more nearshore and benthic carbon sources and teleosts representing prey items associated with the offshore pelagic realm (Table 13 and Figure 17). Despite this, these values do not follow a distinct trend as all of the $\boldsymbol{\delta}^{13}$C values peak in the moderate %W prey item bin, with the low and high bins containing similar mean $\boldsymbol{\delta}^{13}$C values (Figure 17). This makes it hard to discern any significant relationships between $\boldsymbol{\delta}^{13}$C and prey items, potentially because Canary rockfish generally live nearshore, with their deepest depths being recorded at 838 meters (Love et al., 2002), thus the variability in offshore versus nearshore carbon pathways are not too apparent in their diets. There is a significant relationship between $\boldsymbol{\delta}^{13}$C and total mercury concentrations (Table 13), such that individuals with greater average total mercury concentrations source prey items from more pelagic and offshore areas (i.e., more negative $\boldsymbol{\delta}^{13}$C levels). However, this relationship is relatively weak ($R^2 = 0.05$, Figure 20A), thus the effect of food choices on a long-term isotopic analysis and short term prey identification don't appear to have drastic effects on mercury. $\boldsymbol{\delta}^{13}$C values are higher in the northern regions (Figure 10B), and total mercury concentrations in these regions were also higher than their southern counterparts (Figure 13), likely as a function of a more complex food web allowing for Canary rockfish to consume higher TL prey.

Krill and teleosts abundance in the diet of Canary rockfish are significantly correlated with $\boldsymbol{\delta}^{15}$N values (Table 13). Krill %W values decreased with increasing $\boldsymbol{\delta}^{15}$N values, thus individuals with higher $\boldsymbol{\delta}^{15}$N values were less likely to consume large amounts of krill (Figure 18A). However, teleosts were consumed in nearly the same proportion between low and high $\boldsymbol{\delta}^{15}$N fish (Figure 18C), but sexually mature fish consumed more teleosts than sexually immature fish (Figure 5C) and teleosts increased in abundance with increased TL (Figure 19C). This could be explained by possible bias of the TL calculation, which only takes into account the specific prey items identified in the stomach at that one point in time. Whereas, an isotopic measurement such as $\boldsymbol{\delta}^{15}$N, accumulates over months to years and is not as easily influenced by singular items. This illustrates why my study employed both of these measurements as a means of identifying and correcting for bias in dietary information. Another possible bias is that teleosts and krill are the most abundant prey items by weight and number in this study, and found in much higher amounts than the other prey items (Figure 6). Teleosts and krill are often significant prey items when analyzing the GLMs (Table 13) which may be because they contain the most data points across the dataset, and the dataset itself contains lots of zero values, not because they display linear or distinct trends in the dataset. Despite this, given that teleosts' presence, TL, and $\boldsymbol{\delta}^{15}$N drive the higher total mercury concentrations witnessed in the PCA (Figure 21), it would suggest that teleosts are consumed by higher TL individuals and are also conducive to having higher total mercury concentrations.

To synthesize the plethora of data points in this study, PCAs were conducted to draw relationships between all variables studied. These visualizations illustrate teleost consumption explains high concentrations of mercury, while crabs, shrimp, and copepods are common in individuals with lower to moderate mercury levels (Figure 21). It is important to note, that the first PCA containing prey and isotope data does not capture a lot of variance (23.3%), which is a function of the prey dataset containing many zero values. In comparison, the biological and environmental datasets do not contain many zero values and appear to capture a lot more of the dataset variance (70.1% and 67.7%, Figure 23 and 25).

The environmental PCA explained a lot of data variance indicating that these variables could possibly be used to estimate total mercury concentrations. Chlorophyll-a and depth appeared to differentiate these higher total mercury concentrations (Figure 23). This is likely because productive and nearshore environments cause higher rates of methylation due to lower oxygen levels in the water column, therefore allowing mercury bioaccumulation at higher rates in organisms (Fitzgerald et al., 1991; Kim & Fitzgerald, 1986). This would coincide with the study’s early findings in which temperature and chlorophyll-a, a function of latitude and longitude (also related to management region), were significant in describing total mercury concentrations (Table 12 and Figure 13) also similar to the findings of Davis et al. (2016). Therefore, these individuals with higher total mercury concentrations residing in more productive environments align with some of the literature (Zhang et al., 2020), despite other studies that claim total mercury concentrations are higher in cold and lower production environments (Lavoie et al., 2013). The biological PCA encompasses the highest percentage of dataset variance (Figure 23) and the strongest linear correlation between PCA1 and total mercury concentrations (Figure 24), thereby making it the best model for estimating total mercury concentrations in Canary rockfish. Length, weight, and GSI exhibited the strongest correlation with total mercury concentrations, indicating that larger and sexually mature individuals are more likely to have higher mercury levels, which are the individuals typically fished for and consumed by humans. If managers wanted to estimate individuals of high total mercury concentrations, based on this study, they should take measurements of length, weight, liver weight, gonad weight, latitude, longitude, and SST and would be able to estimate total mercury concentrations with high accuracy.

Canary rockfish appear to be an example of a population that appear to be generalists, but upon analyzing individuals, are a population made up of individual specialists (Bolnick et al., 2003; Rudolf & Lafferty, 2011). Bolnick et al. (2003) reported 29 species of fish (literature review analysis) display IS, either through distinct differences in isotopic values, or significant differences in the proportions of prey items found within their diets. It is pertinent to indicate differences at the species level, especially differences that translate into differential partition of resources, as species are typically managed under the assumption that they all behave similarly. Rockfish are a great example of this as their TLs, foraging strategies, and habitat use are quite different as a result of their adaptive radiation and extensive family. Davis et al. (2016) details the differences in TL of rockfish and how this affects their dietary preferences, where they feed in the water column, and habitat utilization. Those with higher TLs tend to feed on pelagic prey items and aggregate either in kelp beds or on rocky reefs bottoms, but it is quite variable without major distinctions across the family. If there are specific individuals or areas in the geographic range in which individuals behave differently or consume different resources, the stock may need to be managed in different ways. Given the push towards ecosystem-based fisheries management in the United States, the protection of resources in which a stock needs to survive (i.e., prey items) is considered to be an objective of protecting or managing a species or stock.

This study shows that these prey item choices can be indicative of isotopic signatures, biological traits, or environmental factors which all in turn affect the total mercury concentrations of their tissues. If these resources change throughout the range or development of a species, it is essential knowledge for managers to the efficiency of the management strategy, and for future ecological models. Considering there were individuals in this study with 0.5 ppm total mercury concentrations, even these mid-trophic level species, that were in the past considered to be relatively healthy to eat in large quantities, may become a threat to human health now and in the future. Mercury concentrations have been on the rise in marine fish since the early 1970s, with Barber et al. (1972) claiming that no fish in their studies, despite large tuna and billfish, were in excess of 0.5 ppm mercury wet weight (The FDA's legal action limit at the time). Thus, finding levels this high now in a species of a mid-trophic level, and with the FDA's legal action limit now at 1.0 ppm, mercury pollution and toxication could become worse in the future. Lower TL species were not a health concern during the 20th century, and are just recently beginning to build traction as a research priority within the mercury literature. This study highlights the importance of analyzing total mercury concentrations in all TL fish as a means of determining if there are species or areas of the ocean that should be avoided for human consumption.

Conclusions

This study details the trophic ecology and total mercury concentrations of Canary rockfish throughout a majority of its range through stomach content, stable isotope, and mercury concentration analysis. The data revealed the important prey items, to the Canary rockfish diet, their range in $\boldsymbol{\delta}^{13}$C and $\boldsymbol{\delta}^{15}$N, and displayed the concentrations of mercury found in dorsal muscle tissues. The analysis identified the biological and environmental factors that cause variance in these values contributing to the spatial, biological, and environmental differences of Canary rockfish throughout the CCS. Specifically, krill and teleosts are the most important prey items, deeming Canary rockfish as specialists. There were several other prey items identified which makes it possible to argue that Canary rockfish diets are determined by opportunity and environmental bottom-up effects on the food web. TLs are affected by chlorophyll-a, SST, and latitude, with individuals sourcing carbon from both pelagic and neritic sources, likely changing throughout their ontogenetic development. This may also be a function of switching habitats and environments throughout the Canary rockfish's life cycle. Total mercury concentrations are related to weight, length, ontogenetic development, SST, chlorophyll-a, and latitude and are best predicted by a mixture of both biological and environmental factors. There are likely hot spots of mercury pollution along the CCS that contribute to some individuals possessing higher total mercury concentrations than others, likely in areas that are susceptible to seasonal or decadal upwelling (La Niña in the CCS) or proximity to anthropogenic pollution or terrestrial weathering runoff sites. The data recorded in this study is important to identify when switching from single-species to ecosystem-based fisheries management as it allows managers to protect the energetic resources necessary for the Canary rockfish stock to perpetuate throughout its range. It is also vital to identify biological traits or environmental conditions conducive to altering the feeding behavior and metabolic processes of a species as it may require different management strategies. Finally, documenting mercury concentrations in all species that are commercially and recreationally consumed is important for informing the public of possible human health issues associated with eating certain types of seafood. Chronicling how mercury concentrations change throughout space and time will allow scientists and fishermen to fish and sell species that are not harmful to human health, or to advise a recommended amount of a species that is healthy to consume. Hopefully this data will inform ecosystem-based models with predator-prey interaction and dietary data to help forecast how ecosystems may change under the impacts of climate change or overfishing.

References

Alava, J. J., Cheung, W. W., Ross, P. S., & Sumaila, U. R. (2017). Climate change–contaminant interactions in marine food webs: Toward a conceptual framework. *Global Change Biology*, *23*(10), 3984-4001.

Alverson, D. L., Pruter, A. T., Ronholt, L. L., & Wilmovsky, N. J. (1964). *A study of demersal fishes and fisheries of the Northeastern Pacific Ocean*. Institute of Fisheries, University of British Columbia.

Andrews, K. S., Nichols, K. M., Elz, A., Tolimieri, N., Harvey, C. J., Pacunski, R., Lowry, D., Yamanaka, K. L., & Tonnes, D. M. (2018). Cooperative research sheds light on population structure and listing status of threatened and endangered rockfish species. *Conservation Genetics*, *19*(4), 865-878.

Barber, R. T., Vijayakumar, A., & Cross, F. A. (1972). Mercury concentrations in recent and ninety-year-old benthopelagic fish. *Science*, *178*(4061), 636-639.

Basnett, B. (2021). *Geographic and ontogenetic variation in the trophic ecology of lingcod (Ophiodon elongatus) along the US West Coast* [Master's thesis, San Jose State University/Moss Landing Marine Laboratories]. Digital Commons at CSUMB.

Bax, N. J. (1998). The significance and prediction of predation in marine fisheries. *ICES Journal of Marine Science*, *55*(6), 997-1030.

Beaudoin, C. P., Tonn, W. M., Prepas, E. E., & Wassenaar, L. I. (1999). Individual specialization and trophic adaptability of northern pike (*Esox lucius*): An isotope and dietary analysis. *Oecologia*, *120*(3), 386-396.

Beckett, J. S., & Freeman, H. C. (1974). Mercury in swordfish and other pelagic species from the Wester Atlantic Ocean. *National Oceanographic and Atmospheric Administration Technical Report NMFS SSRF*, *675*, 154-159.

Behrens, M. D., & Lafferty, K. D. (2012). Geographic variation in the diet of opaleye (*Girella nigricans*) with respect to temperature and habitat. *PLoS One, 7*(9), Article e45901. https://doi.org/10.1371/journal.pone.0045901

Bergmann, C. (1847). *Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*. Göttinger.

Bethea, D. M., Hale, L., Carlson, J. K., Cortés, E., Manire, C. A., & Gelsleichter, J. (2007). Geographic and ontogenetic variation in the diet and daily ration of the bonnethead shark, *Sphyrna tiburo*, from the eastern Gulf of Mexico. *Marine Biology*, *152*, 1009-1020.

Bloom, N. S. (1992). On the chemical form of mercury in edible fish and marine invertebrate tissue. *Canadian Journal of Fisheries and Aquatic Science*s, *49*(5), 1010-1017.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Volker, R.H.W., Schreiber, S.J., Urban, M.C., & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, *26*(4), 183-192.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1-28.

Bosley, K. L., Miller, T. W., Brodeur, R. D., Bosley, K. M., Van Gaest, A., & Elz, A. (2014). Feeding ecology of juvenile rockfishes off Oregon and Washington based on stomach content and stable isotope analyses. *Marine Biology*, *161*(10), 2381-2393.

Braune, B. M. (1987). Comparison of total mercury levels in relation to diet and molt for nine species of marine birds. *Archives of Environmental Contamination and Toxicology*, *16*, 217-224.

Brodeur, R. D., Lorz, H. V., & Pearcy, W. G. (1987). *Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979-1984*. National Marine Fisheries Service/National Oceanographic and Atmospheric Administration.

Bulman, C. M., & Koslow, J. A. (1992). Diet and food consumption of a deep-sea fish, orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae), off southeastern Australia. *Marine Ecology Progress Series. Oldendorf*, *82*(2), 115-129.

Burger, J., & Gochfeld, M. (2007). Risk to consumers from mercury in Pacific cod (*Gadus macrocephalus*) from the Aleutians: Fish age and size effects. *Environmental Research*, *105*(2), 276-284.

Caut, S., Angulo, E., & Courchamp, F. (2009). Variation in discrimination factors ($\boldsymbol{\delta}^{15}$N and $\boldsymbol{\delta}^{13}$C): The effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology*, *46*(2), 443-453.

Checkley, D. M., Jr., & Barth, J. A. (2009). Patterns and processes in the California Current System. *Progress in Oceanography*, *83*(1-4), 49-64.

Chelton, D. B., Bernal, P. A., & McGowan, J. A. (1982). Large-scale interannual physical and biological interaction in the California Current. *Journal of Marine Research*, *40*(4), 1095-1125.

Chen, C., Amirbahman, A., Fisher, N., Harding, G., Lamborg, C., Nacci, D., & Taylor, D. (2008). Methylmercury in marine ecosystems: Spatial patterns and processes of production, bioaccumulation, and biomagnification. *EcoHealth*, *5*(4), 399-408.

Chiba, T., & Sato, S. I. (2016). Climate-mediated changes in predator–prey interactions in the fossil record: a case study using shell-drilling gastropods from the Pleistocene Japan Sea. *Paleobiology*, *42*(2), 257-268.

Chiu, J. (2018). *Diets and stable isotope signatures of yellowtail rockfish (Sebastes flavidus) in Central California* [Master's thesis, San Jose State University/Moss Landing Marine Laboratories]. Digital Commons at CSUMB.

Conover, D. O., & Present, T. M. (1990). Countergradient variation in growth rate: Compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, *83*(3), 316-324.

Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science*, *56*(5), 707-717.

Davis, J. A., Ross, J. R. M., Bezalel, S., Sim, L., Bonnema, A., Ichikawa, G., Heim, W. A., Schiff, K., Eagles-Smith, C. A., & Ackerman, J. T. (2016). Hg concentrations in fish from coastal waters of California and Western North America. *Science of the Total Environment*, *568*, 1146-1156.

Di Lorenzo, M., Vizzini, S., Signa, G., Andolina, C., Palo, G. B., Gristina, M., Mazzoldi, C., & Colloca, F. (2020). Ontogenetic trophic segregation between two threatened smooth-hound sharks in the Central Mediterranean Sea. *Scientific Reports*, *10*(1), 1-15.

Driscoll, C. T., Mason, R. P., Chan, H. M., Jacob, D. J., & Pirrone, N. (2013). Mercury as a global pollutant: Sources, pathways, and effects. *Environmental Science & Technology*, *47*(10), 4967-4983.

Dutton, J., & Fisher, N. S. (2011). Bioaccumulation of As, Cd, Cr, Hg (II), and MeHg in killifish (*Fundulus heteroclitus*) from amphipod and worm prey. *Science of the Total Environment*, *409*(18), 3438-3447.

Ebert, D. A., & Bizzarro, J. J. (2007). Standardized diet compositions and trophic levels of skates (Chondrichthyes: Rajiformes: Rajoidei). *Biology of Skates*, *8*(2-3), 115-131.

Fitzgerald, W. F., Mason, R. P., & Vandal, G. M. (1991). Atmospheric cycling and air-water exchange of mercury over mid-continental lacustrine regions. *Water Air & Soil Pollution*, *56*(1), 745-767.

Flaherty, E. A., & Ben-David, M. (2010). Overlap and partitioning of the ecological and isotopic niches. *Oikos*, *119*(9), 1409-1416.

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, *75*(6), 1259-1268.

Fry, B. (1988). Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography*, *33*(5), 1182-1190.

Fu, C., Xu, Y., Guo, C., Olsen, N., Grüss, A., Liu, H., Barrier, N., Verley, P., & Shin, Y. J. (2020). The cumulative effects of fishing, plankton productivity, and marine mammal consumption in a marine ecosystem. *Frontiers in Marine Science*, *7*, Article 565699. https://doi.org/10.3389/fmars.2020.565699

Gao, Y., Svec, R. A., & Wallace, F. R. (2013). Isotopic signatures of otoliths and the stock structure of Canary rockfish along the Washington and Oregon coast. *Applied Geochemistry*, *32*, 70-75.

Gårdmark, A., & Huss, M. (2020). Individual variation and interactions explain food web responses to global warming. *Philosophical Transactions of the Royal Society B*, *375*(1814), Article 20190449. http://dx.doi.org/10.1098/rstb.2019.0449

Gerking, S. D. (2013). *Feeding ecology of fish.* Elsevier.

Gertseva, V., Matson, S. E., & Cope, J. (2017). Spatial growth variability in marine fish: Example from Northeast Pacific groundfish. *ICES Journal of Marine Science*, *74*(6), 1602-1613.

Gill, T. (1864). Critical remarks on the genera Sebastes and Sebastodes of Ayres. *Proceedings of the Academy of Natural Sciences of Philadelphia, 16*(3), 145-147.

Greenfield, B. K., & Jahn, A. (2010). Mercury in San Francisco bay forage fish. *Environmental Pollution*, *158*(8), 2716-2724.

Hamilton, S. L., Caselle, J. E., Lantz, C. A., Egloff, T. L., Kondo, E., Newsome, S. D., Loke-Smith, K., Pondella, D. J., II, Young, K. A., & Lowe, C. G. (2011). Extensive geographic and ontogenetic variation characterizes the trophic ecology of a temperate reef fish on southern California (USA) rocky reefs. *Marine Ecology Progress Series*, *429*, 227-244.

Hickey, B. M. (1979). The California current system—Hypotheses and facts. *Progress in Oceanography*, *8*(4), 191-279.

Hilton, G. M., Thompson, D. R., Sagar, P. M., Cuthbert, R. J., Cherel, Y., & Bury, S. J. (2006). A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. *Global Change Biology*, *12*(4), 611-625.

Hirons, A. C., Schell, D. M., & Finney, B. P. (2001). Temporal records of $\boldsymbol{\delta}^{13}$C and $\boldsymbol{\delta}^{15}$N in North Pacific pinnipeds: Inferences regarding environmental change and diet. *Oecologia*, *129*, 591-601.

Hodum, P. J., & Hobson, K. A. (2000). Trophic relationships among Antarctic fulmarine petrels: Insights into dietary overlap and chick provisioning strategies inferred from stable-isotope (δ^{15}N and δ^{13}C) analyses. *Marine Ecology Progress Series*, *198*, 273-281.

Hudson, R. J. M., Gherini, S. A., Fitzgerald, W. F., & Porcella, D. B. (1995). Anthropogenic influences on the global mercury cycle: A model-based analysis. *Water, Air, and Soil Pollution*, *80*(1), 265-272.

Hyslop, E. J. (1980). Stomach contents analysis—A review of methods and their application. *Journal of Fish Biology*, *17*(4), 411-429.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), 595-602.

Jonsson, B., & Jonsson, N. (1993). Partial migration: Niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, *3*, 348-365.

Keller, A. A., Frey, P. H., Wallace, J. R., Head, M. A., Wetzel, C. R., Cope, J. M., & Harms, J. H. (2018). Canary rockfishes *Sebastes pinniger* return from the brink: Catch, distribution and life history along the US west coast (Washington to California). *Marine Ecology Progress Series*, *599*, 181-200.

Kendall, A. W., Jr., & Lenarz, W. H. (1986). Status of early life history studies of northeast Pacific rockfishes. *Proceedings of the International Rockfish Symposium, 87*, 99-128.

Kernaléguen, L., Arnould, J. P., Guinet, C., & Cherel, Y. (2015). Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals. *Journal of Animal Ecology*, *84*(4), 1081-1091.

Kidd, K. A., Hesslein, R. H., Fudge, R. J. P., & Hallard, K. A. (1995). The influence of trophic level as measured by δ^{15}N on mercury concentrations in freshwater organisms. *Water, Air, and Soil Pollution*, *80*, 1011-1015.

Kim, J. P., & Fitzgerald, W. F. (1986). Sea-air partitioning of mercury in the equatorial Pacific Ocean. *Science*, *231*(4742), 1131-1133.

Kingsford, M. J. (1992). Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs*, *11*(4), 193-198.

Kolora, S. R. R., Owens, G. L., Vazquez, J. M., Stubbs, A., Chatla, K., Jainese, C., Seeto, K., McCrea, M., Sandel, M. W., Vianna, J. A., Maslenikov, K., Bachtrog, D., Orr, J. W., Milton, L., & Sudmant, P. H. (2021). Origins and evolution of extreme life span in Pacific Ocean rockfishes. *Science*, *374*(6569), 842-847.

Kossak, U. (2006). *How climate change translates into ecological change: Impacts of warming and desalination on prey properties and predator-prey interactions in the Baltic Sea* [Unpublished doctoral dissertation]. Christian-Albrechts-Universität.

Lamborg, C. H., Rolfhus, K. R., Fitzgerald, W. F., & Kim, G. (1999). The atmospheric cycling and air–sea exchange of mercury species in the South and equatorial Atlantic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, *46*(5), 957-977.

Lavoie, R. A., Jardine, T. D., Chumchal, M. M., Kidd, K. A., & Campbell, L. M. (2013). Biomagnification of mercury in aquatic food webs: A worldwide meta-analysis. *Environmental Science & Technology*, *47*(23), 13385-13394.

Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, *88*(1), 42-48.

Le Croizier, G., Schaal, G., Point, D., Le Loc'h, F., Machu, E., Fall, M., Munaron, J. M., Boye, A., Walter, P., Lae, R., & De Morais, L. T. (2019). Stable isotope analyses revealed the influence of foraging habitat on mercury accumulation in tropical coastal marine fish. *Science of the Total Environment*, *650*, 2129-2140.

Loseto, L. L., Stern, G. A., Deibel, D., Connelly, T. L., Prokopowicz, A., Lean, D. R. S., Fortier, L., & Ferguson, S. H. (2008). Linking mercury exposure to habitat and feeding behavior in Beaufort Sea beluga whales. *Journal of Marine Systems*, *74*(3-4), 1012-1024.

Loury, E. K. (2011). Diet of the gopher rockfish (*Sebastes carnatus*) inside and outside of marine protected areas in central California [Master’s thesis, San José State University/Moss Landing Marine Laboratories]. Digital Commons at CSUMB.

Love, M. S., Yoklavich, M., & Thorsteinson, L. K. (2002). *The rockfishes of the Northeast Pacific*. University of California Press.

Madigan, D. J., Litvin, S. Y., Popp, B. N., Carlisle, A. B., Farwell, C. J., & Block, B. A. (2012). Tissue turnover rates and isotopic trophic discrimination factors in the endothermic teleost, Pacific bluefin tuna (*Thunnus orientalis*). *PLoS One*, *7*(11), Article e49220.

Mason, R. P., & Sheu, G. R. (2002). Role of the ocean in the global mercury cycle. *Global Biogeochemical Cycles*, *16*(4), 40-1–40-14.

Mason, R. P., Reinfelder, J. R., & Morel, F. M. (1995). Bioaccumulation of mercury and methylmercury. *Water, Air, and Soil Pollution*, *80*(1), 915-921.

McGowan, J. A., Cayan, D. R., & Dorman, L. M. (1998). Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science*, *281*(5374), 210-217.

McMeans, B. C., Arts, M. T., & Fisk, A. T. (2015). Impacts of food web structure and feeding behavior on mercury exposure in Greenland Sharks (*Somniosus microcephalus*). *Science of the Total Environment*, *509*, 216-225.

Médieu, A., Point, D., Itai, T., Angot, H., Buchanan, P. J., Allain, V. L., Griffiths, S., Gillikan, D. P., Sonke, J. E., Heimbürger-Boavida, L. E., Desgranges, M. M., Menkes, C. E., Madigan, D. J., Brosset, P., Gauthier, O., Tagliabue, A., Bopp, L., Anouk, V., & Lorrain, A. (2022). Evidence that Pacific tuna mercury levels are driven by marine methylmercury production and anthropogenic inputs. *Proceedings of the National Academy of Sciences*, *119*(2), Article e2113032119.

Methot, R. D., & Stewart, I. J. (2005). *Status of the US Canary rockfish resource in 2005.* National Marine Fisheries Service/National Oceanographic and Atmospheric Administration.

Minagawa, M., & Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between δ^{15}N and animal age. *Geochimica et Cosmochimica Acta*, *48*(5), 1135-1140.

Mousseau, T. A. (1997). Ectotherms follow the converse to Bergmann's rule. *Evolution, 51*(2), 630-632.

Musseau, C., Vincenzi, S., Santoul, F., Boulêtreau, S., Jesenšek, D., & Crivelli, A. J. (2020). Within-individual trophic variability drives short-term intraspecific trait variation in natural populations. *Journal of Animal Ecology*, *89*(3), 921-932.

Ohman, M. D., Rau, G. H., & Hull, P. M. (2012). Multi-decadal variations in stable N isotopes of California Current zooplankton. *Deep Sea Research Part I: Oceanographic Research Papers*, *60*, 46-55.

Olson, A. M., Frid, A., dos Santos, J. B. Q., & Juanes, F. (2020). Trophic position scales positively with body size within but not among four species of rocky reef predators. *Marine Ecology Progress Series*, *640*, 189-200.

Páez, Y. C., Betancourt, C. M. A., Sansón, G. G., Kidd, K. A., Curry, R. A., & Aceves, D. K. (2022). Mercury concentrations and stable isotopes (δ^{15}N and δ^{13}C) in fish muscle indicate human impacts in tropical coastal lagoons. *Marine Pollution Bulletin*, *176*, Article 113454.

Parker, S. J., Berkeley, S. A., Golden, J. T., Gunderson, D. R., Heifetz, J., Hixon, M. A., Larson, R., Leaman, B. M., Love, M. S., Musick, J. A., & O'Connell, V. M. (2000). Management of Pacific rockfish. *Fisheries*, *25*(3), 22-30.

Partridge, L., & Coyne, J. A. (1997). Bergmann's rule in ectotherms: Is it adaptive? *Evolution, 51*(2), 632-635.

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, *18*(1), 293-320.

Peterson, C. L., Klawe, W. L., & Sharp, G. D. (1973). Mercury in tunas: A review. *Fishery Bulletin*, *71*(3), 603-613.

Pethybridge, H., Choy, C. A., Logan, J. M., Allain, V., Lorrain, A., Bodin, N., Somes, C. J., Young, J., Menard, F., Langlaid, C., & Duffy, L. A. (2018). A global meta-analysis of marine predator nitrogen stable isotopes: Relationships between trophic structure and environmental conditions. *Global Ecology and Biogeography*, *27*(9), 1043-1055.

Philippsen, J. S., Minte-Vera, C. V., Coll, M., & Angelini, R. (2019). Assessing fishing impacts in a tropical reservoir through an ecosystem modeling approach. *Reviews in Fish Biology and Fisheries*, *29*(1), 125-146.

Pinzone, M., Damseaux, F., Michel, L. N., & Das, K. (2019). Stable isotope ratios of carbon, nitrogen and sulfur and mercury concentrations as descriptors of trophic ecology and contamination sources of Mediterranean whales. *Chemosphere*, *237*, Article 124448.

Pirrone, N., Keeler, G. J., & Nriagu, J. O. (1996). Regional differences in worldwide emissions of mercury to the atmosphere. *Atmospheric Environment*, *30*(17), 2981-2987.

Polis, G. A. (1984). Age structure component of niche width and intraspecific resource partitioning: Can age groups function as ecological species? *The American Naturalist*, *123*(4), 541-564.

Polito, M. J., Brasso, R. L., Trivelpiece, W. Z., Karnovsky, N., Patterson, W. P., & Emslie, S. D. (2016). Differing foraging strategies influence mercury (Hg) exposure in an Antarctic penguin community. *Environmental Pollution*, *218*, 196-206.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, *83*(3), 703-718.

Power, M., Klein, G. M., Guiguer, K. R., & Kwan, M. K. (2002). Mercury accumulation in the fish community of a sub-Arctic lake in relation to trophic position and carbon sources. *Journal of Applied Ecology*, *39*(5), 819-830.

Qamar, N., Panhwar, S. K., & Jahangir, S. (2015). Seasonal variation in diet composition of torpedo trevally, *Megalaspis cordyla* (L) depending upon its size and sex. *Pakistan Journal of Zoology*, *47*(4), 1171-1179.

Raffard, A., Santoul, F., Blanchet, S., & Cucherousset, J. (2020). Linking intraspecific variability in trophic and functional niches along an environmental gradient. *Freshwater Biology*, *65*(8), 1401-1411.

Rice, J. (1995). Food web theory, marine food webs, and what climate change may do to northern marine fish populations. *Canadian Special Publication of Fisheries and Aquatic Sciences,* (121), 561-568.

Riisgård, H., & Hansen, S. (1990). Biomagnification of mercury in a marine grazing food-chain: Algal cells *Phaeodactylum tricornutum*, mussels *Mytilus edulis* and flounders *Platichthys flesus* studied by means of a stepwise-reduction-CVAA method. *Marine Ecology Progress Series*, *62*(3), 259-270.

Ripple, W. J., Estes, J. A., Schmitz, O. J., Constant, V., Kaylor, M. J., Lenz, A., Motley, J. L., Self, K. E., Taylor, D. S., & Wolf, C. (2016). What is a trophic cascade? *Trends in Ecology & Evolution*, *31*(11), 842-849.

Rudolf, V. H. W., & Lafferty, K. D. (2011). Stage structure alters how complexity affects stability of ecological networks. *Ecology Letters*, *14*(1), 75-79.

Shine, R. (1991). Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *The American Naturalist*, *138*(1), 103-122.

Sweeting, C. J., Barry, J. T., Polunin, N. V. C., & Jennings, S. (2007). Effects of body size and environment on diet-tissue $\boldsymbol{\delta}^{13}$C fractionation in fishes. *Journal of Experimental Marine Biology and Ecology*, *352*(1), 165-176.

Syväranta, J., Lensu, A., Marjomäki, T. J., Oksanen, S., & Jones, R. I. (2013). An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. *PloS One*, *8*(2), Article e56094.

Thorson, J. T., & Wetzel, C. (2015). *The status of Canary rockfish (Sebastes pinniger) in the California Current in 2015.* National Marine Fisheries Service, National Oceanographic and Atmospheric Administration.

Tinus, C. A. (2012). Prey preference of lingcod (*Ophiodon elongatus*), a top marine predator: Implications for ecosystem-based fisheries management. *Fishery Bulletin*, *110*, 193-204.

Tissot, B. N., Hixon, M. A., & Stein, D. L. (2007). Habitat-based submersible assessment of macro-invertebrate and groundfish assemblages at Heceta Bank, Oregon, from 1988 to 1990. *Journal of Experimental Marine Biology and Ecology*, *352*(1), 50–64.

US Environmental Protection Agency. (2007). *Method 7473: Mercury in solids and solutions by thermal decomposition, amalgamation, and atomic absorption spectrophotometry*. Author.

Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, *99*(908), 377-390.

Vestfals, C. D. (2009). *Identifying habitat factors for Canary rockfish (Sebastes pinniger) off Washington and Oregon using environmental data and trawl logbooks* [Master's thesis, Oregon State University]. Scholar Archive at Oregon State University.

Vetter, R. D., & Lynn, E. A. (1997). Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera Sebastes and Sebastolobus): Paradigms revisited. *Marine Ecology Progress Series*, *155*, 173-188.

Vojkovich, M. (1998). The California fishery for market squid (*Loligo opalescens*). *California Cooperative Oceanic Fisheries Investigations Report, 39*, 55-60.

Watras, C., & Bloom, N. (1992). Mercury and methylmercury in individual zooplankton: Implications for bioaccumulation. *Limnology and Oceanography*, *37*(6), 1313-1318.

Wimberger, P. H. (1994). Trophic polymorphisms, plasticity, and speciation in vertebrates. In D. J. Stouder, K. L. Fresh, & R. J. Feller (Eds.), *Theory and application in fish feeding ecology* (pp. 19-43). South Carolina University Press.

Wishard, L. N., Utter, F. M., & Gunderson, D. R. (1980). Stock separation of five rockfish species using naturally occurring biochemical genetic markers. *Marine Fisheries Review, 42*(3-4), 64-73.

Yoshino, K., Mori, K., Kanaya, G., Kojima, S., Henmi, Y., Matsuyama, A., & Yamamoto, M. (2020). Food sources are more important than biomagnification on mercury bioaccumulation in marine fishes. *Environmental Pollution*, *262*, Article 113982.

Yurkowski, D. J., Ferguson, S. H., Semeniuk, C. A., Brown, T. M., Muir, D. C., & Fisk, A. T. (2016). Spatial and temporal variation of an ice-adapted predator's feeding ecology in a changing Arctic marine ecosystem. *Oecologia*, *180*(3), 631-644.

Yurkowski, D. J., Ferguson, S., Choy, E. S., Loseto, L. L., Brown, T. M., Muir, D. C., Semeniuk, C. A., & Fisk, A. T. (2016). Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. *Ecology and Evolution*, *6*(6), 1666-1678.

Zhang, Y., Soerensen, A. L., Schartup, A. T., & Sunderland, E. M. (2020). A global model for methylmercury formation and uptake at the base of marine food webs. *Global Biogeochemical Cycles*, *34*(2), Article e2019GB006348.

Zhao, T., Villéger, S., Lek, S., & Cucherousset, J. (2014). High intraspecific variability in the functional niche of a predator is associated with ontogenetic shift and individual specialization. *Ecology and Evolution*, *4*(24), 4649-4657.