GEOGRAPHIC AND ONTOGENETIC VARIATION IN THE TROPHIC ECOLOGY OF LINGCOD (*OPHIODON ELONGATUS*) ALONG THE U.S. WEST COAST

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ABSTRACT

GEOGRAPHIC AND ONTOGENETIC VARIATION IN THE TROPHIC ECOLOGY OF LINGCOD (*OPHIODON ELONGATUS*) ALONG THE U.S. WEST COAST

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Dietary studies of fishes provide an understanding of predator-prey interactions and may be used to inform resource managers about food web dynamics. Along the West Coast of North America, Lingcod (*Ophiodon elongatus*) are top marine predators in rocky-reef habitats and support an economically important fishery. In this study, gut content and stable isotope analyses were used to evaluate differences in the diets of Lingcod collected in U.S. waters from Alaska to Southern California during 2016 and 2017. Overall, Lingcod consumed a wide variety of prey and exhibited both generalist and opportunist feeding strategies. Significant variability in Lingcod diets was driven by factors such as depth, region, sex, and total length. Male Lingcod caught in shallow depths consumed more lower trophic level prey items (e.g. cephalopods) and had more diverse diets. Female Lingcod caught in deep depths consumed more higher trophic level prey items (e.g. groundfishes) and had less diverse diets. Geographic variation in trophic level was associated with environmental conditions of sea surface temperature and primary productivity (i.e., chlorophyll *a*). Southern Lingcod fed more on cephalopods while northern Lingcod fed more on various fish groups. This study fills in data gaps in the trophic ecology of a top marine predator and can inform food web models and fisheries management.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ADFG – Alaska Department of Fish and Game
CD – mean distance to centroid
CDFW – California Department of Fish and Wildlife
CPFV – Commercial Passenger Fishing Vessel
CR – carbon range
EBFM – ecosystem-based fisheries management
ENSO – El Niño Southern Oscillation
GCA – gut content analysis
GLM – generalized linear model
GPS – Global Positioning System
IRI – index of relative importance
MPA – marine protected area
N – number
NND – mean nearest neighbor distance
NOAA – National Oceanic and Atmospheric Administration
NR – nitrogen range
O – frequency of occurrence
ODFW – Oregon Department of Fish and Wildlife
PCA – principal component analysis
PERMANOVA – permutational multivariate analysis of variance
PFMC – Pacific Fishery Management Council
PN – prey-specific abundance by number
PSIRI – prey-specific index of relative importance
PW – prey-specific abundance by weight
SDNND – standard deviation of mean nearest neighbor distance
SEA – standard ellipse area
SIA – stable isotope analysis
SIBER – Stable Isotope Bayesian Ellipses in R
SIMPER – similarity percentage analysis
TA – total area of convex hull
TL – trophic level
W – weight
WDFW – Washington Department of Fish and Wildlife

Introduction

Identifying predator-prey relationships is important for understanding ecological connections and for fishery management purposes. Predators have the capability to affect the structure of prey populations and cause rapid changes in ecosystems through top-down regulation (Shears & Babcock 2002, Peckarsky et al. 2008). Top-down structuring of ecosystems can occur both directly and indirectly. Direct effects occur when predators consume their prey, thus reducing abundance of a species and changing the community composition, whereas indirect effects can occur by causing a change in prey behavior or altering the amount of shared prey resources for other predators (Bax 1998). Cascading shifts in ecosystems create unbalanced food webs, which can be problematic for managers conducting stock assessments or trying to estimate the health of a population.

Diet studies are one way to quantify these predator-prey interactions to improve fisheries management. In general, diet studies can provide information on what a predator has been eating, which provides details on prey availability, predatory feeding habits, and energy intake (Chipps & Garvey 2007). Empirical studies that quantify these food web connections are vital in the shift from traditional single-species management towards a more holistic ecosystem-based fisheries management approach (EBFM; Francis et al. 2007). Managers are able to input dietary data into food web models as a means to predict changes in predator and prey populations (Tinus 2012).

In order to successfully describe a predator's diet, researchers must take into account how their diet may fluctuate. For example, fishes have been described as specialists, generalists, and opportunists (Gerking 1994). Specialists consume specific types of prey, seldom expanding their diets. This strategy is exhibited in fishes that have a readily abundant prey source (Wulff 1994). Generalists, on the other hand, eat a wide variety of prey and are not limited to a specific prey type (Nemeth 1997, Hamilton et al. 2011, Yeager et al. 2014). Opportunists take advantage of prey that are not usually a part of their diets and are often associated with temporal variability in abundance of prey items.

In addition to feeding strategies, marine fish predators have demonstrated diverse spatial, temporal, and ontogenetic variation in their diets (Gerking 1994, Bax 1998). Spatially, diets can be driven by factors such as environmental conditions, prey availability, and habitat. Individuals living in warmer waters experience increased metabolism, leading to increased consumption rates (Bethea et al. 2007). Additionally, prey availability is often spatially and temporally variable, and predators may feed on the most abundant prey, or may selectively target specific prey items (Scharf et al. 2000, Mahe et al. 2007). Along a latitudinal gradient, regional differences in diets may be due to varying abundances in prey as well as the habitat (Simpfendorfer et al. 2001, Sinclair & Zeppelin 2002, Bethea et al. 2007). Smaller fishes may reside in different habitats to avoid predation and even cannibalism by larger, adult fishes (Lowe et al. 1996, Mahe et al. 2007). Temporally, diets can vary seasonally or from year to year, due to changes in oceanographic conditions (e.g., El Niño Southern Oscillation [ENSO]) and shifts in prey availability. For instance, the El Niño phase of warmer water conditions has been accompanied by a decrease in both primary production and fish abundance (Barber & Chavez 1983), but also the temporary appearance of prey species with more southern geographic distributions (Lilly & Ohman 2021). In contrast, La Niña ushers in cooler productive waters, which can greatly increase prey abundance and lead to changes in predator feeding strategies from one year to the next (Hipfner & Galbraith 2013). Certain prey species may fluctuate in abundance due to episodic or sporadic recruitment (e.g., west coast rockfishes; Field & Ralson 2005), which can cause dietary shifts in generalist and opportunistic predators that can take advantage of these resource pulses. Ontogenetically, diets can vary as fish grow in size due to biomechanical constraints on prey acquisition and consumption or due to shifts in habitat by the predator. Gape size and mobility can limit the size of prey that can be consumed (Scharf et al. 2000, Mahe et al. 2007), and as fishes grow in size, their food resources and habitats change (Persson & Crowder 1998). Larger fishes often consume a higher diversity of prey as well as larger prey items compared to their smaller counterparts (Lowe et al. 1996, Scharf et al. 2000, Usmar 2012). These spatial, temporal, and ontogenetic factors should therefore be taken into consideration when deciphering a predator's feeding habits.

Gut content analysis (GCA) is one technique used to describe diets and has been a standard practice used in fish ecology (Hyslop 1980). The traditional GCA involves categorizing stomach contents to provide information on what the predator had recently consumed (Assis 1996). There are different metrics used to report gut contents and each metric has advantages and disadvantages. Metrics include frequency of occurrence, number, volume, and weight. The importance of diet is often expressed by an amount or bulk in the stomach, and a combination of methods is best suited to describe the overall diet of a consumer (Hynes 1950, Hellawell & Abel 1971, Windell 1971, Hyslop 1980). The frequency of occurrence method is a simple way to describe diets by determining the number of stomachs that have a particular prey item; this metric is often presented as a percentage of all stomachs (Frost 1954). This is a quick and straightforward process, but it does not provide an indication of the amount of food in the stomach. The numerical method is more time-intensive, in which the individual numbers of a particular prey item are recorded for all stomachs, and also is often listed as a percentage of all stomachs (Crisp et al. 1978). This method works best when prey items are readily identifiable and of similar size ranges. However, it may overestimate the importance of larger abundances of smaller prey types.

The volumetric method is used to determine the volume of a particular prey item in a stomach and is often listed as a percentage of total volume from all stomachs. This method involves using a graduated measuring tool to calculate the displacement of volume of the particular prey item (Wolfert & Miller 1978). While the volumetric method is widely used to measure bulk, a limitation of this metric is that it may create large errors in volumetric estimates due to water trapped in prey items (Hellawell & Abel 1971). With the gravimetric method, the total weight of a particular prey item is recorded for all stomachs and is often listed as a percentage of all stomachs (Glenn & Ward 1968). This method can be calculated using either wet or dry weights. Taking the wet weight is a quicker route, but the amount of moisture among and within samples varies and has been known to be a source of error. Measuring the dry weight of prey items takes longer as the moisture of the samples must be evaporated before measurements can be made, but it can provide lower error margins when calculating bulk. An important point to consider is that the gravimetric method may overestimate the importance of one large prey item that is slow to digest, while underestimating the importance of prey items that digest rapidly (George & Hadley 1979).

Newer methods have been created in order to account for some of the bias in gut content analyses. For example, the index of relative importance (IRI) integrates multiple metrics. IRI takes the sum of the percentage values of the numerical method and volumetric or gravimetric methods and multiplies by the percentage value of frequency of occurrence (Pinkas 1971). More recently, the prey-specific index of relative importance (PSIRI) has been used in diet studies. PSIRI is a valuable metric that identifies the most important prey items by prey-specific abundances by number and weight and corrects for overestimation of frequency of occurrence (Brown et al. 2012, Loury et al. 2015). However, GCAs do not always reflect all prey sources. Gelatinous and soft-bodied prey items that digest rapidly are often not present by the time the stomach content is analyzed (Whitledge & Rabeni 1997). In addition, GCA only provides information about recent meals consumed by a predator, which may or may not represent typical long-term feeding habits.

Stable isotope analysis (SIA) is another technique used to describe diets and is capable of providing dietary information integrated over longer time periods. SIA has some advantages over GCA, as it is able to account for the prey items that that digest rapidly (Pinnegar & Polunin 1999). These analyses together provide a complementary understanding of the diet of an organism (Davis et al. 2012). The use of stable isotopes are based on ratios of lighter and heavier isotopes in the tissue of an organism. Two common elements used for SIA in diet studies are nitrogen (^{15}N and ^{14}N) and carbon (^{13}C and ^{12}C). These isotopes have been shown to be beneficial to the understanding of feeding ecology and sources of primary production, respectively (Post 2002). Isotopes are naturally occurring forms of the same element with different numbers of neutrons (Hoefs 2015). An element with more neutrons or less neutrons results in heavy or light isotopes of the same element, respectively. A change in the ratio of the heavy and light isotopes from kinetic and chemical processes is called isotopic fractionation (Dalerum & Angerbjörn 2005). The $\delta^{15}N$ ratio provides information on the trophic feeding levels, while $\delta^{13}C$ ratio is an indicator of the dietary carbon source, reflecting the photosynthetic pathways utilized by primary producers (Post 2002). Typically, the consumer's $\delta^{15}N$ is enriched by 3-4‰ relative to their prey (because each trophic step creates an increase in enrichment in the heavier isotope), while the $\delta^{13}C$ changes 0.5-1‰ with an increase in trophic level (Pinnegar & Polunin 1999, MacNeil et al. 2005).

Different tissue types integrate dietary information over different time scales due to tissue-specific turnover rates (i.e., the assimilation of an isotope into the consumer's tissue over time). Tissues with higher turnover rates reflect a more recent feeding history, whereas tissues with low turnover rates integrate information about diets over longer times scales (Post 2002). For example, red blood cells have a quick turnover rate, which is beneficial for asking questions about feeding events within the last days to weeks, whereas bones provide information on dietary patterns accumulated over the course of years (Dalerium & Angerbjörn 2005). White muscle tissue has a turnover rate that provides dietary information from the past several weeks to months (Dalerium & Angerbjörn 2005). Additionally, white muscle tissue samples are less variable in C and N readings than other tissue types and are thus are often the best tissue choice for ecological work (Pinnegar & Polunin 1999).

Along the U.S. West Coast, the Lingcod (*Ophiodon elongatus,* Girard 1883) is a species of fish that plays a role as a top marine predator. Previous Lingcod diet studies have demonstrated that Lingcod exhibit dietary variation along their range. For example, in the San Juan Archipelago, Washington, rocky-reef fishes in the Order Scorpaeniformes (an Order that includes rockfishes) made up approximately 50% of the biomass in Lingcod diets (Beaudreau & Essington 2007). However, along the nearshore Oregon Coast, Lingcod primarily consumed pelagic fishes (46% by number), while rockfishes comprised only 4.7% of prey items, despite visual observations that they were the most abundant potential prey (Tinus 2012). A second study in Oregon also found that rockfishes were uncommon prey items in Lingcod diets, with an average of less than 1% of total biomass (Steiner 1979). Lingcod diets near Morro Bay, California were primarily composed of species in the taxonomic families Octopodidae (on average 32.3% of the numbers of prey), Scorpaenidae (on average 12.6% of the numbers of prey), Engraulidae (on average 11.2% of the numbers of prey), and Paralichthyidae (on average 3.3% of the numbers of prey; Anderson 2016). More recently, Lingcod off the central coast of British Columbia, Canada were reported consuming fishes and octopuses (Olson et al. 2020). These differences in diets support the notion that Lingcod are highly opportunistic (Beaudreau & Essington 2009) and suggest predator-prey relationships can change both spatially and temporally.

In addition to geographic differences, there are aspects of Lingcod life history, such as depths they reside in, size, and sex that are likely to influence their trophic ecology. Lingcod reside in a diverse set of habitats from the shoreline to a depth of at least 427 m (Miller & Geibel 1973). Tagging studies have shown that Lingcod exhibit a high degree of site fidelity (Starr et al. 2004, Starr et al. 2005), with residency correlated to sex, length, and season (Greenley et al. 2016). However, some tagged Lingcod have exhibited exceptional net movements on the scale of 370 km for an adult and 510 km for a juvenile (Cass et al. 1990, Jagielo 1990). As Lingcod age and grow, they migrate to deeper waters, and females usually inhabit deeper depths than males (Miller & Geibel 1973, Hamel et al. 2009). Differences in depth may influence the type and availability of prey. Lingcod are also sexually dimorphic and, similar to other groundfishes, attain larger sizes in the northern part of their range (Miller & Geibel 1973, Lam 2019). Females grow faster and reach larger sizes than their male counterparts (Hamel et al. 2009, Lam 2019). These aspects of Lingcod life history indicate the potential for Lingcod to consume different types or amounts of prey based on their size and sex.

Given that little is known about how Lingcod diets change across their range in a more concise time period, or how life history factors may influence their diets, the goal of this study was to characterize the trophic ecology of Lingcod from Southeast Alaska to Southern California, an area that contains the majority of the U.S. West Coast Lingcod stock. Study objectives were to: (1) Assess geographic differences in Lingcod diets using gut content and stable isotope analyses; (2) Identify and compare male and female Lingcod feeding habits using gut content and stable isotope analyses; (3) Compare Lingcod feeding habits using gut content and stable isotope analyses based on length; and (4) Identify environmental and oceanographic factors that may influence Lingcod feeding habits. This information can then be utilized by fisheries managers and in food web and ecosystem models to better predict the role and impact of this top marine predator in the Gulf of Alaska Ecosystem and the California Current Large Marine Ecosystem.

Materials and Methods

Study Species

Lingcod, in the greenling family *Hexigrammidae*, are important marine predators along their range from Kodiak Island, Alaska to Pt. San Carlos, Baja California, Mexico (Miller & Lea 1972). Early molecular studies indicated that Lingcod are genetically similar throughout their range and exhibit a high degree of gene flow, except for the more isolated population in the Salish Sea (Jagielo et al. 1996, LeClair et al. 2006, Marko et al. 2007). More recently, however, there is evidence for two distinct genetic clusters with a latitudinal break near Point Reyes, California indicating a northern and southern population segment (Longo et al. 2020).

In contrast to other groundfishes, Lingcod are relatively quick to grow and reach maturity. Females reach a maximum size around 119 cm total length, a maximum age of 20 years, and are often mature after 3-5 years. Conversely, males reach a maximum size around 86 cm total length, a maximum age of 14 years, and are mature after 2-3 years (Miller & Geibel 1973, Cass et al. 1990). The largest Lingcod recorded was a female Lingcod caught in Alaskan waters, at 150 cm (total length) and a weight of 32 kg (Cass et al. 1990).

Lingcod are considered a non-migratory species (Hamel et al. 2009), although adults do make a seasonal vertical migration from deeper waters to nearshore waters where they spawn in late Fall through Winter (Wilby 1937, Phillips 1959, Starr et al. 2004). Larger males often move to shallow waters first where they select nesting sites in rocky crevices with strong currents to attain adequate oxygen flow (Giorgi 1981). Males frequently return to the same territory each year and exhibit high nest site fidelity (King & Withler 2005). Females move to shallow waters soon after the males, and the larger and older females often spawn first. During a spawning event, a female will extrude a batch of adhesive eggs to the substrate and the male will fertilize the eggs. The female will then extrude another batch of eggs and the male will fertilize those eggs. This process will continue until spawning has concluded. Afterward, the females leave the nesting sites to return to deeper waters while the males remain to guard the nests. Males guard nests from predators for a period of 5-11 weeks while eggs incubate and leave soon after hatching has concluded. The hatching period typically occurs from early Winter to early Spring (Cass et al. 1990, Silberberg et al. 2001, Hamel at al. 2009).

After a few months in the water column, larval Lingcod (70–80 mm in length) settle to the bottom and take refuge near kelp and eelgrass beds or other structurally complex habitats (Cass et al. 1990, Bassett et al. 2018). Juvenile Lingcod frequent low-relief, soft-sediment habitats and small-rock, mixed substrate habitats inshore, and by September often are found on flat, soft-bottom habitats (Cass et al. 1990). The ontogenetic shift to the soft sediment habitat may be linked to predator avoidance, which includes avoidance of larger, cannibalistic Lingcod (Miller & Geibel 1973, Bassett et al. 2018). As Lingcod age and grow, they tend to move to deeper, moderate-relief rocky habitats (Cass et al. 1990, Bassett et al. 2018).

Lingcod have been a valuable resource in tribal, commercial, and recreational fisheries. Lingcod have traditionally been included in the diets of Indigenous peoples along the Pacific Northwest (McClellan 1975, Gobalet & Jones 1995, McKechnie & Moss 2016). One archaeological study along the central California coast indicated that large inshore fish species, which include Lingcod, comprised over half of Native American diets between 6200 B.C. and A.D. 1830 (Gobalet & Jones 1995). Indigenous peoples of the Pacific Northwest have used multiple methods to catch Lingcod, including lures (made from bone, shell, or wood), spears, nets, seines, and weirs (Cass et al. 1990, Gobalet & Jones 1995). Commercial fishing for Lingcod began in the 1860s in Canada and in the early 1900s for California, Oregon, and Washington (Cass et al. 1990, Haltuch et al. 2018). The Alaskan Lingcod commercial fishery did not develop until 1987, as Lingcod were primarily caught incidentally as part of other targeted fisheries (Gordon 1994). The gear used in the commercial fishery has varied greatly, including the use of jigs, handlines, bottom trawl, and hook-and-line (Cass et al. 1990). In the mid to late 1900s there was a shift in overall landings, from commercial to recreational fisheries. This shift was predominantly due to an increase in use of boat-based recreational anglers (Commercial Passenger Fishing Vessels and private boats) and SCUBA diving, resulting in a spike in the hook-and-line and spear fisheries (Cass et al. 1990, Adams & Starr 2001, Haltuch et al. 2018).

Lingcod reside across multiple jurisdictional marine boundaries, on both international and national levels. Lingcod stocks in Canada are assessed frequently and managed by Fisheries and Oceans Canada. In the United States, Lingcod stocks are assessed frequently but managed by different agencies. The Lingcod fishery in Alaska is managed by the State of Alaska Board of Fisheries and the North Pacific Management Council (Haltuch et al. 2018). Lingcod in waters off Washington, Oregon, and California are assessed by the Pacific Fishery Management Council and modeled as a northern stock (Washington and Oregon) and southern stock (California; Jagielo et al. 1997, Hamel et al. 2009, Haltuch et al. 2018). In 1997, Lingcod were declared overfished from Washington to California, which resulted in new regulations and fishing restrictions, but the population recovered quickly and was declared rebuilt in 2005 (Haltuch et al. 2018). The most recent Lingcod stock assessment in 2017 indicated that Lingcod remain rebuilt; both stocks remain above the minimum stock size threshold of 10% of the estimated unfished spawning biomass. The northern stock was above the target reference point of 40% of the estimated unfished spawning biomass (at 57.9%), whereas the southern stock was below the target reference point, in the precautionary zone (at 32.1%; Haltuch et al. 2018).

Study System

Southeast Alaska spans 6 degrees of latitude and is exposed to the Alaska Coastal Current, which runs North along the southern coast of Alaska (Stabeno et al. 1995). The U.S. West Coast spans 16 degrees of latitude and is exposed to several currents: the California Current, Davidson Current, and Southern California Countercurrent. The California Current runs South along this stretch from British Columbia, Canada to Baja California, Mexico, bringing cool, productive, nutrient-rich waters during Spring, Summer, and early Fall (Checkley & Barth 2009). The Davidson Current runs North from Baja California, Mexico to Oregon and is a weaker countercurrent that brings warmer water during the late Fall and Winter (Reid & Schwartzlose 1962). The warmer, Southern California countercurrent becomes entrained in the general southward California Current, moving waters up and around the Channel Islands off the coast of southern California in all seasons except Spring (Bray et al. 1999). The favorable conditions of cold, nutrient-rich waters promote growth of primary producers at the base of the food web (Walsh 1972). These currents are important determinants of the temperature and productivity in the study region and thus are important drivers of primary and secondary production, which affect overall productivity of the NE Pacific Ocean. This in turn may cause geographic variation in Lingcod diets. In addition, the broad geographic range of the study region encompasses a variety of habitat types and water depths. The rocky reef habitat provides shelter for groundfishes and other marine fauna in both shallow and deep waters and was the primary focus of habitat types during collections for this study.

Sample Collection Techniques

For this study, chartered Commercial Passenger Fishing Vessels (CPFVs) were used to conduct hook-and-line fishing out of 19 different port locations (i.e. “sites”) distributed along the Alaska, Washington, Oregon, and California coasts (Figure 1). The goal was to obtain approximately 100 Lingcod per site, representing a wide array of sizes from both sexes, from both deep and nearshore rocky-reef habitats. Juvenile Lingcod, which typically reside in low relief and soft bottom habitats (Bassett et al. 2018) were not targeted and therefore were less likely to be caught and included in this study.

The majority of sampling occurred from April–October 2016 in Washington, Oregon, and California. Additional sites were sampled in January and March 2016, and January 2017. Alaska was sampled in May 2017. A subset of Lingcod samples from Oregon were provided by the ODFW Marine Reserves Program. Lingcod samples were then grouped into 6 regions: Alaska (Yakutat, Sitka, and Craig), Vancouver (Neah Bay and La Push), Columbia (Westport, Garibaldi, Newport, and Coos Bay), Eureka (Brookings and Eureka), Monterey (Fort Bragg, Bodega Bay, San Francisco, and Monterey), and Conception (Morro Bay, Santa Barbara, Long Beach, and San Diego). Regional designations were set using current management areas from the Pacific Coast Groundfish Fishery Management Plan, based on considerations of stock distributions, historical catch statistics, biological factors, and administrative ease (PFMC (Pacific Fishery Management Council) 2011). Collection of biological specimens were conducted with approval from the San Jose State University Institutional Animal Care and Use Committee (protocol #964), and federal (NOAA SRP #31-2016, #31-2017), and state permits (AK #CF-17-006, WA #16-138, WA #17-024, OR #20237, OR #21074, CA #6477).

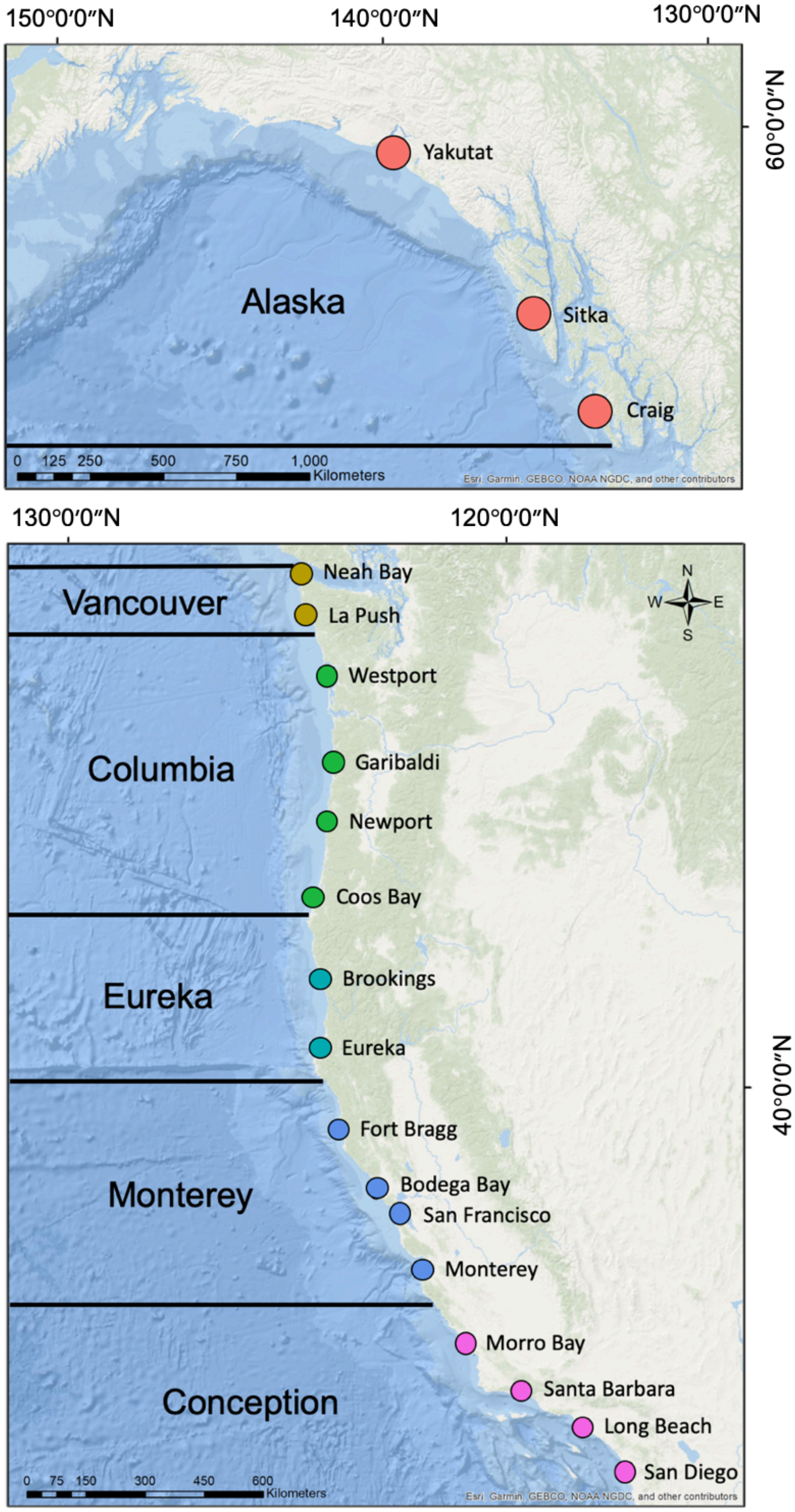


Figure 1. Map of the study area, indicating port locations and regions for collections of Lingcod (*Ophiodon elongatus*).

Lingcod Collections

For each fishing drift, the latitude and longitude of drift start and stop locations and time of day were recorded using a Garmin© GPS unit. Depth and seafloor relief were recorded from the ship's echosounder. All fishing conducted for this project used hook-and-line fishing gear. Anglers used a variety of combinations of terminal tackle, including copper pipes, bars, jigs, and bait. Bycatch primarily consisted of rockfishes from the genus Sebastes, and total lengths of each individual were recorded before being released alive. Rockfishes captured in deep water or showing signs of barotrauma were immediately returned back to capture depth by use of SeaQualizer© descending devices.

Lingcod were euthanized using the cranial concussion method once they were landed on the boat. Lingcod may regurgitate after being brought to the surface. To the best of our capabilities, all regurgitated items were retained. Captured Lingcod were measured (total length to the nearest cm) and weighed (to the nearest 0.1 kg). Each fish was assigned a code based on skin color (blue or brown). This code was determined by visually observing external body colors and the color in the mouth, and assessed a second time during dissections when observing the inner body cavities. Lingcod were sexed visually; males have a conical papilla that is easily identified, while females lack this external feature. Small Lingcod, whose sex can be difficult to discern, were confirmed during dissection by observing the presence of testes or ovaries. A gill tissue sample was collected and stored in 95% ethanol for genetic analysis. Each fish was then tagged using a tagging gun, plastic t-bar tags, and waterproof paper strips with a unique code. A subset of collections were placed in heavy duty plastic bags for parasite analysis. All Lingcod were placed in coolers with ice until returning to port.

Dissections

Before starting dissections, a handheld caliper was used to measure the body depth (to the nearest mm) of the widest point on each individual, which was usually located between the top of the head and just under the pelvic fins. Gape size also was measured. Prior to measuring gape size, the mouth was stretched open to ensure rigor mortis did not inhibit the true gape potential. Gape was recorded as the distance (in mm) from the center of the top jaw to the center of the bottom jaw when the maxillary flared forward and exposed the connecting skin tissue around the mouth. The second dorsal fin rays (rays 4-8) were removed and frozen, and the sagittal otoliths were removed and carefully dried with a paper towel for ageing. Two white muscle tissue samples were collected just below the first dorsal fin region on the left side of each Lingcod. These tissue samples were placed in 1.8 mL cryogenic vials, labeled with a unique code, and frozen for stable isotope analysis. Lingcod organ weights were measured to 0.1 g using a portable Ohaus Scout® SPX2201 balance. Gonads were used to confirm the external sex, then were weighed and assigned a maturity stage based on categories described by Silberberg et al. (2001). The intestines, gall bladder, and any connective tissues were removed prior to weighing the liver, as a proxy for energy storage. The stomach was cut from the top of the esophagus to the junction between the pyloric caeca and intestine. The whole stomach weight was recorded, which included the stomach lining and contents, and the weight of the stomach contents alone. For prey items that were identifiable and in good condition, a small piece of fleshy muscle tissue was removed and frozen for prey stable isotope analysis. Stomach contents were then placed in individual jars and preserved in 95% ethanol for later analysis.

Gut Content Analysis

Each preserved gut content sample was poured through a 1 mm test sieve. Prey items were sorted into the lowest taxonomic groups possible and weighed to the nearest 0.1 g. Standard methods were used to quantify gut contents using prey indices; these indices include percent frequency of occurrence (%O), percent prey-specific abundance by number ($\%PN_i$), percent prey-specific abundance by weight ($\%PW_i$), and percent prey-specific index of relative importance (%PSIRI) (Hyslop 1980, Cortés 1997, Brown et al. 2012, Loury et al. 2015). Trophic level was determined using the trophic level equation by Cortés (1999) and generalized prey categories by Ebert & Bizzarro (2007; Appendix 1). Two diversity indices were utilized to estimate gut content diversity (Simpson diversity index and Shannon diversity index).

These metrics were calculated using the following formulas:

1. Percent frequency of occurrence (%O):

$$\%O_i=\frac{n_i}{n}*100$$

In which, n_i = number of stomachs that have a prey item (i) and n = the number of stomachs sampled.

2. Percent prey-specific abundances by number and weight ($\%PN_i$, $\%PW_i$):

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

In which, A_{ij} = abundance by number or weight for a prey item (i) in a stomach (j), and n_i = number of stomachs that have a prey item (i).

3. Percent prey-specific index of relative importance (%PSIRI):

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

In which, PN_i = prey-specific abundance by number of a prey item (i), PW_i = prey-specific abundance by weight of a prey item (i), and O_i = occurrence of a prey item (i).

4. Trophic level (TL):

$$TL_k = 1 + \left(\sum_{j=1}^{n} P_j * TL_j \right)$$

In which, TL_k = trophic level of species k, P_j = proportion of prey category j in the diet of species k, n = total number of prey categories, and TL_j = trophic level of prey category j.

5. Simpson index (D):

$$\mathrm{D} = \frac{1}{\sum_{i=1}^{s} {p_i}^2}$$

In which, p_i = in an individual stomach, the proportion of a prey item found divided by the total number of prey items found in that stomach.

6. Shannon index (H):

$$\mathrm{H} = -\sum_{i=1}^{s} p_i \ln p_i$$

In which, p_i = in an individual stomach, the proportion of a prey item found divided by the total number of prey items found in that stomach.

For this study there were 2,074 Lingcod collected, of which 1,321 Lingcod stomachs contained sufficient gut contents to analyze (Appendix 2). Stomachs from these Lingcod contained 104 different types of prey items. These numbers include Lingcod collected from Puget Sound, however many of those samples were lost during shipping which greatly reduced the sample size for that area. Thus, Puget Sound Lingcod were excluded from analyses and are only reported in Appendix 2 for anecdotal purposes. After removing the Puget Sound samples there were 1,949 Lingcod, in which 1,272 Lingcod stomachs contained gut contents (Table 1). Prey items that were unusual (e.g. shell fragments), fishing gear, Petromyzontidae and Chondrichthyes fishes, algae, parasites, unidentified organic matter, and prey that were only present in Puget Sound, were removed before analysis (see Appendix 1 “Other/Unknown” category). This reduced the 104 prey items to 61 prey items for analysis. This also eliminated 14 more Lingcod as they only contained prey items that were already excluded as described above, reducing the 1,272 Lingcod stomachs with gut contents to 1,258 Lingcod stomachs with gut contents available for analysis (Table 1).

Table 1. Total number of Lingcod collected for this study and for gut content analysis, by region.

Region	Total # of Stomachs for this study	# of Stomachs with Contents	# of Stomachs for Analysis
Alaska	196	144	140
Vancouver	197	160	160
Columbia	427	324	323
Eureka	201	159	158
Monterey	541	244	239
Conception	387	241	238
All Regions	1,949	1,272	1,258

Not all prey species occurred in each of the sampling regions, and there were numerous rare prey items that only occurred once or only in one region. Additionally, due to high rates of digestion, many prey items were not identifiable to genus or species and were therefore grouped into higher taxonomic levels to allow for statistical comparisons. For these reasons, the 61 types of prey items from the 1,258 Lingcod stomachs were sorted into 8 high-level taxonomic prey groups: 1) Crustacea and Gastropoda, 2) Cephalopoda, 3) Unidentified Teleostei, 4) Scorpaenidae, 5) Demersal Fishes, 6) Semi-Pelagic Fishes, 7) Pleuronectiformes, and 8) Gadiformes. Prey groups were determined by a minimum threshold of 2% PSIRI.

Stable Isotope Analysis

Isotopic ratios are expressed in parts per thousand (‰) differences from a standard reference material (Vienna Pee Dee Belemnite for C and atmospheric nitrogen for N), such that $\delta X = (R_{sample}/R_{standard} - 1) \times 1000$, in which, X is ^{15}N or ^{13}C, R is the corresponding ratio of ^{15}N:^{14}N or ^{13}C:^{12}C, and δ is the measure of heavy to light isotope in the tissue sample (Pinnegar & Polunin 1999).

The SIA consisted of 519 Lingcod across all 6 regions. Lingcod that were selected for the SIA were subsampled from the total Lingcod collected for this study due to costs associated with SIA and overall processing time. Within each region, a variety of females, males, adults, and juveniles of different sizes were selected, as well as samples of fish that were being used for auxiliary studies.

Muscle tissue samples were collected from relatively intact prey samples in the gut contents of Lingcod in each region for the stable isotope analysis. However, there were not enough samples of one prey type across all regions to use in a mixing model (e.g. MixSIAR; Stock & Semmens 2013). These broad prey categories were pooled across all regions for a general understanding of prey isotopes: Clupeidae (n=19), Sebastes (n=50), Pleuronectiformes (n=5), and Octopoda (n=22). For Clupeidae and Sebastes prey samples, white muscle tissue was removed from the upper left dorsal region. For Pleuronectiformes, white muscle tissue was removed from the upper dorsal region of the eyed-side of the fish. Octopoda muscle tissue samples were collected from the mantle and an arm.

Samples were freeze-dried in 1.8 mL twist-top cryovials at the Marine Analytical Laboratory at the University of California, Santa Cruz. The tops of the vials were twisted halfway open to allow sufficient airflow into the vial and then placed in a Labconco Corporation FreeZone 4.5 L Benchtop Freeze Dry System™. To ensure the samples were entirely dried, they stayed in the system for 48 hours. Samples were then taken back to Moss Landing Marine Laboratories and ground into powder using a ball mill machine and a 5 mm stainless steel pestle ball. Samples were left in the ball mill machine for a minimum of 2 minutes or until the samples were homogenized.

All stable isotope samples were shipped to the Stable Isotope Laboratory at Idaho State University for analysis. The powder was measured to the nearest 0.01 mg and placed in a tin capsule. Trays containing samples were placed in an Elemental Combustion System 4010™ interfaced to a Delta V™ Advantage mass spectrometer through the Thermo Scientific™ ConFlo IV system to ascertain stable isotope signatures. Each tray was run with international standards and blanks to ensure accuracy and allow for corrections if necessary.

Statistical Analyses

Both univariate and multivariate techniques were utilized to assess geographic, ontogenetic, and sex-specific variability in Lingcod diets determined from gut content and stable isotope data. All analyses were conducted using the statistical software R version 3.6.3 and PRIMER v7 (R Core Team 2020, Clarke & Gorley 2015).

Gut Contents. In order to assess sample size sufficiency, a prey accumulation curve was created for each region by each of the 8 high-level taxonomic prey groups using the Vegan Community Ecology package (Oksanen et al. 2013). Sufficient sample size for this number of prey groups is visually confirmed once the curve reaches an asymptote. This was statistically confirmed with a linear regression, when the last five points of the slope (b) of the linear regression was ≤ 0.05.

A permutational multivariate analysis of variance (PERMANOVA) was used to test the effects of multiple factors (region, sex, depth, length) on the abundance of the 8 high-level taxonomic prey groups by %N and %W in order to determine which factors explained variability in the diet. Region and sex were categorical factors while depth and length were continuous factors. A Bray-Curtis similarity matrix was created from 4^{th} root transformed diet data. All models were permuted 9,999 times. Each factor and interaction were tested individually and ranked based on high r^2 and pseudo-F values. The final models were created by adding high ranking factors until p-values were no longer statistically significant ($p>0.05$).

A similarity percentage analysis (SIMPER) was used to assess the similarities and dissimilarities of diets within and among regions. As with the PERMANOVA, a Bray-Curtis similarity matrix was created from 4^{th} root transformed diet data. A variance inflation factor (VIF) was calculated to check for multicollinearity. A principal component analysis (PCA) was used to help further examine which prey categories contributed most to dietary differences among regions. In order to examine similarities and dissimilarities among regions, the mean and ± 1 standard error (SE) for each region was plotted on principal component axis 1 (PC1) and principal component axis 2 (PC2). Additional bar graphs were created to visually describe significant factors. Trophic level and Simpson's and Shannon's diversity indices were determined using all 1,258 Lingcod stomachs and their associated prey items.

Stable Isotopes. A generalized linear model (GLM) was used to test the effects of multiple factors (region, sex, depth, length) on $\delta^{13}C$ and on $\delta^{15}N$, and a VIF was calculated to check for multicollinearity. Boxplots and biplots were created for significant factors to visually aid the GLM. For both the carbon and nitrogen models, a Tukey Honest Significant Difference (Tukey HSD) pairwise comparison was used to distinguish which regions were the driving forces behind the significant differences. An analysis of covariance (ANCOVA) was then utilized in order to test whether the sex of Lingcod influences $\delta^{15}N$ while controlling for depth and length.

The Stable Isotope Bayesian Ellipses in R (SIBER) package was used to examine dietary diversity by region, sex, length, and depth (Jackson et al. 2011). Using SIBER, all Lingcod were plotted in bivariate stable isotope space and isotopic standard ellipse areas (SEAs) were created for each factor. Mean ellipses were used to identify overlap and how isotopic niches differ. Larger ellipses indicated a greater diversity in diets and smaller ellipses indicated less diversity.

Using SIBER, Layman metrics (Layman et al. 2007) were also calculated for each factor to quantify isotopic niches and to better understand trophic diversity. Within a group of Lingcod (e.g. by region), these metrics include 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 NND (SDNND). NR is calculated as the distance between the maximum and minimum $\delta^{15}N$ values. This represents the degree of trophic diversity consumed in a group. A larger NR indicates greater trophic diversity in the diet and a smaller NR indicates less trophic diversity in the diet. CR is calculated as the distance between the maximum and minimum $\delta^{13}C$ values. This represents the degree of basal resources consumed in a group. A larger CR indicates multiple basal resources in the diet and a smaller CR indicates less basal resources in the diet. TA is calculated as the total area of the $\delta^{13}C$-$\delta^{15}N$ in bivariate space. This represents the total niche space occupied, in which larger TA values indicate greater trophic diversity and smaller TA values indicate less trophic diversity in a group. CD is calculated as the average Euclidean distance to the centroid (the mean $\delta^{13}C$ and $\delta^{15}N$ value). This metric is beneficial in that it provides an average of the trophic diversity within a group, whereas TA may be more influenced by outliers. NND is calculated as the mean of the Euclidean distances to the nearest neighbor. This provides information on the density of the $\delta^{13}C$-$\delta^{15}N$ values, in which larger NND values indicated more differences in the trophic niches and smaller NND values indicate more similarities in the trophic niches of that group. SDNND represents the evenness of the bivariate density, in which larger values indicate more variability in the trophic niches and smaller values indicate less variability of trophic niches of that group.

Linear regressions were used to test the effects of two oceanographic factors, sea surface temperature (SST) and chlorophyll a (Chl *a*), on $\delta^{13}C$, $\delta^{15}N$, and Layman metrics. Both SST (^{o}C) and Chl *a* (mg/m^3) data were obtained from NASA's Earthdata EOSDIS Giovanni Visualization data portal (https://giovanni.gsfc.nasa.gov/ Accessed October 8, 2018). These data were collected at a 4x4 km box resolution using NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) satellites. Data were selected from the closest locations to this study's collection sites and averaged over 12 years (2005 to 2017) for each region in order to capture the fluctuations over time.

Results

There were 598 female (48%) and 660 male (52%) Lingcod with gut contents available for analysis. The total lengths of all 1,258 Lingcod ranged from 27–115 cm (mean and SD of 68.3 ± 13.4 cm) and exhibited an overall increase in size from South to North (Figure 2). Total lengths of females ranged from 33.3–115 cm (mean and SD of 76.1 ± 13.0 cm). Total lengths of males ranged from 27–90 cm (mean and SD of 61.2 ± 9.0 cm).

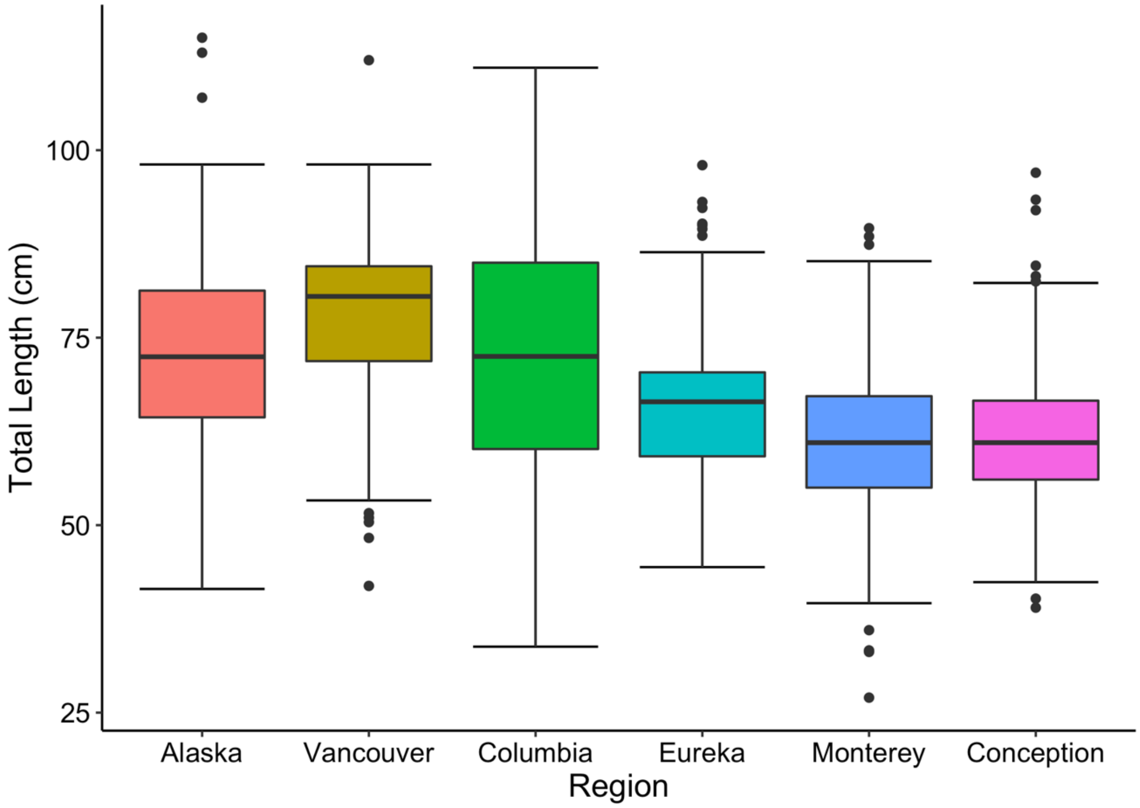


Figure 2. Box plot of total lengths (cm) of 1,258 Lingcod used for dietary analysis, by region. The horizontal line inside each box represents the median length for that region, the colored box represents the interquartile range (IQR), the horizontal bars above and below the box are ± 1.5 * IQR, and the black dots represent outliers.

There was a wide array of prey found from the 1,258 Lingcod stomachs (Table 2). Overall, Lingcod primarily consumed fishes. By prey group, the most important and most frequently occurring were the Unidentified Teleostei (49.25% PSIRI, 60.81% O), Cephalopoda (22.53% PSIRI, 31.88% O), and Scorpaenidae (11.90% PSIRI, 15.02% O; Table 3). However, the most important prey groups by prey-specific abundance by number and weight followed a different trend. Unidentified Teleostei still had the highest prey-specific abundance by number (81.15% PN), followed by Semi-Pelagic Fishes (76.64% PN), and Gadiformes (76.30% PN). The prey groups with the highest prey-specific abundance by weight were Scorpaenidae (83.49% PW), Semi-Pelagic Fishes (83.03% PW), and Gadiformes (82.12% PW).

By prey item, Unidentified Teleostei comprised close to half (48.9% PSIRI) of the importance of Lingcod diets, followed by Octopodidae (19.1% PSIRI) and Sebastes spp. (9.4% PSIRI). These prey items were also the most frequently occurring across all regions (Unidentified Teleostei 60.1% O, Octopodidae 27.3% O, Sebastes spp. 12.0% O).

Table 2. Lingcod gut contents listed with dietary metrics. There were 61 types of prey items, from 1,258 Lingcod stomachs, and sorted into 8 prey groups. An asterisk indicates less than 0.1%.

Prey Group	Prey Item	# Stomachs	%O	%N	%PN	%W	%PW	%PSIRI
Crustacea & Gastropoda	**Unidentified Crustacea**	2	0.2	0.1	62.5	0.1	56.3	0.1
	Eucarida	1	0.1	0.1	100.0	0.1	100.0	0.1
	Decapoda	5	0.4	0.1	33.3	*	10.7	0.1
	Pleuroncodes planipes	17	1.4	0.9	65.7	1.2	86.8	1.0
	Brachyura	2	0.2	0.1	41.7	*	1.8	*
	Cancridae	2	0.2	0.1	42.5	*	28.2	0.1
	Cancer	1	0.1	0.1	75.0	*	11.6	*
	Caridea	8	0.6	0.3	42.1	0.3	39.6	0.3
	Heptacarpus	1	0.1	*	50.0	0.1	64.3	*
	Crangon	1	0.1	*	25.0	0.1	97.4	*
	Paguroidea	1	0.1	*	33.3	*	3.7	*
	Lithodidae	1	0.1	*	25.0	*	3.0	*
	Paguridae	1	0.1	0.1	100.0	0.1	100.0	0.1
	Pagurus	2	0.2	*	18.8	0.1	55.5	0.1
	Unidentified Gastropoda	9	0.7	0.4	49.0	0.1	16.5	0.2
	Trichotropis cancellata	3	0.2	0.1	27.8	0.1	30.9	0.1
	Anabathridae	1	0.1	*	50.0	*	33.3	*
	Calliostoma	1	0.1	*	50.0	*	13.6	*
	Columbellidae	1	0.1	0.1	100.0	0.1	100.0	0.1
	Cylichnidae	1	0.1	*	60.0	*	57.1	*
	Littorinidae	2	0.2	*	11.1	*	14.8	*
	Littorina plena	1	0.1	*	50.0	*	25.0	*
	Muricidae	2	0.2	0.1	36.8	*	10.6	*
	Nucella	1	0.1	*	16.7	*	6.0	*
	Ocenebra	1	0.1	0.1	75.0	0.1	92.3	0.1
	Rissoidae	1	0.1	*	16.7	*	10.7	*
	Trochidae	3	0.2	*	10.2	*	3.7	*
	Volutacea	1	0.1	0.1	66.7	*	1.0	*
Cephalopoda	Cephalopoda	11	0.9	0.6	64.4	0.6	71.8	0.6
	Octopodidae	344	27.3	20.3	74.3	17.9	65.4	19.1
	Octopus dofleini	22	1.7	1.3	76.3	1.6	93.5	1.5
	Loligo opalescens	38	3.0	1.5	49.4	1.1	37.2	1.3
	Octopoteuthis deletron	1	0.1	*	50.0	0.0	50.0	*
Unidentified Teleostei	Unidentified Teleostei	756	60.1	49.0	81.6	48.8	81.2	48.9
	Fish egg mass	10	0.8	0.3	41.8	0.3	43.6	0.3
Scorpaenidae	Scorpaenidae	30	2.4	1.8	76.3	1.9	80.7	1.9
	Sebastes spp.	151	12.0	8.8	73.4	9.9	82.8	9.4
	Sebastes flavidus	1	0.1	0.1	100.0	0.1	100.0	0.1
	Sebastes jordani	2	0.2	0.1	75.0	0.2	99.2	0.1
	Sebastes melanops	2	0.2	0.2	100.0	0.2	100.0	0.2
	Sebastes mystinus	1	0.1	0.1	100.0	0.1	100.0	0.1
	Sebastes semicinctus	1	0.1	*	42.9	*	54.7	*
	Sebastes zacentrus	2	0.2	0.2	100.0	0.2	100.0	0.2
Demersal Fishes	Cottidae	10	0.8	0.5	63.3	0.6	79.9	0.6
	Leptocottus armatus	5	0.4	0.3	73.6	0.3	71.8	0.3
	Enophyrs bison	1	0.1	*	50.0	0.1	65.0	*
	Hexagrammidae	2	0.2	0.1	75.0	0.1	58.5	0.1
	Ophiodon elongatus	2	0.2	0.1	37.5	0.1	59.5	0.1
	Anoplopoma fimbria	4	0.3	0.3	87.5	0.3	96.6	0.3
	Ammodytes personatus	5	0.4	0.3	68.3	0.4	98.9	0.3
	Ophiidae	21	1.7	0.9	54.3	0.9	55.3	0.9
Semi-Pelagic Fishes	*Scomber japonicus*	1	0.1	0.1	100.0	0.1	100.0	0.1
	Clupeidae	15	1.2	1.2	100.0	1.2	100.0	1.2
	Clupea pallasii	18	1.4	0.8	55.9	1.0	68.0	0.9
Pleuronectiformes	Pleuronectiformes	30	2.4	1.5	60.8	1.9	81.2	1.7
	Citharichthys sordidus	1	0.1	0.1	100.0	0.1	100.0	0.1
	Atheresthes stomias	3	0.2	0.1	55.6	0.2	65.2	0.1
	Microstomus pacificus	1	0.1	*	50.0	0.1	97.9	0.1
	Parophrys vetulus	2	0.2	0.1	58.3	0.2	97.3	0.1
Gadiformes	Gadiformes	26	2.1	1.4	67.1	1.5	70.5	1.4
	Merluccius productus	82	6.5	5.2	79.2	5.6	85.8	5.4

Table 3. Lingcod gut content prey groups and several standard dietary metrics: frequency of occurrence (%O), abundance by number (%N), prey-specific abundance by number (%PN), abundance by weight (%W), prey-specific abundance by weight (%PN), and prey-specific index of relative importance (%PSIRI).

Prey Groups	%O	%N	%PN	%W	%PW	%PSIRI
Unidentified Teleostei	60.81	49.35	81.15	49.15	80.83	49.25
Cephalopoda	31.88	23.73	74.46	21.32	66.88	22.53
Scorpaenidae	15.02	11.25	74.90	12.54	83.49	11.90
Gadiformes	8.59	6.55	76.30	7.05	82.12	6.80
Crustacea & Gastropoda	4.61	2.78	60.27	2.51	54.34	2.64
Demersal Fishes	3.97	2.47	62.16	2.78	70.01	2.63
Semi-Pelagic Fishes	2.70	2.07	76.64	2.24	83.03	2.16
Pleuronectiformes	3.02	1.80	59.43	2.40	79.60	2.10

A PERMANOVA model was used to determine factors that significantly influenced Lingcod diets (Table 4). A model was created for both abundance by number and by weight; however, as both models were nearly identical, only abundance by number results are shown. Depth, region, sex, and the interaction between depth and region were all important variables that significantly influenced Lingcod diets. Length and gape exhibited a strong positive correlation (Pearson’s correlation 0.73, n = 1,240, $p<0.001$). However, in both models, length and gape were not significant when other factors were included and were therefore excluded in further analysis. No other factors exhibited high levels of collinearity (variance inflation factor scores all <5).

The first model included the Unidentified Teleostei prey group, while the final model did not. The Unidentified Teleostei prey group is a vague grouping of unidentified bony fishes but comprised nearly half of the importance of Lingcod diets (49.25% PSIRI; Table 3). Removing the Unidentified Teleostei prey group for statistical purposes greatly reduced variance and created a stronger model without changing the order of the variables or reducing their significance as in the first model. The first model explained 12.78% of the variability in Lingcod diets by number, and the final model explained 24.4% of the variability in Lingcod diets by number.

Table 4. Permutational multivariate analysis of variance (PERMANOVA) models indicating variables that exhibit significant differences in Lingcod gut contents using abundance by number. The first model included the Unidentified Teleostei prey group (8 prey groups), while the final model did not (7 prey groups). Pseudo *F* is a means of determining within group and between group variability, where higher Pseudo *F* values indicate a more explanatory variable for the model, and was used to rank the variables.

Model	Variable	df	Pseudo *F*	r^2	*p*-value
Final Model (Without Unidentified Teleostei)	Depth	1	131.741	0.13209	0.0001
	Region	5	14.896	0.07468	0.0001
	Sex	1	3.556	0.00357	0.0123
	Depth x Region	5	6.716	0.03367	0.0001
	Residuals	754		0.756	
First Model (With Unidentified Teleostei)	Depth	1	83.732	0.05866	0.0001
	Region	5	10.041	0.03517	0.0001
	Sex	1	2.695	0.00189	0.0495
	Depth x Region	5	9.172	0.03213	0.0001
	Residuals	1245		0.87216	

Depth was the most important variable in the PERMANOVA models, and in the final model it explained 13.2% of the variability in Lingcod diets. In order to better understand the influence of depth on Lingcod diets by region and sex, these data were grouped into shallow (<30m), moderate (30-60m), and deep (>60m) water depth bins. More female Lingcod were collected in deeper depths, and more male Lingcod were collected in shallower depths. Of the 7 prey groups included, Cephalopoda was the most important prey group for Lingcod in the shallow (<30m) and moderate (30-60m) water depth bins by abundance by number at 64.6% and 58.1%, respectively (Figure 3). In contrast, the most important prey group for Lingcod in the deep (>60m) water depth bin was Gadiformes at 36.1%. In all three depth bins, Scorpaenidae was the second most important prey group (shallow 14.5%; moderate 24.3%; deep 22.7%). The least amount of Cephalopoda and the largest amount of Gadiformes were in the Vancouver region, where deeper fishing occurred and where the highest proportion of female Lingcod were caught.

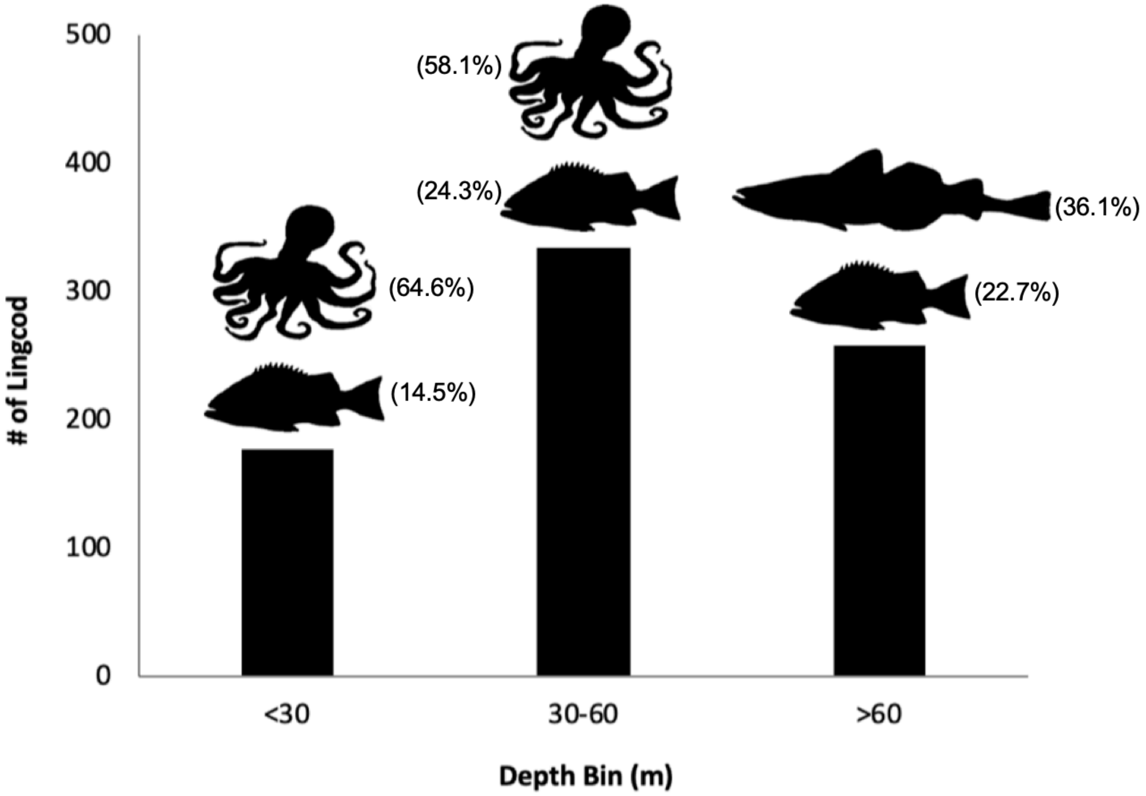


Figure 3. The number of Lingcod per depth bin (m), and the most important prey groups by abundance by number (N) contributing to that depth bin above each bar. Numbers next to each icon indicate %N for that depth bin. Cephalopoda was the most important prey group for the shallow (<30m) and moderate (30-60m) depth bins, while Gadiformes was the most important prey group for the deep (>60m) depth bin. Scorpaenidae was the second most important prey group in each depth bin.

Region explained 7.4% of the variance in the final model. A principal component analysis (PCA) was used to visually assess regional similarities and dissimilarities in Lingcod diets by abundance by number (Figure 4). Based on the results from the PERMANOVA, the 7 prey groups used in the final model were used in the PCA. Then, the average principal component scores for each region were plotted onto the PCA. Principal component 1 (PC1) explained 21.9% of the variation and principal component 2 (PC2) explained 17.7% of the variation. Overall, the PCA explained a moderate amount of variation. This is likely due to the fact that these Lingcod consumed a wide variety of prey which created a large dataset with many zeros. PC1 primarily described regions where Lingcod consumed Cephalopoda (positive values), while PC2 primarily described regions where Lingcod consumed Scorpaenidae (positive values) and Gadiformes (negative values). The clearest pattern seen here is from the high levels of Gadiformes, followed by Semi-Pelagic Fishes, consumed by Lingcod in the Vancouver region. Another clear pattern is the high levels of Cephalopoda consumed by Lingcod in the Eureka, Monterey, and Conception regions. The Alaska region separated out from the rest of the regions as being primarily influenced by Scorpaenidae. The Columbia region exhibited the least clear pattern among all regions, because it was influenced by multiple prey groups.

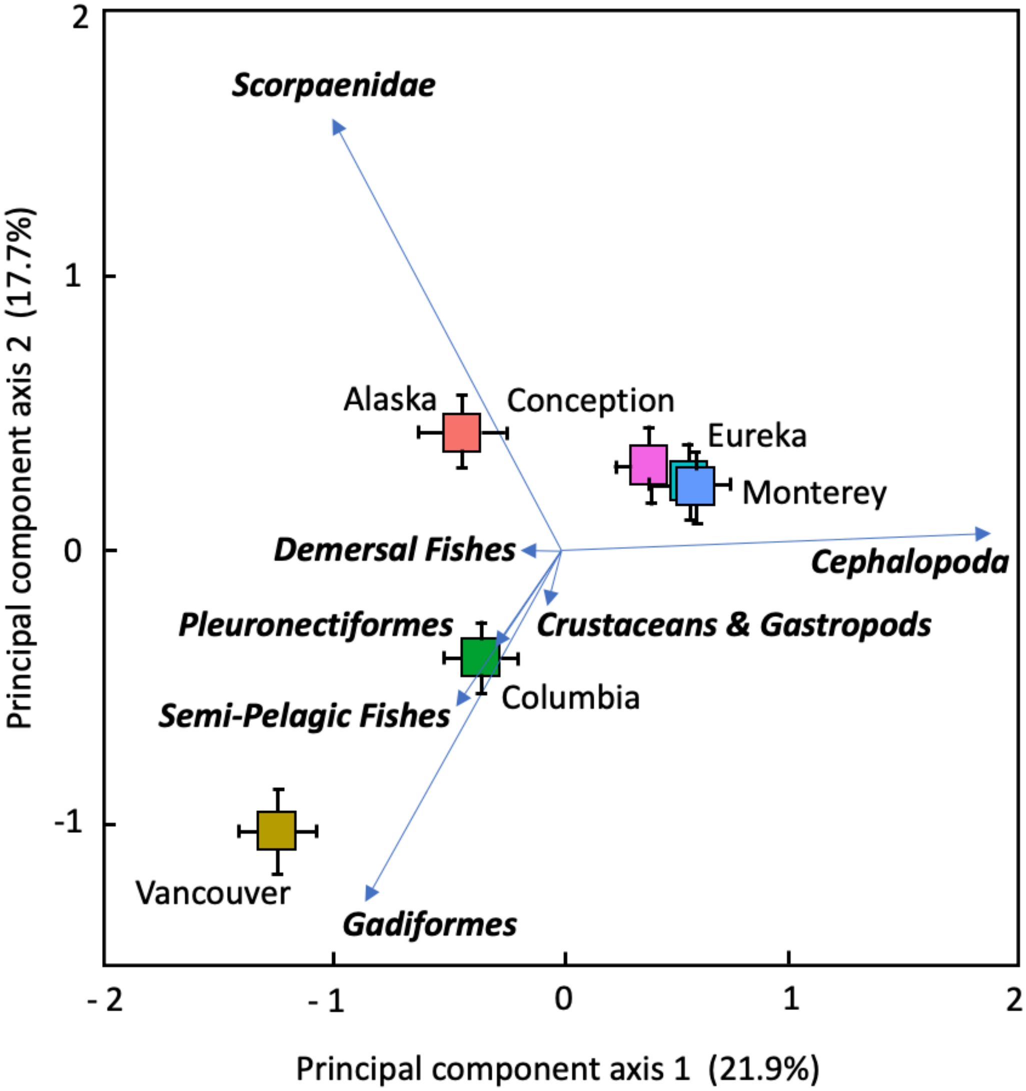


Figure 4. Principal component analysis (PCA) of Lingcod gut contents abundance by number from 7 prey groups. Squares indicate the average principal component score for each region and their error bars represent ± 1 standard error. Lines indicate the eigenvector values for each prey group. Principal component 1 explained 21.9% of the variation and principal component 2 explained 17.7% of the variation.

In addition to the PERMANOVA and PCA, a similarity percentage (SIMPER) analysis was used to identify which of the 7 prey groups contributed to regional similarities (Table 5) and dissimilarities (Table 6) by abundance by number. In various combinations, 4 of the 7 prey groups (Cephalopoda, Gadiformes, Scorpaenidae, and Semi-Pelagic Fishes) contributed to the top 80% of similarities within each region. The average similarity within a region column indicates how similar Lingcod diets are to one another within a region, in which lower percentages suggest higher diversity of prey in Lingcod diets and higher percentages suggest lower diversity of prey in Lingcod diets. Alaska had the least similarity to itself (25.38%; i.e. more diverse diets), while Eureka had the most similarity to itself (53.24%; i.e. less diverse diets).

Table 5. Results of similarity percentage (SIMPER) analysis of Lingcod gut-content prey groups using abundance number by region (excluding the Unidentified Teleostei prey group). The second column indicates how similar that region is to itself, while the last column indicates the cumulative percentage of the prey groups that contribute the top 80% of that similarity.

Region	Average Similarity within a Region %	Prey Group	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum.%
Alaska	25.38	Scorpaenidae	1.23	14.3	0.42	56.33	56.33
		Cephalopoda	0.92	7.11	0.31	28.02	84.36
Vancouver	29.69	Gadiformes	1.37	17.76	0.48	59.8	59.8
		Semi-Pelagic Fishes	1	8.86	0.33	29.83	89.63
Columbia	26.98	Cephalopoda	1.16	12.89	0.39	47.76	47.76
		Gadiformes	1.02	10.04	0.34	37.2	84.96
Eureka	53.24	Cephalopoda	2.3	48.78	1.07	91.62	91.62
Monterey	52.72	Cephalopoda	2.28	48.68	1.05	92.34	92.34
Conception	46.11	Cephalopoda	2.12	38.66	0.94	83.84	83.84

Table 6. Pairwise comparisons of Lingcod gut contents, using abundance by number, between regions (ranked in order of ascending dissimilarity) indicating each region's dissimilarity to one another.

Regions	Ave. Dissimilarity %
Vancouver & Monterey	92.91
Vancouver & Conception	92.36
Vancouver & Eureka	92.09
Vancouver & Alaska	89.53
Vancouver & Columbia	80.8
Alaska & Columbia	80.38
Alaska & Monterey	72.46
Conception & Columbia	71.9
Alaska & Eureka	71.87
Alaska & Conception	71.32
Columbia & Monterey	70.36
Columbia & Eureka	69.54
Conception & Monterey	51.09
Conception & Eureka	50.66
Monterey & Eureka	46.72

The variety of prey items was greatest in Alaska when compared to other regions; 33 types of prey items were identified from 140 stomachs (Appendix 2). The wider array of Crustacea and Gastropoda prey items are associated with the stomachs that contained fish egg masses. The most important prey groups for Alaska were Scorpaenidae (56.33%) and Cephalopoda (28.02%) for a cumulative total of 84.63% (Table 5). The Scorpaenidae prey group was primarily composed of rockfishes (Sebastes spp.), and the Cephalopoda prey group was primarily composed of octopuses (Octopodidae) followed by market squid (*Loligo opalescens*). The prey accumulation curve reached an asymptote, indicating that there were enough samples collected and analyzed to describe the diet of Lingcod in the Alaska region at the prey group level (b=0.000, Figure 5).

There were 16 types of prey items from 160 stomachs in the Vancouver region (Appendix 4). It was the most dissimilar among all regions, with at least 80% average dissimilarity between each region (Table 6). The most important prey groups for Vancouver were Gadiformes (59.8%) and Semi-Pelagic Fishes (29.83%) for a cumulative total of 89.63% (Table 5). Gadiformes primarily consisted of Pacific Hake (*Merluccius productus*) and other species from the order Gadiformes. Semi-Pelagic Fishes primarily consisted of Pacific Herring (*Clupea pallasii*) and members of the family Clupeidae. Additionally, this region had the least amount of Cephalopoda in Lingcod diets across all regions. The prey accumulation curve reached an asymptote, indicating that there were enough samples collected and analyzed to describe the diet of Lingcod in the Vancouver region at the prey group level (b=0.000, Figure 5).

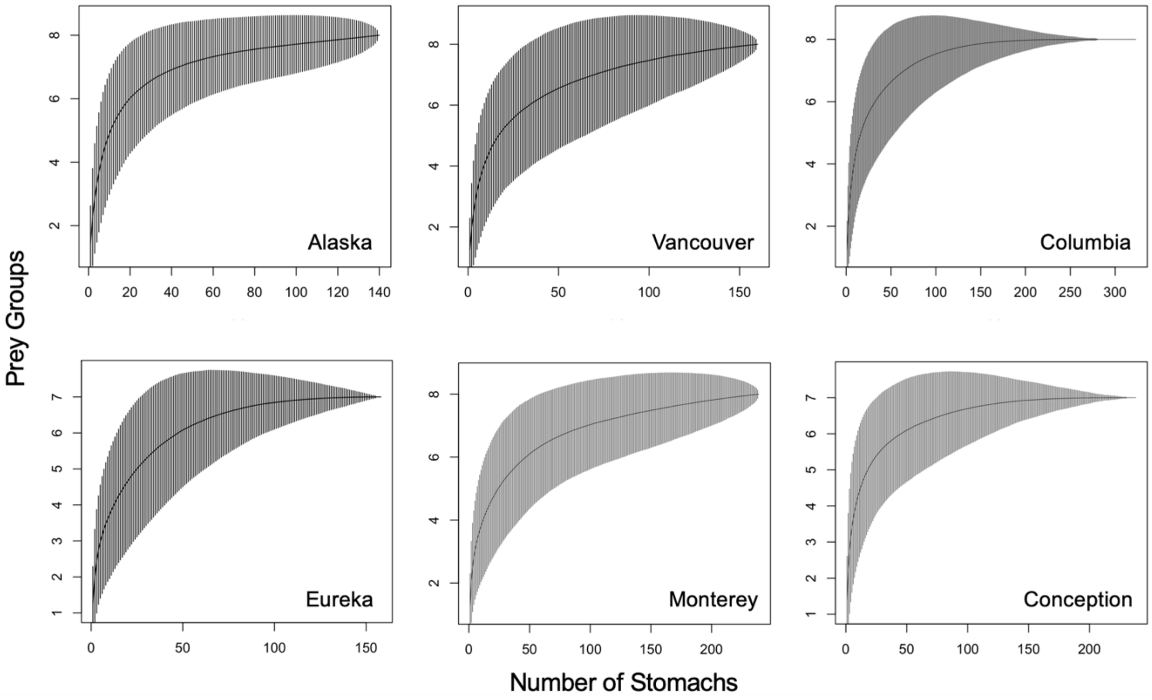


Figure 5. Prey accumulation curves for Lingcod, by region and prey group. The curved horizontal line represents the mean while the vertical lines represent the 95% confidence intervals around the mean. Note that the y-axis scale changes to 7 prey groups for Eureka and Conception (no Semi-Pelagic Fishes), and the x-axis changes based on number of stomachs for that region.

There were 22 types of prey items from 323 stomachs in the Columbia region (Appendix 5). The most important prey groups for Columbia were Cephalopoda (47.76%) and Gadiformes (37.2%) for a cumulative total of 84.96% (Table 5). The Cephalopoda prey group was primarily composed of octopuses (Octopodidae), and there were several instances in which Lingcod had consumed Giant Pacific Octopuses (*Octopus dofleini*). In one instance, the beak of a rare pelagic squid, *Octopoteuthis deletron,* was found in the stomach of a

Lingcod. The prey accumulation curve reached an asymptote, indicating that there were enough samples collected and analyzed to describe the diet of Lingcod in the Columbia region at the prey group level (b=0.000, Figure 5).

Eureka, Monterey, and Conception regions exhibited strong similarities with one another. The most important prey group for all three of these regions was Cephalopoda for a total of 91.62%, 92.34%, and 83.43%, respectively (Table 5). This pattern is also clear in the PCA, showing a clustering and some overlap of the three regions (Figure 4). There were 18 types of prey items from 158 stomachs in the Eureka region (Appendix 6), 24 types of prey items from 239 stomachs in the Monterey region (Appendix 7), and 18 types of prey items from 238 stomachs in the Conception region (Appendix 8). In the Eureka and Monterey regions, the Cephalopoda prey group was primarily composed of octopuses (Octopodidae), and there were several instances in which Lingcod had consumed Giant Pacific Octopuses (*Octopus dofleini*). In the Conception region, the Cephalopoda prey group was composed primarily of octopuses (Octopodidae), but also with an influence of market squid (*Loligo opalescens*). After Cephalopoda, Scorpaenidae (Sebastes spp.) was the most consumed prey group for Lingcod in these three regions. Correspondingly, these three regions were the least dissimilar to one another (Table 6). The Conception region was the furthest South and contained higher numbers of Demersal Fishes (Ophiidae) and Pelagic Red Crabs (*Pleuroncodes planipes*). The prey accumulation curves reached an asymptote, indicating that there were enough samples collected and analyzed to describe the diet of Lingcod in the Eureka (b=0.000), Monterey (b=0.000), and Conception (b=0.000) regions at the prey group level (Figure 5).

There were 41 types of prey items from 598 female Lingcod stomachs (Appendix 9) and 45 types of prey items from 660 male stomachs (Appendix 10). Female Lingcod ate 1,317 individual prey items with a combined weight of 38,234 g, whereas male Lingcod ate 1,625 individual prey items with a total weight of 15,093 g. Female Lingcod stomachs contained an average of 63.9 g of prey (SE of ± 5.3 g), whereas male stomachs contained an average of 22.9 g of prey (SE of ± 1.6 g). This means that on average, female Lingcod ate more than 2.7 times the amount of weight in prey compared to male Lingcod, due primarily to the fact that female Lingcod attain larger sizes than males. However, on a per weight basis, a hypothetical male and female Lingcod each weighing 3.5 kg would have 35.2 g and 36.2 g of prey in their stomachs, respectively. The prey accumulation curves reached an asymptote, indicating that there were enough samples collected and analyzed to describe the diet of female (b=0.000, Figure 6A) and male (b=0.000, Figure 6B) Lingcod at the prey group level.

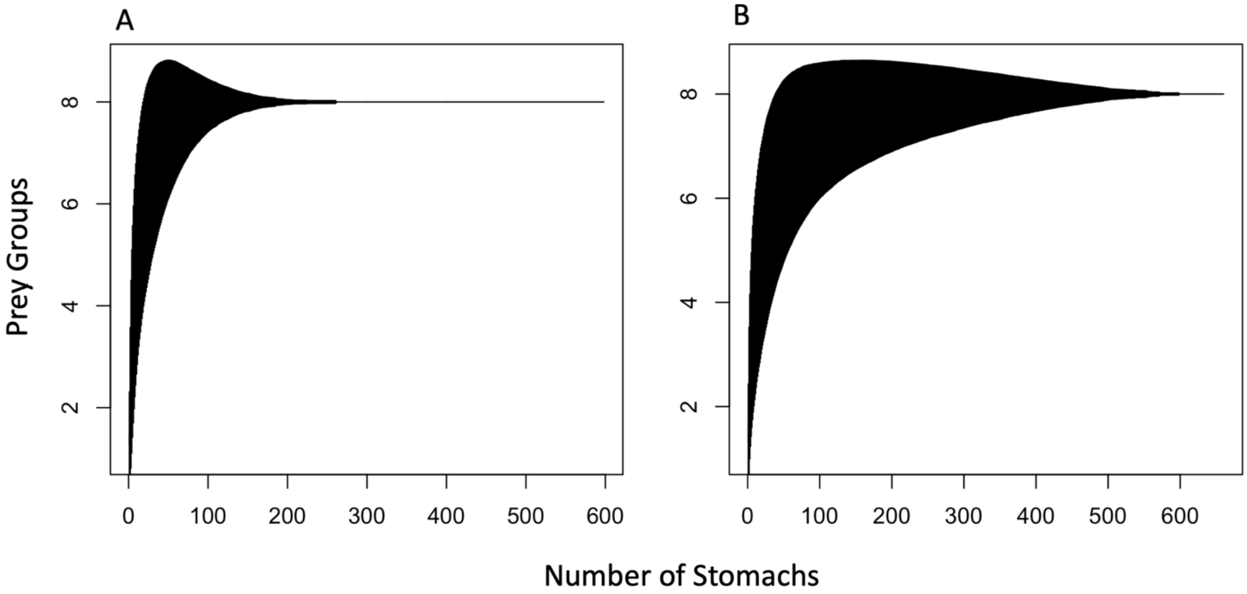
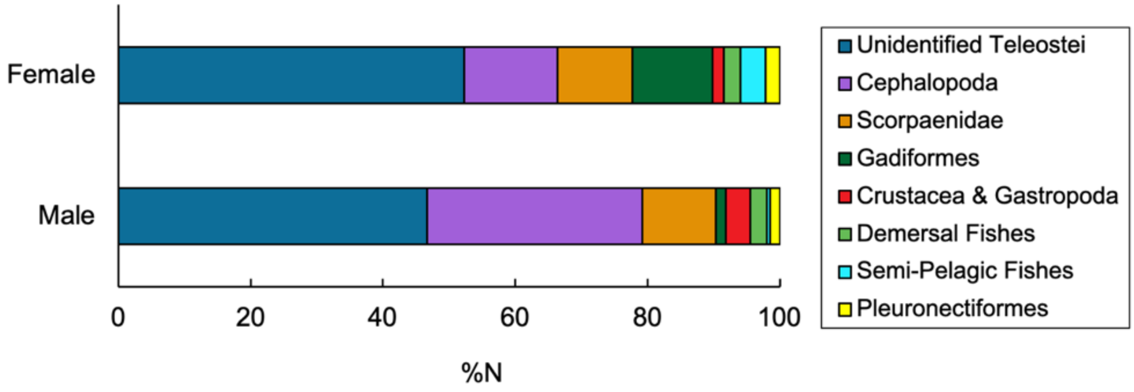


Figure 6. Prey accumulation curves for A) female and B) male Lingcod, by prey group. The shaded areas denote the 95% confidence intervals around the means.

Sex explained only 0.3% of the variation in Lingcod diets but was still a significant variable in both PERMANOVA models. Most prominently, as a whole, male Lingcod ate 2.3 times the amount of Cephalopoda compared to female Lingcod by both abundance and weight (Figure 7). This also held true on a regional basis; male Lingcod consistently consumed more Cephalopoda than female Lingcod with the exception of abundance by weight in the Alaska region. Male Lingcod also ate 2.2 times the abundance and 2.8 times the weight of Crustacea and Gastropoda compared to female Lingcod. On a regional basis, male Lingcod consistently consumed more Crustacea and Gastropoda compared to female Lingcod, with the exception of abundance by number in the Eureka region, and in the Vancouver region. However, there were only 14 male Lingcod collected in the Vancouver region, potentially limiting the full understanding of male Lingcod diets from that area. Female Lingcod ate 8 times the abundance by number and 6 times the abundance by weight of Gadiformes than did male Lingcod. Female Lingcod also ate 7.6 times the abundance by number and 8.4 times the abundance by weight of Semi-Pelagic Fishes compared to male Lingcod. These last two trends were primarily driven by the diets of Lingcod in the Vancouver region, as Gadiformes and Semi-Pelagic Fishes were found in the diets of males and females in a variety of quantities among all other regions.

A)



B)

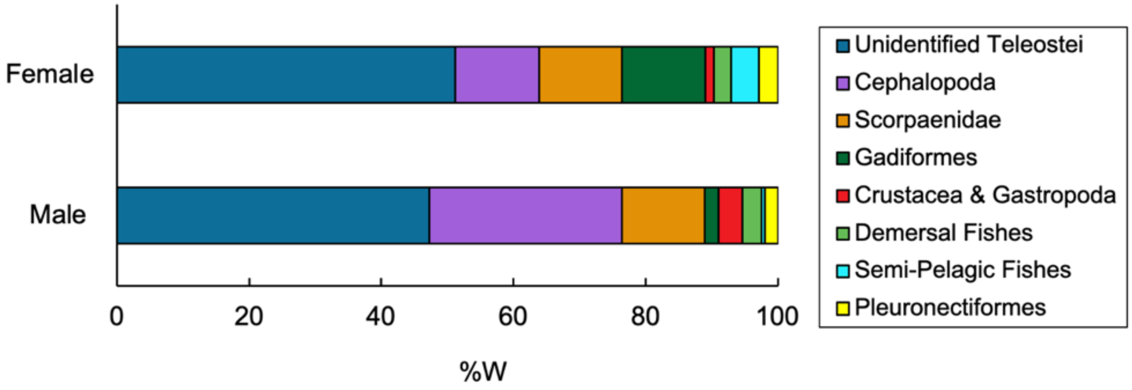


Figure 7. Lingcod gut content prey groups by sex for A) percent abundance by number (%N) and B) percent abundance by weight (%W).

Trophic level and diversity indices exhibited consistent similarities among one another (Table 7). Lingcod trophic levels ranged from 3.10 to 4.24, with a mean of 4.20. The lower values correspond to invertebrate dominated diets, while higher values correspond to fish dominated diets. As previously described (Table 2 and Table 3), the majority of these Lingcod diets consisted of fishes, which explains the overall high mean trophic levels. The trophic level equation (see methods) used in this study assumed that all Lingcod occupied the same trophic level. However, smaller Lingcod do not eat as high a trophic level as larger Lingcod, and the lengths of Lingcod were not accounted for in the equation, potentially creating a bias. Simpson’s diversity index ranged from 1 to 4.53, with a mean of 1.27. A ‘1’ indicates no diversity (only one type of prey in a stomach). Shannon’s diversity index ranged from 0 to 1.51, with a mean of 0.19. A ‘0’ indicates no diversity (only one type of prey in a stomach). The trophic levels and diversity indices indicated that Lingcod from the Alaska and Conception regions fed at a lower trophic level and had more diverse diets (Table 7). Similarly, Lingcod that were male, or from shallow waters ate at a lower trophic level and had more diverse diets. Conversely, Lingcod from the Vancouver and Columbia regions, and Lingcod that are female, or from deep waters fed at a higher trophic level and had the least diverse diets.

Table 7. Mean overall Lingcod trophic levels and diversity indices by region, sex, length, and depth. All three metrics were calculated using Lingcod gut contents.

		Trophic Level	Simpson Index	Shannon Index
Region	Alaska	4.16 ± 0.2	1.43 ± 0.7	0.29 ± 0.4
	Vancouver	4.23 ± 0.1	1.19 ± 0.4	0.14 ± 0.3
	Columbia	4.22 ± 0.1	1.20 ± 0.4	0.15 ± 0.3
	Eureka	4.21 ± 0.1	1.26 ± 0.5	0.18 ± 0.3
	Monterey	4.21 ± 0.1	1.24 ± 0.4	0.18 ± 0.3
	Conception	4.19 ± 0.2	1.37 ± 0.6	0.26 ± 0.4
Sex	Female	4.22 ± 0.1	1.23 ± 0.5	0.17 ± 0.3
	Male	4.19 ± 0.1	1.31 ± 0.5	0.22 ± 0.3
Length	Small	4.21 ± 0.1	1.23 ± 0.5	0.17 ± 0.3
	Large	4.21 ± 0.1	1.28 ± 0.5	0.20 ± 0.3
Depth	Shallow	4.18 ± 0.2	1.36 ± 0.6	0.25 ± 0.4
	Moderate	4.20 ± 0.1	1.27 ± 0.5	0.19 ± 0.3
	Deep	4.23 ± 0.1	1.23 ± 0.5	0.17 ± 0.3
Total	All	4.21 ± 0.1	1.27 ± 0.5	0.19 ± 0.3

Stable Isotope Analysis

Stable isotopes were analyzed from 257 female (49.5%) and 262 male (50.5%) Lingcod. The total lengths of all 519 Lingcod used for SIA ranged from 33.8–115 cm (mean and SD of 65.5 ± 13.4 cm). Female total lengths ranged from 39.6–115 cm (mean and SD of 71.1 ± 14.4 cm). Male total lengths ranged from 33.8–88.5 cm (mean and SD of 60.0 ± 9.6 cm). The overall range for $\delta^{13}C$ was -19.34‰ to -15.32‰ with a mean of -16.98‰, and the overall range for $\delta^{15}N$ was 14.59‰ to 18.29‰ with a mean of 16.51‰ (Table 8).

Table 8. Total numbers of Lingcod white muscle tissue samples used for the stable isotope analysis, and means, by region.

Region	# Lingcod Used for SIA from White Muscle Tissue	Mean $\delta^{13}C$ ± SD (‰)	Mean $\delta^{15}N$ ± SD (‰)	Mean C:N ± SD
Alaska	66	-17.81 ± 0.7	15.80 ± 0.5	3.32 ± 0.1
Vancouver	50	-16.64 ± 0.6	16.36 ± 0.4	3.37 ± 0.0
Columbia	72	-16.86 ± 0.5	16.60 ± 0.5	3.41 ± 0.1
Eureka	94	-16.69 ± 0.4	16.43 ± 0.4	3.33 ± 0.1
Monterey	130	-16.75 ± 0.5	16.53 ± 0.4	3.33 ± 0.1
Conception	107	-17.25 ± 0.8	17.02 ± 0.5	3.35 ± 0.1
All Regions	519	-16.98 ± 0.7	16.51 ± 0.6	3.35 ± 0.1

The $\delta^{13}C$ values indicate the source of primary production, in which the more negative values imply a pelagic carbon source and the less negative values imply a benthic carbon source. The highest mean $\delta^{13}C$ regional values were observed in the most northern and southern regions, Alaska and Conception, respectively. The mean $\delta^{13}C$ values from middle four regions clustered close to one another with relatively lower values. This indicates that the Alaska and Conception regions were more influenced by pelagic carbon sources while the middle four regions were not. The $\delta^{15}N$ values are a proxy for trophic level, in which lower values represent lower trophic levels and higher values represent higher trophic levels. There was a latitudinal trend observed, in which the mean $\delta^{15}N$ values increased from North to South. This indicates that overall, Lingcod from southern regions were eating higher trophic level prey. There is also the potential that there were baseline shifts in $\delta^{15}N$ values along this range. The Columbia region was interesting in that it had slightly higher $\delta^{13}C$ and $\delta^{15}N$ values compared to the regions above and below. Furthermore, the Columbia region also exhibited the highest mean C:N ratio among all regions. In general, a C:N ratio >3.5 indicates that there is high lipid content and potential to bias $\delta^{13}C$ values. Lingcod sampled across all regions exhibited similar C:N ratios with mean values <3.5, indicating relatively lean fish.

Lingcod white muscle tissue $\delta^{13}C$ and $\delta^{15}N$ values were plotted as an average by region (Figure 8). As indicated in the table above, the Alaska and Conception regions were more similar to one another in being influenced by more pelagic prey sources. Most prominently, the Alaska region separated out from the rest of the regions with the lowest δ^{13}C and δ^{15}N values. Also, the Conception region exhibited the highest δ^{15}N values. The middle four regions exhibited a large amount of overlap and fall between the Alaska and Conception regions.

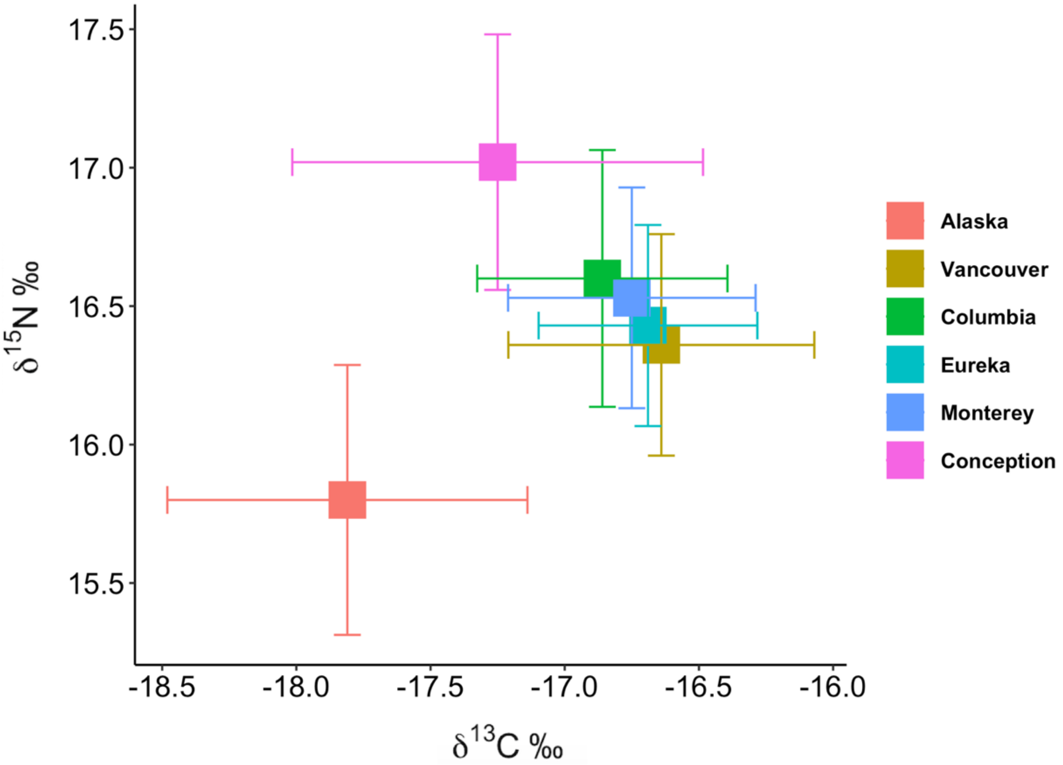


Figure 8. Relationship between Lingcod white muscle tissue carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope mean values with standard deviations, by region.

A GLM was used to determine factors that had a significant influence on Lingcod $\delta^{13}C$ and $\delta^{15}N$ values (Table 9). No factors exhibited high levels of collinearity (variance inflation factor scores all <5). Region was the only variable that significantly influenced the Lingcod $\delta^{13}C$ values. However, depth, sex, length, and region were all significant variables that influenced Lingcod $\delta^{15}N$ values.

Table 9. Generalized linear models (GLM) indicating variables that exhibit significant differences in Lingcod carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values.

Model	Variable	Estimate	SE	t value	p-value
Carbon	Depth	0.000488	0.000941	0.519	0.604145
	Sex	-0.077900	0.067430	-1.155	0.248544
	Length	0.000349	0.002691	0.13	0.896862
	Region	0.065590	0.019410	3.38	**<0.001**
Nitrogen	Depth	0.003311	0.000547	6.056	**<0.001**
	Sex	-0.113424	0.039168	-2.896	**0.00394**
	Length	0.011639	0.001563	7.446	**<0.001**
	Region	0.211063	0.011273	18.724	**<0.001**

For the carbon model, significant differences were predominantly driven by the Alaska and Conception regions (Tukey HSD, $p<0.0001$; Figure 9A). Lingcod from these regions exhibited the lowest average $\delta^{13}C$ values compared to Lingcod from the middle regions. This implies that Lingcod from the Alaska and Conception regions consumed prey with more pelagic carbon sources. Average $\delta^{13}C$ values were higher in the Vancouver, Columbia, Eureka, and Monterey regions, which implies that the Lingcod from these regions were eating more benthic and less pelagic food sources. For the nitrogen model, significant differences were also driven by the Alaska and Conception regions (Tukey HSD, $p<0.0001$; Figure 9B). In general, the average $\delta^{15}N$ values increased from northern to southern regions; they were lowest in the Alaska region and highest in the Conception region, with the exception of the Columbia region which exhibited significantly higher average $\delta^{15}N$ values compared to the Vancouver region (Tukey HSD, $p<0.027$). This implies Lingcod in the Alaska region consumed lower trophic level prey while those in the Conception region consumed higher trophic level prey, or that there are underlying baseline shifts in isotope signatures. Lingcod in the Vancouver, Columbia, Eureka, and Monterey regions were consuming relatively mid-range trophic level prey.

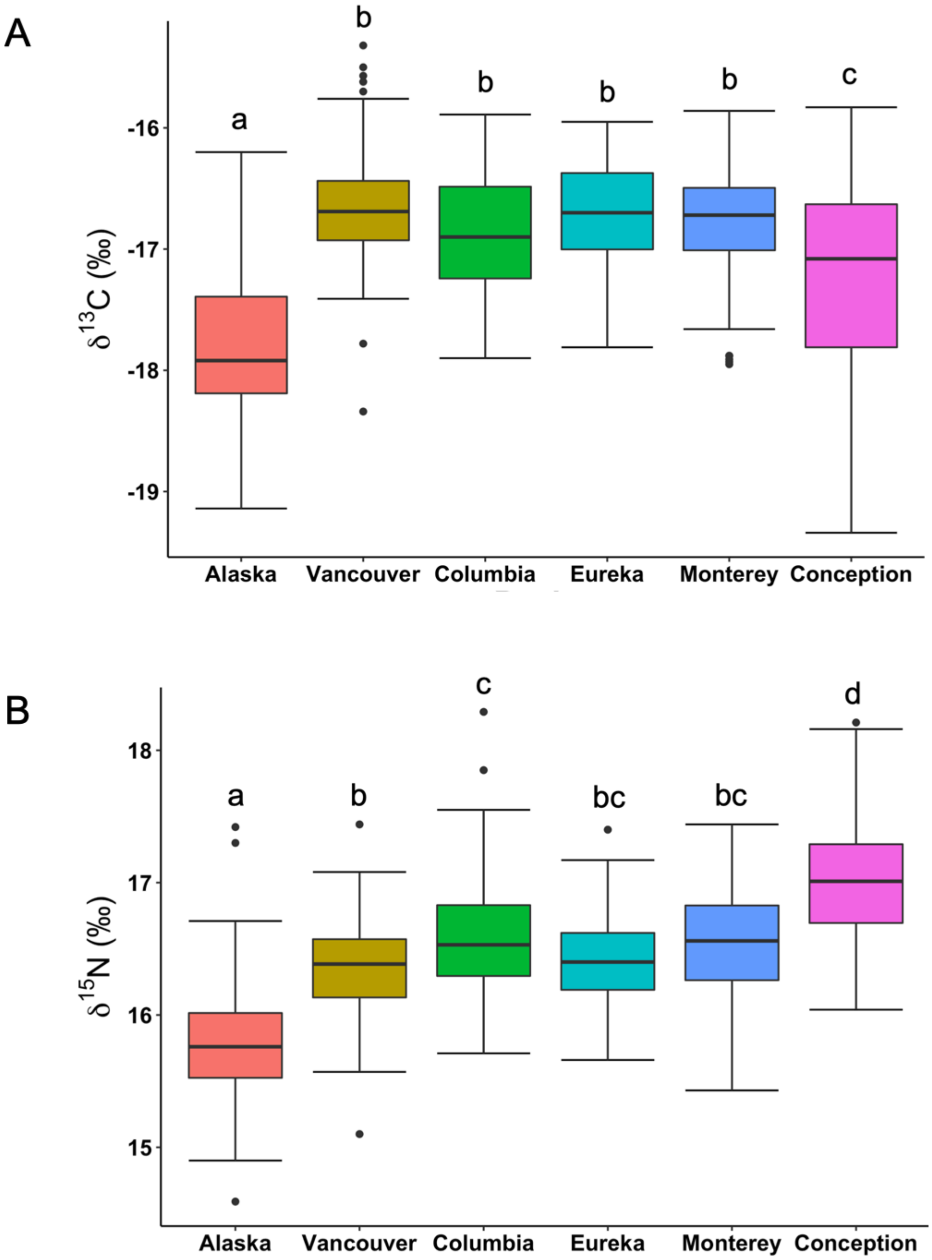


Figure 9. Box plots of stable isotope values of Lingcod by region for A) carbon ($\delta^{13}C$) and B) nitrogen ($\delta^{15}N$). The horizontal line inside the boxes represent the median value, the colored boxes represent the interquartile range (IQR), the horizontal bars above and below the box are ± 1.5 * IQR, and the black dots represent outliers. Letters above boxes represent Tukey Honest Significant Difference pairwise comparisons of regions, in which different letters indicate significant differences.

Within every region, $\delta^{15}N$ values were higher in Lingcod caught at deeper depths (Figure 10A). This indicates that Lingcod at deeper depths were consuming higher trophic level prey than Lingcod at shallower depths. Similarly, across all regions $\delta^{15}N$ values obtained from larger Lingcod were higher than smaller lingcod (Figure 10B). This indicates that larger Lingcod are consuming higher trophic level prey than smaller Lingcod.

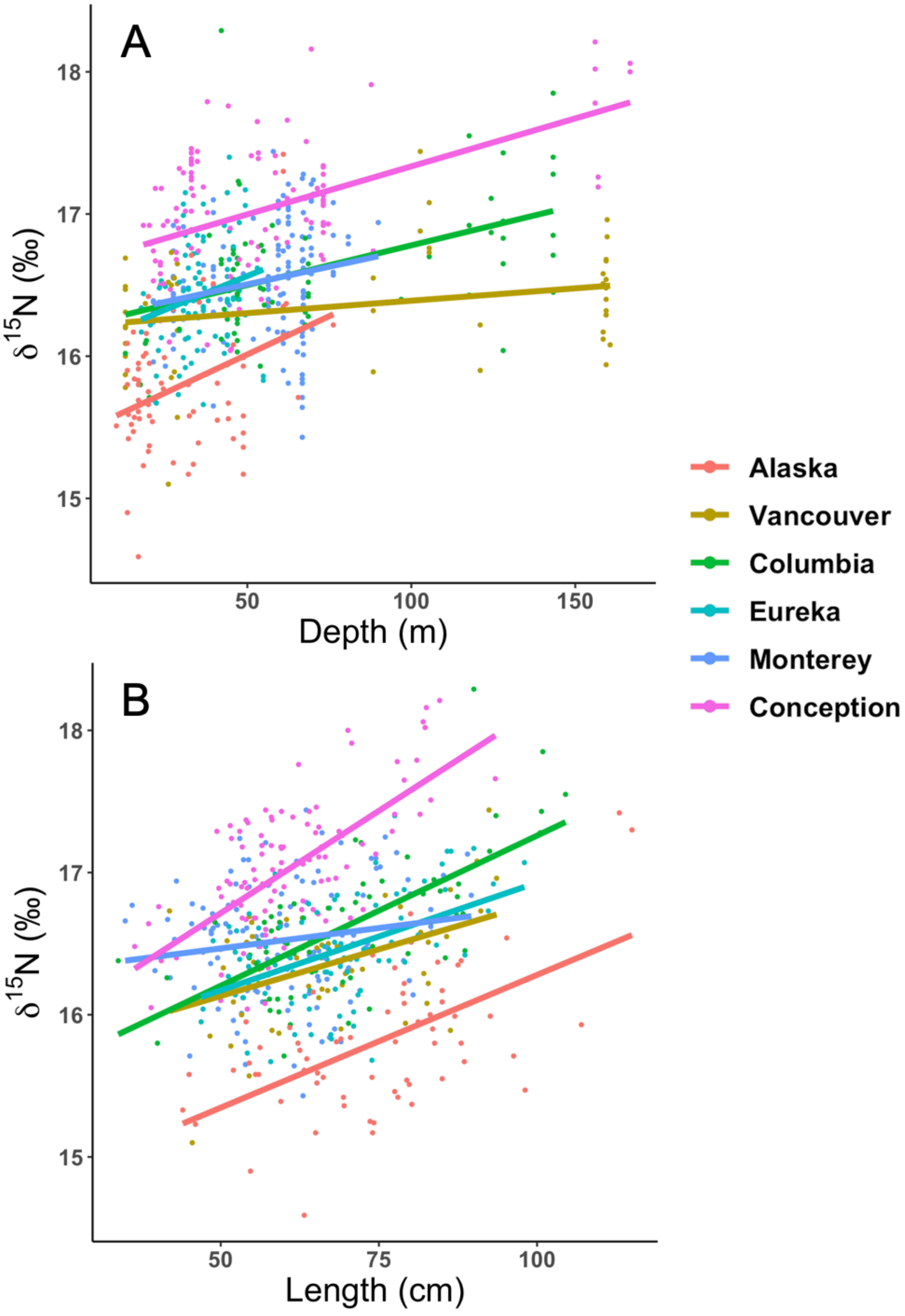


Figure 10. Relationship of Lingcod white muscle tissue nitrogen ($\delta^{15}N$) values to A) Lingcod capture depths and B) Lingcod total lengths, by region. Best fit lines were plotted for each region.

On average, $\delta^{15}N$ values measured in female Lingcod were consistently higher than those from males across all regions (Figure 11). An ANCOVA was then utilized to test for differences in $\delta^{15}N$ between female and male Lingcod while controlling for depth and length (Table 10). There was a significant effect of Lingcod sex on $\delta^{15}N$ after controlling for the effect of depth, in which $\delta^{15}N$ increased with depth in both male and female Lingcod at a similar rate (Figure 12A). There was also a significant effect of Lingcod sex on $\delta^{15}N$ after controlling for the effect of the length, in which, as Lingcod grew in length, $\delta^{15}N$ increased in females and decreased in males (Figure 12B).

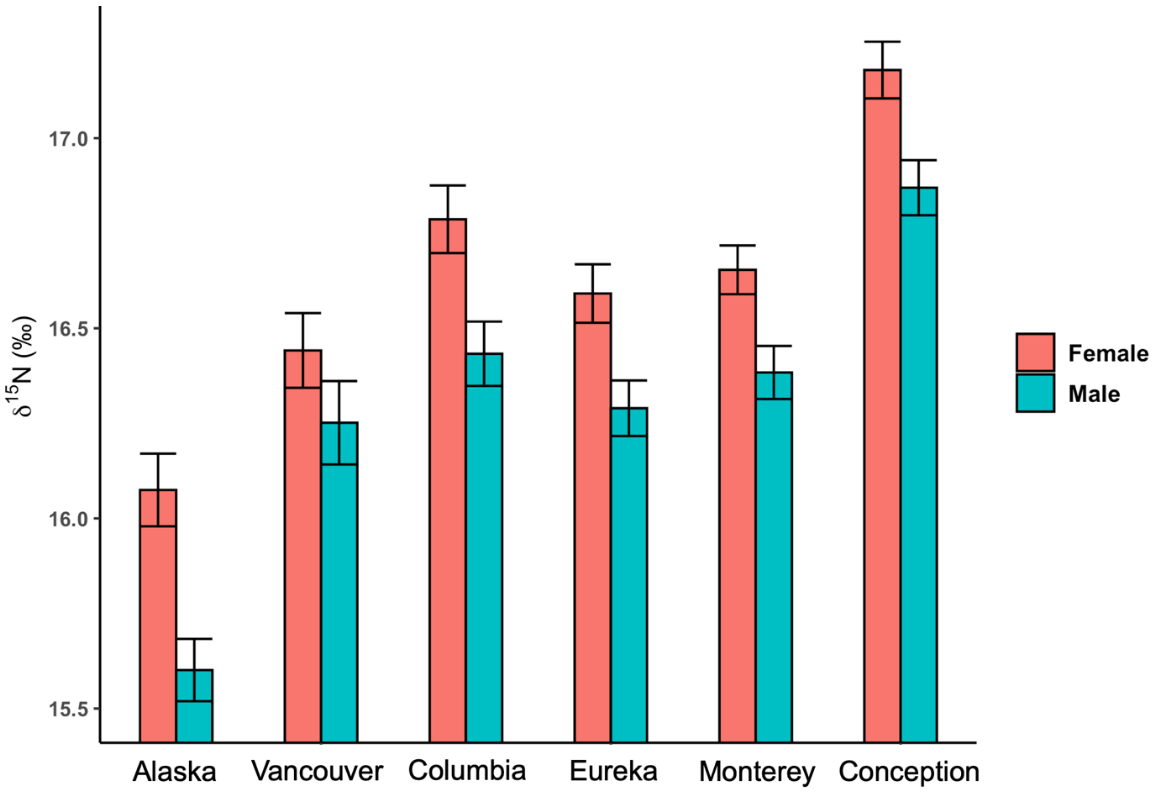


Figure 11. Bar plots showing the mean and standard error of nitrogen ($\delta^{15}N$) stable isotope values obtained from Lingcod white muscle tissues, by sex and region.

Table 10. Analysis of covariance (ANCOVA) models used to determine effects of sex, length, and depth on Lingcod white muscle tissue $\delta^{15}N$ values.

Model	**Variable**	**df**	**F**	***p*-value**
Sex & Depth	Sex	1	12.4799	**0.0004**
	Depth	1	25.3349	**<0.0001**
	Sex x Depth	1	0.8706	0.3512
	Residuals	515		
Sex & Length	Sex	1	5.8495	**0.0159**
	Length	1	10.0521	**0.0016**
	Sex x Length	1	13.2631	**0.0003**
	Residuals	515		

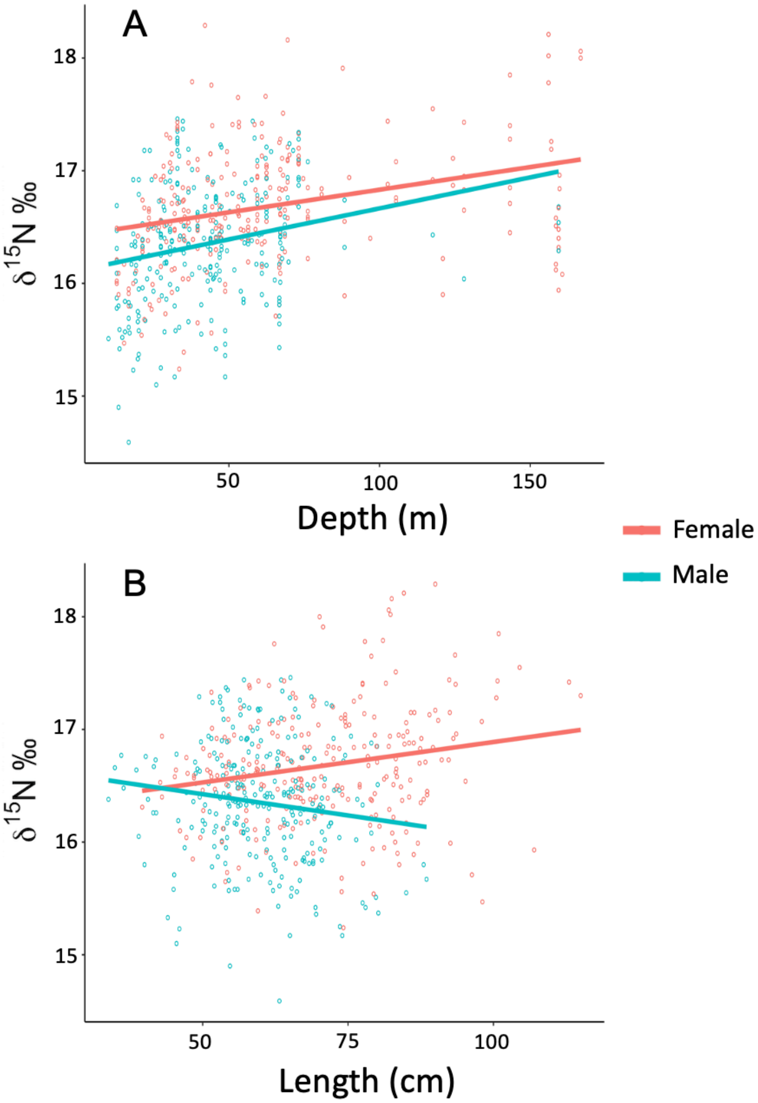


Figure 12. Relationship of Lingcod white muscle tissue nitrogen ($\delta^{15}N$) values to A) Lingcod capture depths and B) Lingcod total lengths. Best fit lines were plotted for each sex, pooled across all regions.

Results of the Bayesian modelling conducted in the SIBER package in R indicated differences in isotopic dietary diversity among regions. In order to visually assess the size of the dietary niche among regions, the standard ellipse areas for each region were plotted both separately (Figure 13) and overlapping for comparison purposes (Figure 14A). The Alaska and Conception regions exhibited the largest dietary niche compared to other regions, driven primarily by the wider ranges of $\delta^{13}C$ values. In contrast, the Eureka and Monterey regions exhibited the smallest dietary diversity (Figure 14B). The Alaska and Conception regions overlapped the least, while the Vancouver, Columbia, Eureka, and Monterey regions largely overlapped one another in isotopic space.

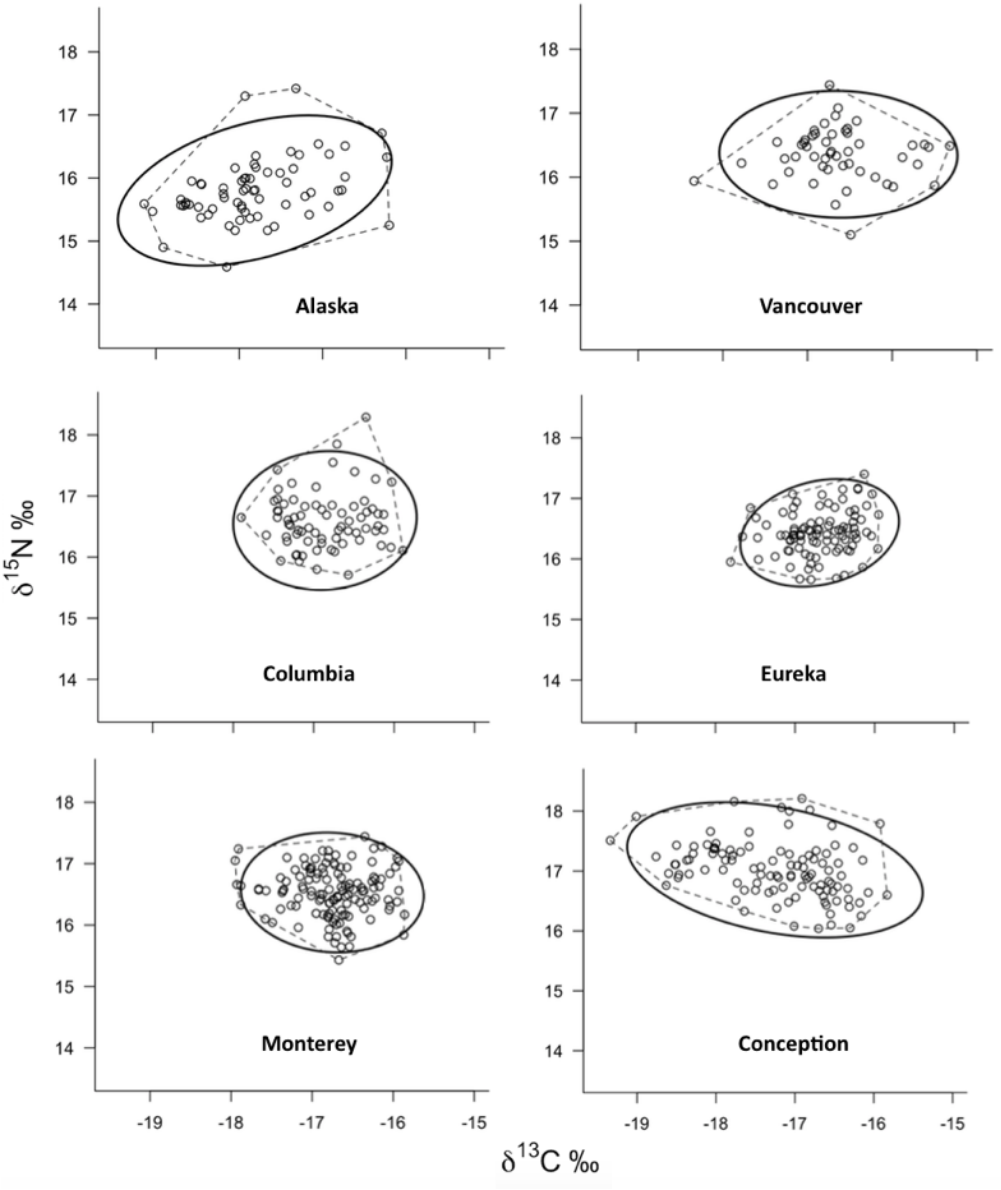


Figure 13. Lingcod white muscle tissue stable isotope biplots, by region. Each point indicates an individual. The dotted lines represent that region's convex hull. The bold ellipses are that population's standard ellipse. Larger standard ellipse areas indicate a larger dietary niche, and smaller standard ellipse areas indicate a smaller dietary niche.

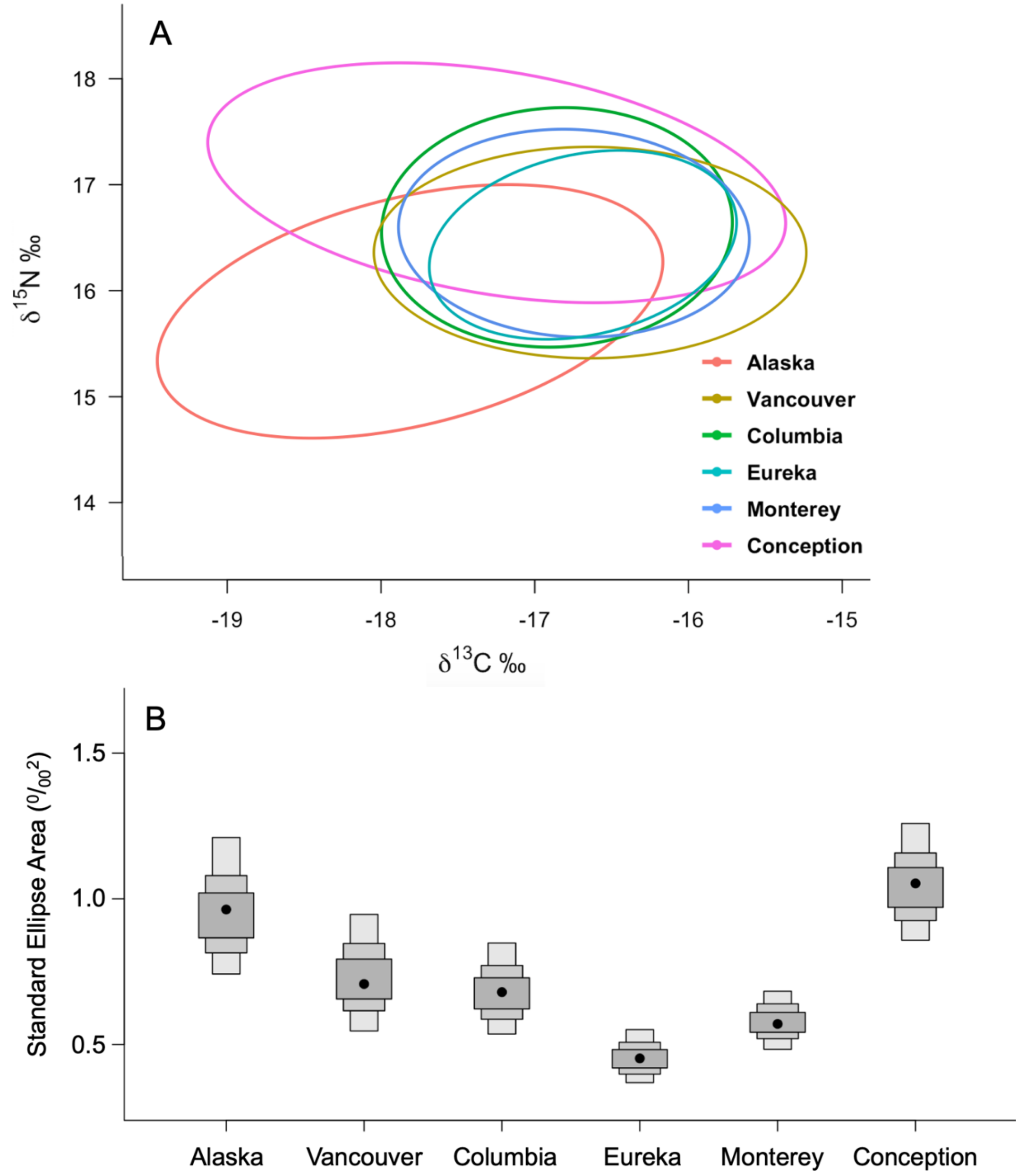


Figure 14: A) Stable isotope biplot of Lingcod white muscle tissue nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) values. Each ellipse represents a region's standard ellipse area. B) Standard ellipse area (‰^{2}) values plotted for each region. Gray boxes represent the 50%, 75%, and 95% credible intervals. Black dots represent the mode.

Layman metrics were calculated for each region, by sex, length, and depth (Table 11). Alaska exhibited the largest nitrogen range, whereas Conception exhibited the largest carbon range. Eureka had the smallest isotopic niche, as indicated by TA, whereas Alaska and Conception had the largest. The CD and NND values indicate that Lingcod from the Eureka and Monterey regions had the least trophically diverse diets, and Lingcod from the Conception and Alaska regions had the most trophically diverse diets. Furthermore, NND and SDNND indicate that Lingcod from Alaska, Vancouver, and Conception had more variety in their trophic niches, while Lingcod from Columbia, Eureka, and Monterey had more similarities in their trophic niches with less variability.

Table 11. Layman metrics calculated from Lingcod white muscle tissue nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) values, by region. 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.

		NR	CR	TA	CD	NND	SDNND
Region	Alaska	2.83	2.94	5.72	0.70	0.15	0.16
	Vancouver	2.34	3.02	3.84	0.59	0.16	0.13
	Columbia	2.58	2.01	3.24	0.59	0.13	0.10
	Eureka	1.74	1.86	2.30	0.48	0.10	0.07
	Monterey	2.01	2.09	3.11	0.54	0.08	0.06
	Conception	2.17	3.51	5.39	0.80	0.14	0.10
Sex	Female	3.05	4.02	9.16	0.71	0.08	0.09
	Male	2.87	3.64	8.00	0.75	0.08	0.08
Length (cm)	Small	2.47	3.29	6.51	0.69	0.11	0.11
	Large	3.70	4.02	10.99	0.76	0.07	0.08
Depth (m)	Shallow	2.73	3.82	7.14	0.89	0.12	0.11
	Moderate	3.12	2.93	6.60	0.67	0.08	0.08
	Deep	2.78	3.48	6.61	0.68	0.09	0.10

Overall, larger, female Lingcod exhibited larger isotopic niches, and carbon and nitrogen ranges, whereas smaller, male Lingcod exhibited smaller isotopic niches and carbon and nitrogen ranges (Figure 15 and 16). SEA's indicate that female Lingcod were eating slightly higher on the food web and that male Lingcod had slightly higher trophic diversity (Figure 15). Small Lingcod (<55cm) exhibited less dietary diversity compared to large Lingcod (>55cm; Figure 16). Most strikingly, Lingcod collected from shallow depths had the largest trophic diversity and isotopic niches (Figure 17). This indicates that compared to Lingcod caught at other depths, shallow water Lingcod have the largest trophic diversity, occupy the largest isotopic niche, and consume prey with a wider array of basal $\delta^{13}C$ sources.

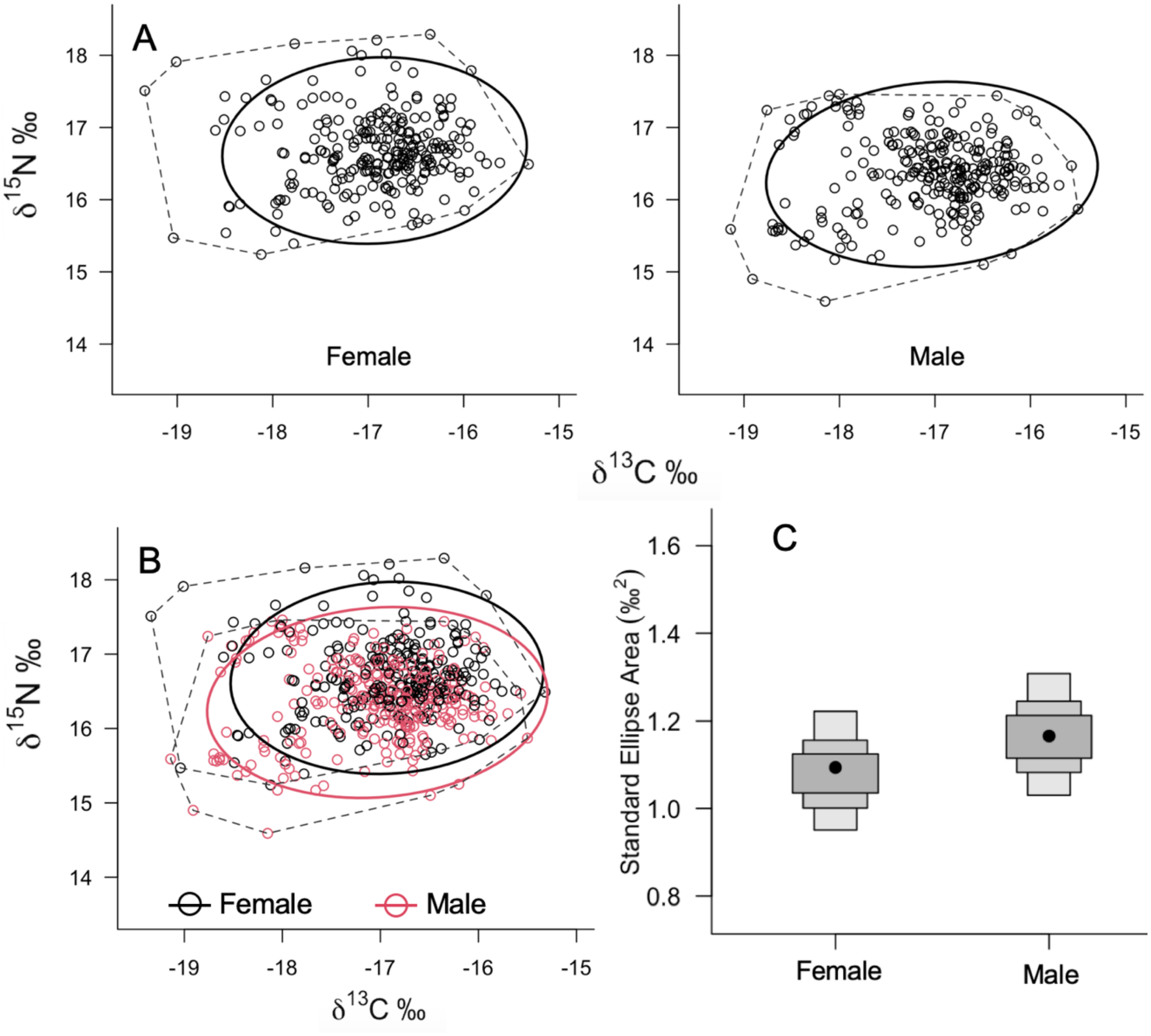


Figure 15. A) Individual stable isotope standard ellipse areas (SEA) of Lingcod, by sex. Each point indicates an individual. The dotted lines represent that region's convex hull. The bold ellipses are that population's standard ellipse. B) Overlapping SEA's, by sex. C) Standard ellipse area (‰^{2}) values plotted for each sex. Gray boxes represent the 50%, 75%, and 95% credible intervals. Black dots represent the mode. Female Lingcod (n = 257), male Lingcod (n = 262).

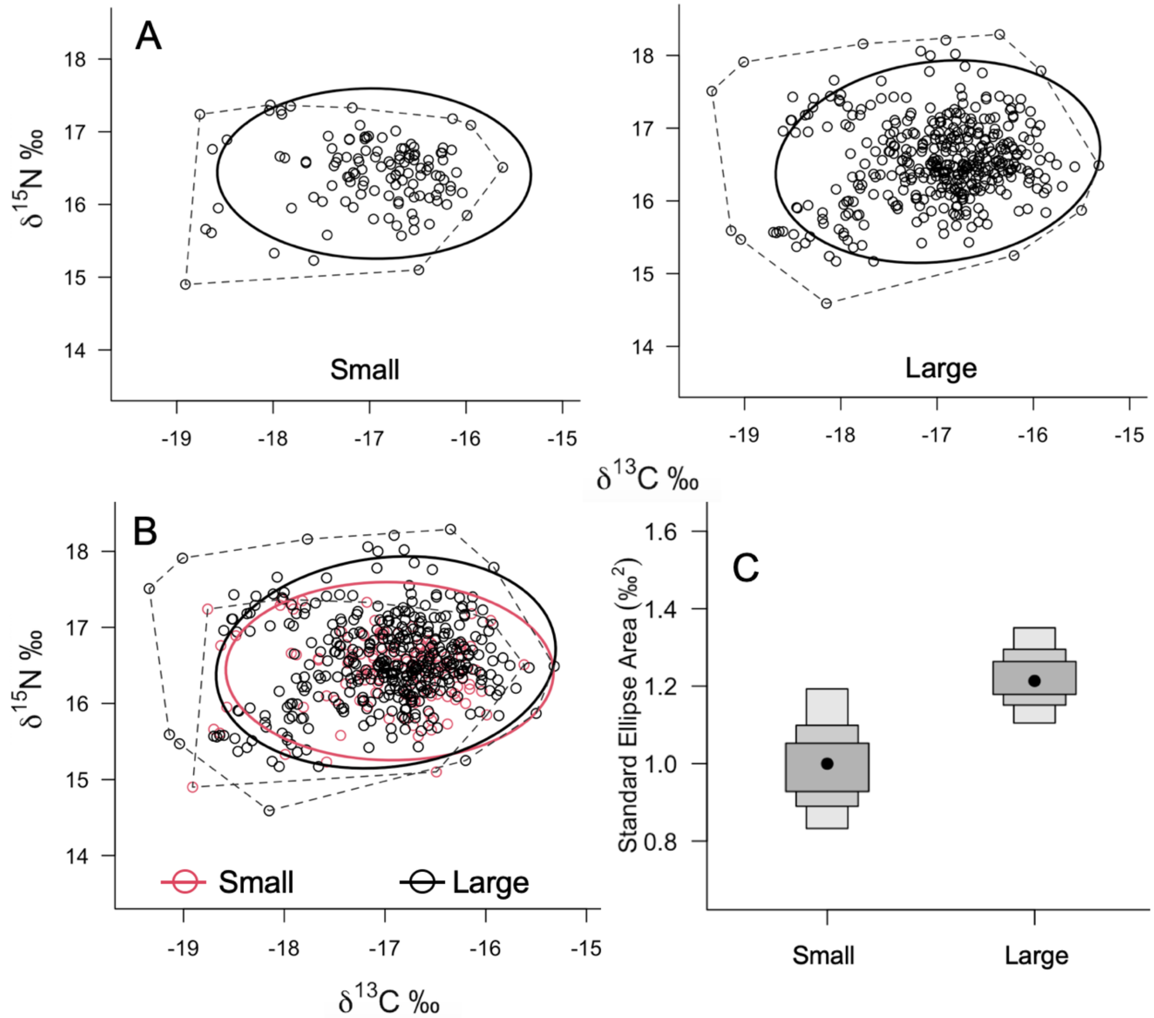


Figure 16. A) Individual stable isotope standard ellipse areas (SEA) of Lingcod, by size (total length (cm)). Each point indicates an individual. The dotted lines represent that region's convex hull. The bold ellipses are that population's standard ellipse. B) Overlapping SEA's, by size. C) Standard ellipse area (‰^{2}) values plotted for each size. Gray boxes represent the 50%, 75%, and 95% credible intervals. Black dots represent the mode. Small Lingcod <55cm (n=120), Large Lingcod >55cm (n=399).

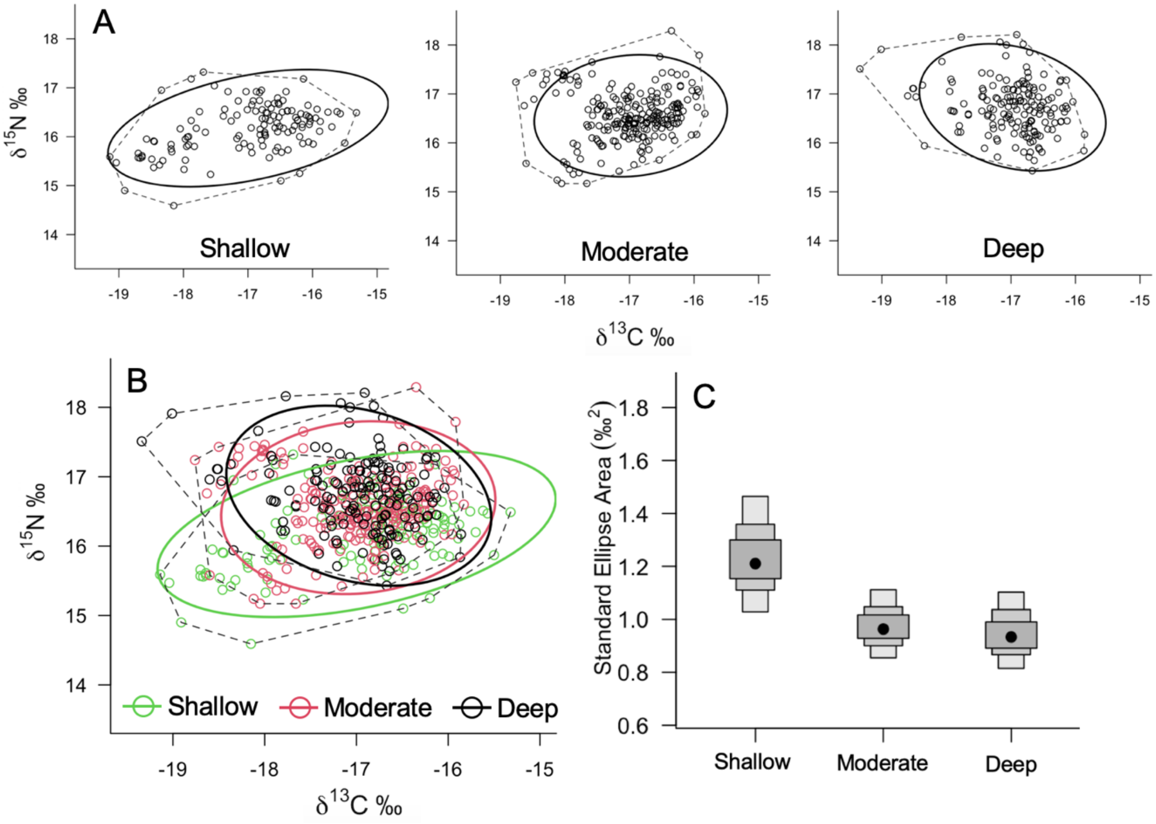


Figure 17. A) Individual stable isotope standard ellipse areas (SEA) of Lingcod, by depth (m). Each point indicates an individual. The dotted lines represent that region's convex hull. The bold ellipses are that population's standard ellipse. B) Overlapping SEA's, by depth. C) Standard ellipse area (‰^{2}) values plotted for each depth. Gray boxes represent the 50%, 75%, and 95% credible intervals. Black dots represent the mode. Shallow <30m (n=129), Moderate 30-60m (n=226), Deep >60m (n=164).

The four most common prey types were plotted in bi-variate isotopic space with Lingcod samples to visually compare the predator and prey isotope values (Figure 18). On average, Lingcod $\delta^{15}N$ values were ~ 2‰ higher than the four prey types. There was a general agreement between the gut content and stable isotope analysis, where Lingcod in the Eureka, Monterey, and Conception regions were consuming more Octopoda (higher $\delta^{13}C$ and $\delta^{15}N$). Also, Lingcod in the Alaska region were consuming more Sebastes (lower $\delta^{13}C$ and $\delta^{15}N$). However, these four prey types were not evenly sampled across all regions, and gut contents confirmed that Lingcod consumed a much wider array than just these four prey types presented here.

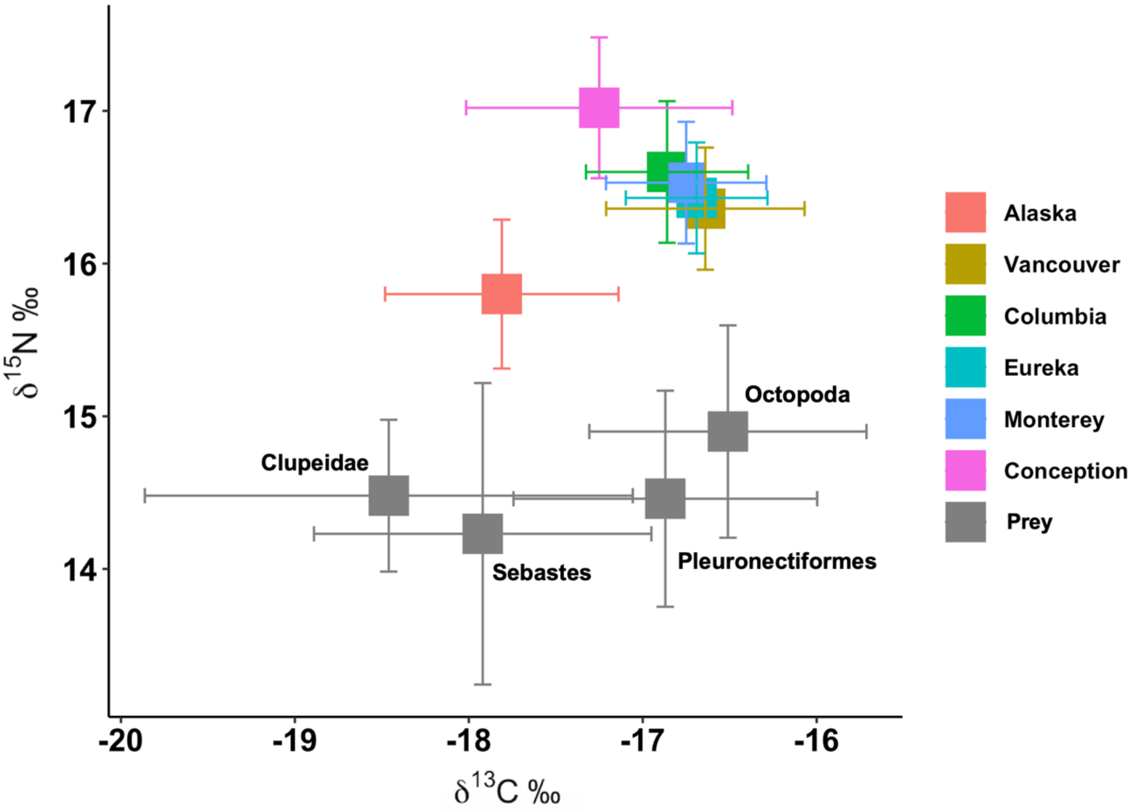


Figure 18. Average muscle tissue stable isotope values ($\delta^{15}N$ & $\delta^{13}C$) with standard deviations of Lingcod, by region, and 4 common prey types pooled across all regions; Clupeidae (n=19), Sebastes (n=50), Pleuronectiformes (n=5), Octopoda (n=22).

There were significant relationships between isotope values and environmental factors SST and Chl *a*. As expected, SST increased from North to South. Lingcod $\delta^{15}N$ values exhibited a strong positive relationship with SST (Linear regression, $F_{1,517} = 276.4$, $r^2 = 0.45$, p = <0.001; Figure 19A) and a negative relationship with Chl *a* (Linear regression, $F_{1,517} = 76.96$, $r^2 = 0.13$, p = <0.001; Figure 19B). This indicates that Lingcod from warmer regions, and regions with lower primary productivity in the water column, consume higher trophic level prey. Conversely, Lingcod from colder regions, and regions with higher primary productivity in the water column, consume lower trophic level prey. There were no significant relationships between $\delta^{13}C$ values and SST (Linear regression, $F_{1,517} = 0.02$, $r^2 = 0.00$, $p = 0.90$) or $\delta^{13}C$ and Chl a (Linear regression, $F_{1,517} = 2.13$, $r^2 = 0.00$, $p = 0.15$). There were no significant relationships between SST and Layman metrics (Linear regression, NR: $F_{1,4}$ = 1.06, $r^2 = 0.21$, $p = 0.36$; CR: $F_{1,4} = 0.39$, $r^2 = 0.09$, $p = 0.57$; TA: $F_{1,4} = 0.05$, r^2 = 0.01, $p = 0.84$; CD: $F_{1,4} = 0.94$, $r^2 = 0.19$, $p = 0.39$; NND: $F_{1,4} = 0.20$, $r^2 = 0.05$, p = 0.67). Finally, there were no significant relationships between Chl *a* and each layman metric (Linear regression, NR: $F_{1,4} = 0.53$, $r^2 = 0.12$, $p = 0.51$; CR: $F_{1,4}$ = 2.83, $r^2 = 0.41$, $p = 0.17$; TA: $F_{1,4} = 0.71$, $r^2 = 0.15$, $p = 0.45$; CD: $F_{1,4} = 1.33$, r^2 = 0.25, $p = 0.31$; NND: $F_{1,4} = 0.00$, $r^2 = 0.00$, $p = 0.97$).

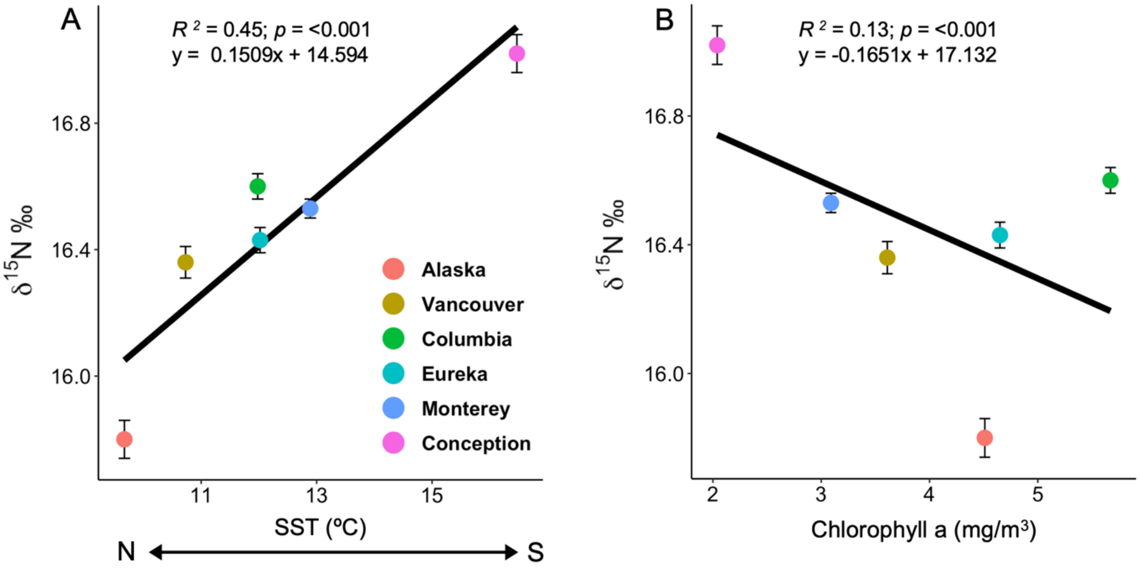


Figure 19. Average nitrogen ($\delta^{15}N$) Lingcod white muscle tissue isotope values with standard error bars plotted against A) the 12-year average sea surface temperature (SST) values and B) the 12-year average chlorophyll *a* (Chl *a*) values, by region. A linear regression was conducted, and the best-fit line was plotted.

Discussion

In this study along the U.S. West Coast, Lingcod diets were explored using gut content analysis and stable isotope analysis, and factors were identified that influence Lingcod feeding ecology. The results indicated that although Lingcod feed on a wide variety of prey, their diets were significantly influenced by biological factors (sex and length) and environmental factors (geographic region, depth, SST, and Chl *a*). These findings emphasize that Lingcod are both generalists and opportunists, and exhibit spatial, temporal, and ontogenetic variation in their diet.

The basis in which predators exhibit variability in their diets has been well documented (Murdoch 1969, Mehl 1989, Gerking 1994, Bax 1998). For example, the most abundant prey available may vary by location creating geographic differences in diet within a fish species (Bethea et al. 2007, Mahe et al. 2007). These geographic differences may occur at both large and small scales. Large scale latitudinal differences in diets have been seen in another predatory groundfish species, the Pacific Hake (*Merluccius productus*), from British Columbia, Canada to Southern California, U.S.A. (Buckley & Livingston 1997). Similar to Lingcod, *M. productus* also exhibited an increase in size with latitude and had diets that were primarily composed of fishes. In comparison, California Sheephead (*Semicossyphus pulcher*) have exhibited geographic variation in diets over small spatial scales (Hamilton et al. 2011). The SIMPER analysis indicated that the three southern regions had the highest average similarities within a region, while the three northern regions had the lowest average similarities within a region. These findings imply that Lingcod diets should be carefully assessed as they can vary at both large and small spatial scales.

Shifts in prey sources have also been linked to biological factors such as ontogeny and sex (Werner & Gilliam 1984, Kingsford 1992, Bethea et al. 2007, Qamar et al. 2015). In the Chukchi Sea for example, several species of fishes, such as Saffron Cod (*Eliginus gracilis*), Bering Flounder (*Hippoglossoides robustus*), and Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*) have demonstrated ontogenetic shifts in their diets (Marsh et al. 2017). Off the coast of Western Australia, Tiger Sharks (*Galeocerdo cuvier*) have demonstrated differences in diet due to both ontogeny and sex (Simpfendorfer et al. 2001). Similar to Lingcod, *G. cuvier* females attained larger sizes than males. Female sharks consumed larger prey and male sharks consumed smaller prey. The GCA confirmed that Lingcod followed similar trends seen in *G. cuvier*. In general, fishes have exhibited an increasingly larger diversity of prey as they age and grow (Lowe et al. 1996, Usmar 2012). Lingcod followed this trend within both the GCA and SIA. Larger Lingcod consumed larger, and higher trophic level ($\delta^{15}N$) prey as well as a wider diversity of prey compared to smaller Lingcod.

Environmental factors, including temperature and depth, have created variability in fish abundances and fish diets (Barber & Chavez 1983, Félix-Hackradt et al. 2014). Temperature differences may cause changes in feeding behavior; as basal metabolism increases with warmer temperatures, there is an increased demand for extra energy (Bethea et al. 2007, Behrens & Lafferty 2012). Temperature was an important factor that influenced Lingcod feeding ecology; however this pattern could also be driven by differences in latitude. Differences in depth may provide differences in prey sources. For example, the diet composition of the Orange Roughy (*Hoplostethus atlanticus*) was significantly influenced by depth, shifting from fish in shallower waters to crustaceans in deeper waters (Bulman & Coslow 1992). Indeed, Lingcod also exhibited a shift in diet by depth, having consumed more cephalopods in shallower and moderate depths and more gadids in deeper depths.

Lingcod gut content results from this study both paralleled and countered previous studies on Lingcod. For example, Lingcod diets from the two northern regions (Alaska and Vancouver) were dominated by fishes (Scorpaenidae and Gadiformes, respectively), whereas the four southern regions were dominated by cephalopods. This is in concurrence with findings from studies off the coast of Canada (Olson et al. 2020) and central California (Anderson 2016), who also found that Lingcod diets were primarily composed of fishes and cephalopods. Another study conducted off the coast of Washington reported that rockfishes (family Scorpaenidae) were consistently important prey across multiple seasons, years, and locations (Beaudreau & Essington 2007). Although the study presented here did not directly address multiple seasons across several years or differences inside and outside marine protected areas (MPAs), rockfishes were a major food source for all Lingcod across all depths. However, Steiner (1979) found octopuses contributed 19.2% of the total biomass, while rockfishes contributed less than 1% of total biomass to Lingcod diets from rocky reef habitats in central Oregon. Similarly, in central Oregon during dive surveys, Tinus (2012) found that rockfishes were the most abundant potential prey, but only consisted of 4.7% by number of Lingcod diets. In my study, Scorpaenidae accounted for 8.6% by number for the Columbia region and 11.25% for the entire range. These numbers also likely underrepresented the true amount of Scorpaenidae consumed, as this group likely accounted for a large portion of the Unidentified Teleostei prey group. Overall, while Lingcod demonstrated a broad latitudinal gradient in prey composition, it could also be said that regional differences in diet were simply a result of regional differences in prey availability.

Stable isotope results presented here are similar to the other studies that have reported basal Lingcod $\delta^{13}C$ and $\delta^{15}N$ values. In central California, muscle tissue of six Lingcod (likely small juveniles) were collected from seabird prey samples, having mean $\delta^{13}C$ values of -18.3 ± 0.5, and mean $\delta^{15}N$ values of 12.5 ± 0.3 (Sydeman et al. 1997). Using bone midden samples from Haidi Gwaii, Canada, Szpak et al. (2009) ascertained that three Lingcod samples had mean $\delta^{13}C$ values of -10.4 ± 0.8, and mean $\delta^{15}N$ values of 17.2 ± 0.6. However, it is unknown how Lingcod bone and muscle tissue stable isotope values compare to one another. More recently, white muscle tissue of Lingcod from British Columbia, Canada had $\delta^{13}C$ values between -16 and -19, and $\delta^{15}N$ values between 15 and 17 (Olson et al. 2020), similar to the values reported in the current study.

Similar to the gut contents, Lingcod stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) also exhibited significant differences based on geographic region. The GLM results indicated that region was the only variable that significantly influenced Lingcod $\delta^{13}C$ values. Isoscapes, or broad geographic variation in isotope values, are still in development for many ocean systems (Graham et al. 2010). Although there are currently no isoscape delineations to compare to, the change in $\delta^{13}C$ across this study's relatively large geographic area was expected. Tukey HSD comparisons indicated the Alaska and Conception regions drove these differences with relatively lower $\delta^{13}C$ signatures and larger variability compared to other regions. Lower $\delta^{13}C$ values indicate more pelagic influences (Hobson et al. 1994). While the middle four regions were exposed to the California Current, the Alaska and Conception regions were exposed to the Alaska Current and the Southern California Countercurrent, respectively. The differences in current systems could be driving the differences seen in the GLM, in which the Alaska and Conception regions were exposed to more pelagic current influences as indicated by the lower $\delta^{13}C$ values. Indeed, Lingcod from the Conception region also had the largest amount of Crustacea and Gastropoda in their diet compared to other regions. Pelagic Red Crabs (*Pleuroncodes planipes*) were the dominant prey source in the Crustacea and Gastropoda prey group in the Conception region, suggesting that prey composition could be driving the lower $\delta^{13}C$ values.

However, the Alaska region Lingcod did not consume pelagic prey sources such as *P. planipes*. It is unknown if the differences in Alaska were driven by another prey source that were not seen in the gut content analysis, or if differences were driven in isoscapes or differences in sampling year. Tukey HSD results identified that the Alaska and Conception regions also drove the $\delta^{15}N$ differences among regions, and Vancouver to an extent as well. These three regions also exhibited the largest amount of dietary diversity as indicated by the relatively larger TA and CD. This is supported by the gut content diversity indices for the Alaska and Conception regions.

The SST and Chl *a* data demonstrated further spatial patterns in Lingcod isotope values. As expected, SST steadily increased from North to South, while Chl *a* tended to decrease. The $\delta^{15}N$ values also followed this trend from North to South and formed a significant positive relationship, which suggested Lingcod consumed prey from higher trophic levels at warmer temperatures. The prey isotope samples indicate that Octopoda had the highest $\delta^{15}N$ values compared to other prey sources, and Octopoda were also more common in the southern regions. It is unknown if Octopoda were truly at a higher trophic level compared to other prey sources, as there is also the potential that there was a latitudinal shift in the baseline $\delta^{15}N$ values (Graham et al 2010). As mentioned previously, isoscapes may be influencing the basal isotope values along the U.S. West Coast and could be the reasoning for this discrepancy. This pattern conflicts with trophic level calculations from the gut contents, in which with the exception of

Alaska, trophic levels decreased from North to South. Furthermore, Lingcod in the Alaska region were influenced by the Alaska coastal current and were collected in 2017, whereas Lingcod in the Conception region were collected from Fall and Winter 2016 and were influenced by the Southern California Countercurrent. Lingcod from the middle regions were collected closer temporally, during Summer 2016 and exposed to the California Current. The significant negative relationship between $\delta^{15}N$ and Chl *a* did not follow as straightforward a trend that for temperature, but this analysis indicated that Lingcod in areas with lower Chl *a* concentrations were eating at higher trophic levels. Surprisingly, SST and Chl *a* factors (the latter associated with primary production) did not show any significant relationships with $\delta^{13}C$ values. Although the linear regressions for $\delta^{13}C$ and SST, $\delta^{13}C$ and Chl a, and $\delta^{13}C$ and each Layman metric were not significant they were also noisy (i.e. low r^2 values), implying there may be other explanatory factors that were not accounted for in this study.

There were temporal influences on Lingcod isotope values, likely caused by environmental fluctuations. While temporal comparisons among regions were not feasible due to differences in sampling periods, they did provide interesting insight. The majority of this study (the lower 5 regions) was conducted in 2016 during an ENSO cycle, in which the El Niño phase of warmer water was prevalent. Pelagic Red Crabs (*P. planipes*) in California are indicative of an El Niño event, in which warmer water species are advected northward from Baja

California, Mexico (Stewart et al. 1984). There were *P. planipes* in Lingcod stomachs from the Conception region. This may explain the more negative $\delta^{13}C$ values in the Conception region than would have been expected, given higher consumption of these pelagic prey sources. Average isotope values from the lower 5 regions were higher than those Lingcod from the Alaska region, which were collected in May 2017. The average $\delta^{13}C$ and $\delta^{15}N$ isotope values for Lingcod in British Columbia, Canada in 2015-2016 (Olson et al. 2020) fall directly between the average $\delta^{13}C$ and $\delta^{15}N$ isotope values of Alaska region and the lower 5 regions. This suggests there was a decreasing gradient in average isotope values from South to North. However, differences seen in the isotopes of Lingcod from the Alaska region could also be a result of the current systems, isoscapes, or El Niño conditions strongly influencing the waters in the lower 5 regions. In addition to environmental drivers, differences could be attributed to prey preference (more Crustacea & Gastropoda consumed in Alaska), spatial variation in prey, or biological factors such as differences in the sampling rates of Lingcod sexes or sizes.

Lingcod diets exhibited significant differences in diet based on sex and depth captured. Overall, $\delta^{15}N$ was consistently greater in Lingcod caught at deeper depths and was greater in females compared to males across all regions. This supports the GCA results, in which female Lingcod consumed more Gadiformes and Semi-Pelagic Fishes (higher trophic level prey), and male Lingcod consumed more Cephalopoda and Crustacea and Gastropoda (lower trophic level prey).

Additionally, Lingcod from deeper depths consumed more Gadiformes (higher trophic level prey), while Lingcod from shallower and moderate depths consumed more Cephalopoda (lower trophic level prey). This may also be a result of the abundances of these prey sources in these depth ranges.

Larger fish may select larger prey items, or items that have a higher caloric intake. For example, a fish will have a higher caloric value than an octopus (Phillips & Brockway 1959, Goodman-Low et al. 1999). The Eastern Pacific red octopus (*Octopus rubescens*) is the most common shallow-water, nearshore species of octopus in the North Pacific Ocean (Hochberg & Fields 1980). Results presented here support that the small, often male, Lingcod living nearshore consume octopuses more than rockfishes. Olson (2020) reported that ontogenetic shifts in Lingcod diets were less apparent than expected, as all size classes consumed both fishes and octopuses. In this study, female Lingcod residing at deeper depths were consuming larger and higher trophic level prey items, such as the Pacific Hake (*Merluccius productus*) and had less diverse diets. Moreover, male Lingcod caught in shallower depths consumed smaller and lower trophic level prey items, such as *O. rubescens,* and had more diverse diets. It is unknown if Octopoda truly had higher $\delta^{15}N$ values compared to other prey sources without being able to account for the potential baseline shifts in isotopic values across this broad geographic range. Although Olson (2020) found that gape was an important factor in Lingcod diet, results from Tinus (2012) indicate that gape was not. In the current study, Lingcod exhibited a strong correlation between gape and length, where larger Lingcod have larger mouths, with the potential to consume larger prey. Length was a stronger factor to include in the isotope models than gape, which is why it was excluded.

Lingcod consumed fishes and cephalopods from a broad spectrum of prey types, suggesting they are generalists. However, pelagic fishes (Semi-Pelagic Fishes prey group) were the most prominent taxa in the Vancouver region, supporting the notion that Lingcod were opportunistically consuming transient schools of fishes. Also, Lingcod stomachs in the Conception region contained Pelagic Red Crabs, an uncommon prey source that is usually only available to Lingcod in U.S. waters during the El Niño warmer water phase, further supporting an opportunistic feeding strategy. This stresses the point that Lingcod feeding strategies vary across time and broad geographic regions, and that future diet studies and food web models should account for these variable feeding strategies in top marine predators.

Fisheries Management Implications and Future Directions

Diet analyses inform food web models and can ultimately be used in EBFM (Bizzarro et al. 2017). EBFM incorporates predator-prey relationships as a means to improve current management (Pikitch et al. 2004, Link et al. 2011). EBFM has the capacity to predict changes in predator and prey populations based on trophic dynamics (Tinus 2012). Lingcod are top marine predators along their range, making them a prime choice for use in food web models. Incorporating ecological information such as diet data into existing techniques may improve fisheries management worldwide (Link et al. 2011). In contrast to EBFM's holistic approach, current fisheries management strategies use stock complexes and single-species fisheries stock assessments. These traditional methods have been unsuccessful in preventing collapses of populations worldwide (Simberloff 1998, Pikitch et al. 2004). In addition, the traditional methods do not include feeding habits of predators. Including Lingcod feeding ecology data into current fisheries management can help better predict fluctuations in populations of both Lingcod and their various prey. Currently, the lack of diet studies available for food web models hinders EBFM's implementation (Essington & Punt 2011). More diet data, such as from the current study, will contribute to the greater body of knowledge necessary to implement EBFM. Food web models such as Ecopath with Ecosim (EwE) software are utilized worldwide to address complex marine ecosystems and management approaches (Polovina 1984, Pauly et al. 2000). These types of models include diet data obtained from stomach content and stable isotope analyses (Heymans et al. 2016). The gut content and stable isotope data accumulated from the current study will be used in food web models and to improve the management of Lingcod and their prey.

Future studies on Lingcod diet and trophic ecology should consider 1) a narrower sampling period and 2) directed prey collections alongside Lingcod sampling. Sampling Lingcod across a broad geographic range gave valuable insight into overall Lingcod diet diversity and key factors that influence their feeding ecology. However, sampling could be conducted on a more concise timeline. For example, given the results above, rescheduling due to poor weather conditions and between sportfishing trips should be more strongly accounted for in an effort to further minimize spatial and temporal variation. Directed prey collections should be considered in addition to Lingcod collections. Using a mixing model (e.g. MixSIAR), it is possible to assess the contribution of prey sources in a predator’s diet (Stock et al. 2018). In this study, tissue samples were collected from intact prey found in Lingcod stomachs, however, there were not enough of any given species in Lingcod stomachs across all regions to conduct a mixing model. Although Lingcod consumed a large quantity of rockfishes across their range, there was no specific species that was found in Lingcod gut contents across all regions, and often stomach contents were too digested to identify beyond the Sebastes genus. Even within a rockfish species, there is a large amount of variability in isotopic values (B. Finney, pers comm). Therefore, it is recommended to simultaneously obtain white muscle tissue samples from common rockfish species across the desired study range, and to conduct diving collections for octopuses (ideally *Octopus rubescens*). In addition to the use in a mixing model, the octopus isotope samples would also help establish an isotope baseline to standardize the variation in isotope signatures across ocean isoscapes.

Conclusion

This study provided a synopsis of Lingcod diets and trophic ecology, using both gut content and stable isotope analyses, across the majority of the Lingcod's range. Overall, the information generated here adds to the greater body of knowledge of gut content and stable isotope analyses. More specifically, this study emphasizes that Lingcod exhibit both generalist and opportunist feeding strategies, with spatial, temporal, and ontogenetic variations in their diets. The results highlighted that sex, length, geographic region, depth, SST, and Chl *a* are all important factors that influence Lingcod feeding habits. These data are valuable for future food web models as they fill in data gaps of a top marine predator and more clearly describe predator-prey interactions in the North Pacific Ocean. This is particularly valuable as fisheries management shifts towards the ecosystem-based fisheries management approach. With overall worldwide declines in recreationally and commercially valuable fish stocks and implications of climate change, understanding how a top marine fish predator may respond is valuable to take into consideration.

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APPENDIX

Appendix 1. Prey categories used for trophic level calculations, adopted from Ebert and Bizzarro (2007).

Prey Category	Trophic Level
Fishes	3.24
Cephalopods	3.2
Decapod Crustaceans	2.52
Other Crustaceans	2.4
Other Molluscs	2.1

Appendix 2. All 104 types of prey items from 1,321 Lingcod stomachs listed as percent frequency of occurrence, sectioned out by region and prey group.

	All	Puget Sound	Alaska	Vancouver	Columbia	Eureka	Monterey	Conception
# stomachs	1321	50	144	160	324	159	244	240
Prey Items	%O							
Crustacea & Gastropoda								
Unidentified Crustacea	0.4	6	0.7				0.4	
Eucarida	0.2	4						0.4
Decapoda	0.4		0.7		0.6	0.6	0.4	
Pleuroncodes planipes	1.3							7.1
Brachyura	0.2		1.4					
Cancridae	0.2		1.4					
Cancer	0.1					0.6		
Caridea	0.8	4	0.7		1.2	0.6	0.4	0.4
Heptacarpus	0.1						0.4	
Crangon	0.1						0.4	
Paguroidea	0.1		0.7					
Lithodidae	0.1		0.7					
Paguridae	0.1		0.7					
Pagurus	0.2		0.7				0.4	
Unidentified Gastropoda	0.8	2	4.2			0.6	0.4	0.4
Trichotropis cancellata	0.2		2.1					
Anabathridae	0.1					0.6		
Calliostoma	0.1			0.6				
Columbellidae	0.1		0.7					
Cylichnidae	0.1				0.3			
Littorinidae	0.2		0.7		0.3			
Littorina plena	0.1						0.4	
Muricidae	0.3	4	1.4					
Nucella	0.1						0.4	
Ocenebra	0.1							0.4
Rissoidae	0.1		0.7					
Trochidae	0.2		1.4				0.4	
Volutacea	0.1			0.6				
Cephalopoda								
Cephalopoda	0.8		0.7	0.6		1.3	0.8	2.1
Octopodidae	26.0		11.8	1.9	17.3	39.0	48.0	37.1
Octopus dofleini	1.7	2	1.4		2.2	7.5	0.4	
Loligo opalescens	3.0	2	6.9			0.6	1.2	10.0
Octopoteuthis deletron	0.1				0.3			
Unidentified Teleostei								
Unidentified Teleostei	59.4	58	59.7	64.4	66.7	55.3	51.2	57.5
Fish egg mass	1.1	8	6.9					

Appendix 2. (continued)

	All	Puget Sound	Alaska	Vancouver	Columbia	Eureka	Monterey	Conception
# stomachs	1321	50	144	160	324	159	244	240
Prey Items	%O							
Scorpaenidae								
Scorpaenidae	2.3		0.7	1.9	1.5	3.1	4.9	1.7
Sebastes spp.	12.0	14	23.6	6.3	7.7	10.7	9.8	17.1
Sebastes flavidus	0.2	2			0.3			
Sebastes jordani	0.2				0.6			
Sebastes melanops	0.2		1.4					
Sebastes mystinus	0.1							0.4
Sebastes semicinctus	0.1							0.4
Sebastes zacentrus	0.2			1.3				
Demersal Fishes								
Cottidae	0.9	4	2.1		0.3	1.9	1.2	
Leptocottus armatus	0.4		1.4		0.6	0.6		
Enophyrs bison	0.1					0.6		
Hexagrammidae	0.2							0.8
Ophiodon elongatus	0.2		0.7				0.4	
Anoplopoma fimbria	0.3		1.4	0.6	0.3			
Ammodytes personatus	0.5	2	2.8		0.3			
Ophiidae	1.6					0.6	2.5	5.8
Semi-Pelagic Fishes								
Scomber japonicus	0.1						0.4	
Clupeidae	1.1			8.8	0.3			
Clupea pallasii	1.4	2	0.7	8.8	0.9			
Pleuronectiformes								
Pleuronectiformes	2.4	4	3.5	1.3	3.7	1.3	2.0	1.7
Citharichthys sordidus	0.1						0.4	
Atheresthes stomias	0.2			1.9				
Microstomus pacificus	0.1				0.3			
Parophrys vetulus	0.2			1.3				
Gadiformes								
Gadiformes	2.2	6	3.5	7.5	2.5			0.4
Merluccius productus	6.3	2		16.3	14.8	2.5	0.8	0.8

Appendix 2. (continued)

	All	Puget Sound	Alaska	Vancouver	Columbia	Eureka	Monterey	Conception
# stomachs	1321	50	144	160	324	159	244	240
Prey Items	%O							
Other/Unknown								
Arthropoda	0.2		1.4					
Thecostraca	0.1		0.7					
Elthusa spp.	0.1						0.4	
Elthusa californica	0.2							0.8
Elthusa vulgaris	0.2						0.8	
Pasiphaea pacifica	0.1	2						
Pandalus	0.2	6						
Sabellariidae	0.2	4			0.3			
Phragmatopoma	0.1						0.4	
Phyllochaetopterus	0.1					0.6		
Serpulidae	0.1							0.4
Scleractinia	0.1							0.4
Ophiuroidea	0.2		1.4					
Hydrozoa	0.1		0.7					
Leptothecata	0.1				0.3			
Athecata	0.1						0.4	
Tunicata	0.1				0.3			
Pyrosoma	0.4						0.8	1.3
Mollusca	0.1						0.4	
Bivalvia	0.3		0.7		0.3	0.6	0.4	
Heterodonta	0.1		0.7					
Pteriomorpha	0.1				0.3			
Pectinidae	0.1		0.7					
Chlamys hastata	0.1		0.7					
Buccinidae	0.1	2						
Onychoteuthis borealijaponica	0.1	2						
Petromyzontidae	0.5				0.9	1.3	0.4	
Rajiformes (egg case)	0.1					0.6		
Bathyraja kincaidii (egg case)	0.1				0.3			
Sebastes emphaeus	0.1	2						
Embiotocidae	0.2	4						
Cymatogaster aggregata	0.2	4						
Unidentified algal matter	0.4	2	2.1					0.4
Scytosiphon	0.1		0.7					
Phyllospadix	0.1							0.4
Chlorophyta	0.1		0.7					
Rhodophyta	0.2							1.3
Dumontia alaskana	0.1		0.7					
Cryptopleura	0.1							0.4
Shell fragments	0.5		3.5			0.6		0.4
Unidentified parasite	1.0		2.1	0.6	1.2	0.6		1.7
Unidentified organic matter	3.3	8	13.2	0.6	1.5	1.3	2.9	2.1
Fishing gear	0.2				0.3			0.4

Appendix 3. Alaska region Lingcod gut contents listed with dietary metrics. There were 33 types of prey items from 140 stomachs.

Prey Group	**Prey Item**	**# Stomachs**	**%O**	**%N**	**%PN**	**%W**	**%PW**	**%PSIRI**
Crustacea & Gastropoda	**Unidentified Crustacea**	1	0.7	0.2	25.0	0.1	12.6	0.1
	Decapoda	1	0.7	0.2	33.3	0.0	0.4	0.1
	Brachyura	2	1.4	0.6	41.7	0.0	1.8	0.3
	Cancridae	2	1.4	0.6	42.5	0.4	28.2	0.5
	Caridea	1	0.7	0.2	33.3	0.0	5.9	0.1
	Paguroidea	1	0.7	0.2	33.3	0.0	3.7	0.1
	Lithodidae	1	0.7	0.2	25.0	0.0	3.0	0.1
	Paguridae	1	0.7	0.7	100.0	0.7	100.0	0.7
	Pagurus	1	0.7	0.0	4.2	0.2	31.0	0.1
	Unidentified Gastropoda	6	4.3	2.3	54.8	0.9	20.1	1.6
	Trichotropis cancellata	3	2.1	0.6	27.8	0.7	30.9	0.6
	Columbellidae	1	0.7	0.7	100.0	0.7	100.0	0.7
	Littorinidae	1	0.7	0.0	2.1	0.0	1.1	0.0
	Muricidae	2	1.4	0.5	36.8	0.2	10.6	0.3
	Rissoidae	1	0.7	0.1	16.7	0.1	10.7	0.1
	Trochidae	2	1.4	0.1	5.3	0.1	5.1	0.1
Cephalopoda	Cephalopoda	1	0.7	0.2	33.3	0.2	33.3	0.2
	Octopodidae	17	12.1	7.9	65.2	7.0	58.0	7.5
	Octopus dofleini	2	1.4	0.6	43.3	0.7	52.5	0.7
	Loligo opalescens	10	7.1	3.3	45.8	2.7	38.1	3.0
Unidentified Teleostei	Unidentified Teleostei	86	61.4	46.0	75.0	45.0	73.2	45.5
	Fish egg mass	10	7.1	3.0	41.8	3.1	43.6	3.0
Scorpaenidae	Scorpaenidae	1	0.7	0.7	100.0	0.7	100.0	0.7
	Sebastes spp.	34	24.3	17.9	73.6	20.3	83.7	19.1
	Sebastes melanops	2	1.4	1.4	100.0	1.4	100.0	1.4
Demersal Fishes	Cottidae	3	2.1	0.8	38.9	1.7	77.6	1.2
	Leptocottus armatus	2	1.4	0.9	62.5	0.9	62.5	0.9
	Ophiodon elongatus	1	0.7	0.4	50.0	0.7	98.0	0.5
	Anoplopoma fimbria	2	1.4	1.4	100.0	1.4	100.0	1.4
	Ammodytes personatus	4	2.9	2.3	79.2	2.8	99.0	2.5
Semi-Pelagic Fishes	*Clupea pallasii*	1	0.7	0.7	100.0	0.7	100.0	0.7
Pleuronectiformes	Pleuronectiformes	5	3.6	2.1	60.0	2.8	78.9	2.5
Gadiformes	Gadiformes	5	3.6	2.9	80.0	3.6	99.7	3.2

Appendix 4. Vancouver region Lingcod gut contents listed with dietary metrics. There were 16 types of prey items from 160 stomachs.

Prey Group	Prey Item	# Stomachs	%O	%N	%PN	%W	%PW	%PSIRI
Crustacea & Gastropoda	Calliostoma	1	0.6	0.3	50.0	0.1	13.6	0.2
	Volutacea	1	0.6	0.4	66.7	0.0	1.0	0.2
Cephalopoda	Cephalopoda	1	0.6	0.6	100.0	0.6	100.0	0.6
	Octopodidae	3	1.9	1.0	55.6	0.6	33.8	0.8
Unidentified Teleostei	Unidentified Teleostei	103	64.4	56.2	87.4	52.8	82.0	54.5
Scorpaenidae	Scorpaenidae	3	1.9	1.5	77.8	1.5	81.9	1.5
	Sebastes spp.	10	6.3	4.8	77.6	5.4	86.6	5.1
	Sebastes zacentrus	2	1.3	1.3	100.0	1.3	100.0	1.3
Demersal Fishes	*Anoplopoma fimbria*	1	0.6	0.3	50.0	0.5	86.4	0.4
Semi-Pelagic Fishes	Clupeidae	14	8.8	8.8	100.0	8.8	100.0	8.8
	Clupea pallasii	14	8.8	5.1	58.1	6.6	75.1	5.8
Pleuronectiformes	Pleuronectiformes	2	1.3	0.5	41.7	0.9	69.4	0.7
	Parophyrs vetulus	2	1.3	0.7	58.3	1.2	97.3	1.0
	Atheresthes stomias	3	1.9	1.0	55.6	1.2	65.2	1.1
Gadiformes	Gadiformes	12	7.5	5.3	70.4	5.8	76.9	5.5
	Merluccius productus	26	16.3	12.1	74.3	12.7	78.4	12.4

Appendix 5. Columbia region Lingcod gut contents listed with dietary metrics. There were 22 types of prey items from 323 stomachs.

Prey Group	Prey Item	# Stomachs	%O	%N	%PN	%W	%PW	%PSIRI
Crustacea & Gastropoda	Decapoda	2	0.6	0.3	41.7	0.2	25.1	0.2
	Caridea	4	1.2	0.6	50.8	0.6	51.7	0.6
	Cylichnidae	1	0.3	0.2	60.0	0.2	57.1	0.2
	Littorinidae	1	0.3	0.1	20.0	0.1	28.6	0.1
Cephalopoda	Octopodidae	56	17.3	13.5	77.7	12.4	71.3	12.9
	Octopus dofleini	7	2.2	1.9	85.7	2.1	97.2	2.0
	Octopoteuthis deletron	1	0.3	0.2	50.0	0.2	50.0	0.2
Unidentified Teleostei	Unidentified Teleostei	216	66.9	56.9	85.0	55.6	83.2	56.2
Scorpaenidae	Scorpaenidae	5	1.5	1.5	100.0	1.5	100.0	1.5
	Sebastes spp.	25	7.7	6.3	81.4	6.8	88.2	6.6
	Sebastes flavidus	1	0.3	0.3	100.0	0.3	100.0	0.3
	Sebastes jordani	2	0.6	0.5	75.0	0.6	99.2	0.5
Demersal Fishes	Cottidae	1	0.3	0.1	33.3	0.2	50.3	0.1
	Leptocottus armatus	2	0.6	0.4	71.4	0.4	67.0	0.4
	Anoplopoma fimbria	1	0.3	0.3	100.0	0.3	100.0	0.3
	Ammodytes personatus	1	0.3	0.1	25.0	0.3	98.7	0.2
Semi-Pelagic Fishes	Clupeidae	1	0.3	0.3	100.0	0.3	100.0	0.3
	Clupea pallasii	3	0.9	0.3	30.6	0.2	24.0	0.3
Pleuronectiformes	Pleuronectiformes	12	3.7	2.6	68.8	3.1	83.7	2.8
	Microstomus pacificus	1	0.3	0.2	50.0	0.3	97.9	0.2
Gadiformes	Gadiformes	8	2.5	1.5	60.4	1.2	49.5	1.4
	Merluccius productus	48	14.9	12.2	81.9	13.0	87.6	12.6

Appendix 6. Eureka region Lingcod gut contents listed with dietary metrics. There were 18 types of prey items from 158 stomachs.

Prey Group	Prey Item	# Stomachs	%O	%N	%PN	%W	%PW	%PSIRI
Crustacea & Gastropoda	Decapoda	1	0.6	0.2	33.3	0.0	2.9	0.1
	Cancer	1	0.6	0.5	75.0	0.1	11.6	0.3
	Caridea	1	0.6	0.2	33.3	0.5	76.2	0.3
	Unidentified Gastropoda	1	0.6	0.2	33.3	0.0	3.5	0.1
	Anabathridae	1	0.6	0.3	50.0	0.2	33.3	0.3
Cephalopoda	Cephalopoda	2	1.3	0.9	75.0	1.2	92.3	1.1
	Octopodidae	62	39.2	28.7	73.1	25.5	65.1	27.1
	Octopus dofleini	12	7.6	6.0	78.5	7.4	97.6	6.7
	Loligo opalescens	1	0.6	0.2	33.3	0.0	0.2	0.1
Unidentified Teleostei	Unidentified Teleostei	88	55.7	46.1	82.9	47.3	84.9	46.7
Scorpaenidae	Scorpaenidae	5	3.2	2.8	90.0	2.5	80.0	2.7
	Sebastes spp.	17	10.8	9.3	86.6	9.2	85.7	9.3
Demersal Fishes	Cottidae	3	1.9	1.5	77.8	1.4	73.4	1.4
	Leptocottus armatus	1	0.6	0.6	100.0	0.6	100.0	0.6
	Enophyrs bison	1	0.6	0.3	50.0	0.4	65.0	0.4
	Ophiidae	1	0.6	0.1	20.0	0.0	1.0	0.1
Pleuronectiformes	Pleuronectiformes	2	1.3	0.4	33.3	1.1	87.1	0.8
Gadiformes	*Merluccius productus*	4	2.5	1.5	58.3	2.5	98.2	2.0

Appendix 7. Monterey region Lingcod gut contents listed with dietary metrics. There were 24 types of prey items from 239 stomachs.

Prey Group	Prey Item	# Stomachs	%O	%N	%PN	%W	%PW	%PSIRI
Crustacea & Gastropoda	**Unidentified Crustacea**	1	0.4	0.4	100.0	0.4	100.0	0.4
	Decapoda	1	0.4	0.1	16.7	0.0	0.1	0.0
	Caridea	1	0.4	0.1	33.3	0.1	25.0	0.1
	Heptacarpus	1	0.4	0.2	50.0	0.3	64.3	0.2
	Crangon	1	0.4	0.1	25.0	0.4	97.4	0.3
	Pagurus	1	0.4	0.1	33.3	0.3	80.0	0.2
	Unidentified Gastropoda	1	0.4	0.3	66.7	0.1	20.0	0.2
	Littorina plena	1	0.4	0.2	50.0	0.1	25.0	0.2
	Nucella	1	0.4	0.1	16.7	0.0	6.0	0.0
	Trochidae	1	0.4	0.1	20.0	0.0	1.1	0.0
Cephalopoda	Cephalopoda	2	0.8	0.4	50.0	0.5	61.0	0.5
	Octopodidae	117	49.0	40.3	82.3	35.9	73.3	38.1
	Octopus dofleini	1	0.4	0.2	50.0	0.4	100.0	0.3
	Loligo opalescens	3	1.3	0.7	56.6	0.4	34.2	0.6
Unidentified Teleostei	Unidentified Teleostei	125	52.3	39.8	76.2	42.1	80.5	41.0
Scorpaenidae	Scorpaenidae	12	5.0	3.3	64.9	3.6	72.4	3.4
	Sebastes spp.	24	10.0	7.4	74.0	9.0	89.9	8.2
Demersal Fishes	Cottidae	3	1.3	1.0	83.3	1.2	98.4	1.1
	Ophiodon elongatus	1	0.4	0.1	25.0	0.1	21.0	0.1
	Ophiidae	6	2.5	1.8	70.8	1.5	61.2	1.7
Semi-Pelagic Fishes	*Scomber japonicus*	1	0.4	0.4	100.0	0.4	100.0	0.4
Pleuronectiformes	Pleuronectiformes	5	2.1	1.5	73.3	1.7	80.1	1.6
	Citharichthys sordidus	1	0.4	0.4	100.0	0.4	100.0	0.4
Gadiformes	*Merluccius productus*	2	0.8	0.8	100.0	0.8	100.0	0.8

Appendix 8. Conception region Lingcod gut contents listed with dietary metrics. There were 18 types of prey items from 238 stomachs. There were no Semi-Pelagic Fishes in this region.

Prey Group	Prey Item	# Stomachs	%O	%N	%PN	%W	%PW	%PSIRI
Crustacea & Gastropoda	Eucarida	1	0.4	0.4	100.0	0.4	100.0	0.4
	Pleuroncodes planipes	17	7.1	4.7	65.7	6.2	86.8	5.4
	Caridea	1	0.4	0.1	33.3	0.0	3.0	0.1
	Unidentified Gastropoda	1	0.4	0.1	12.5	0.0	4.6	0.0
	Ocenebra	1	0.4	0.3	75.0	0.4	92.3	0.4
Cephalopoda	Cephalopoda	5	2.1	1.4	65.0	1.5	69.9	1.4
	Octopodidae	89	37.4	24.2	64.7	20.2	54.1	22.2
	Loligo opalescens	24	10.1	5.1	50.6	3.9	38.8	4.5
Unidentified Teleostei	Teleostei unknown	138	58.0	46.4	80.0	46.8	80.8	46.6
Scorpaenidae	Scorpaenidae	4	1.7	0.9	56.3	1.3	76.5	1.1
	Sebastes spp.	41	17.2	10.6	61.4	12.5	72.5	11.5
	Sebastes mystinus	1	0.4	0.4	100.0	0.4	100.0	0.4
	Sebastes semicinctus	1	0.4	0.2	42.9	0.2	54.7	0.2
Demersal Fishes	Hexagrammidae	2	0.8	0.6	75.0	0.5	58.5	0.6
	Ophiidae	14	5.9	2.9	49.7	3.3	56.6	3.1
Pleuronectiformes	Pleuronectiformes	4	1.7	0.8	45.8	1.4	81.1	1.1
Gadiformes	Gadiformes	1	0.4	0.1	16.7	0.1	15.5	0.1
	Merluccius productus	2	0.8	0.8	100.0	0.8	100.0	0.8

Appendix 9. Female Lingcod gut contents listed with dietary metrics. There were 41 types of prey items from 598 stomachs.

Prey Group	Prey Item	# Stomachs	%O	%N	%PN	%W	%PW	%PSIRI
Crustacea & Gastropoda	**Unidentified Crustacea**	1	0.2	0.2	100.0	0.2	100.0	0.2
	Decapoda	4	0.7	0.2	33.3	0.1	13.3	0.2
	Pleuroncodes planipes	5	0.8	0.6	68.7	0.7	81.5	0.6
	Cancridae	2	0.3	0.1	42.5	0.1	28.2	0.1
	Cancer	1	0.2	0.1	75.0	0.0	11.6	0.1
	Caridea	2	0.3	0.1	26.7	0.1	29.6	0.1
	Unidentified Gastropoda	1	0.2	0.0	25.0	0.0	3.6	0.0
	Calliostoma	1	0.2	0.1	50.0	0.0	13.6	0.1
	Cylichnidae	1	0.2	0.1	60.0	0.1	57.1	0.1
	Littorinidae	1	0.2	0.0	20.0	0.0	28.6	0.0
	Nucella	1	0.2	0.0	16.7	0.0	6.0	0.0
	Volutacea	1	0.2	0.1	66.7	0.0	1.0	0.1
Cephalopoda	Cephalopoda	4	0.7	0.5	68.8	0.4	62.6	0.4
	Octopodidae	90	15.1	10.8	71.7	9.3	62.0	10.1
	Octopus dofleini	13	2.2	1.6	71.4	1.9	89.0	1.7
	Loligo opalescens	14	2.3	1.2	52.2	0.9	39.5	1.1
	Octopoteuthis deletron	1	0.2	0.1	50.0	0.1	50.0	0.1
Unidentified Teleostei	Unidentified Teleostei	366	61.2	52.0	85.0	51.0	83.4	51.5
	Fish egg mass	2	0.3	0.2	66.7	0.2	53.6	0.2
Scorpaenidae	Scorpaenidae	19	3.2	2.4	75.0	2.6	82.3	2.5
	Sebastes spp.	64	10.7	8.1	75.4	8.9	83.5	8.5
	Sebastes flavidus	1	0.2	0.2	100.0	0.2	100.0	0.2
	Sebastes jordani	1	0.2	0.1	50.0	0.2	98.4	0.1
	Sebastes melanops	1	0.2	0.2	100.0	0.2	100.0	0.2
	Sebastes mystinus	1	0.2	0.2	100.0	0.2	100.0	0.2
	Sebastes zacentrus	2	0.3	0.3	100.0	0.3	100.0	0.3
Demersal Fishes	Cottidae	3	0.5	0.4	77.8	0.4	73.4	0.4
	Leptocottus armatus	2	0.3	0.3	100.0	0.3	100.0	0.3
	Enophyrs bison	1	0.2	0.1	50.0	0.1	65.0	0.1
	Ophiodon elongatus	2	0.3	0.1	37.5	0.2	59.5	0.2
	Anoplopoma fimbria	4	0.7	0.6	87.5	0.6	96.6	0.6
	Ammodytes personatus	1	0.2	0.2	100.0	0.2	100.0	0.2
	Ophiidae	10	1.7	0.8	47.0	0.8	48.2	0.8
Semi-Pelagic Fishes	Clupeidae	14	2.3	2.3	100.0	2.3	100.0	2.3
	Clupea pallasii	16	2.7	1.5	55.0	1.9	69.5	1.7
Pleuronectiformes	Pleuronectiformes	15	2.5	1.6	63.9	2.0	80.8	1.8
	Atheresthes stomias	2	0.3	0.2	58.3	0.3	97.3	0.3
	Microstomus pacificus	3	0.5	0.3	55.6	0.3	65.2	0.3
	Parophrys vetulus	1	0.2	0.1	50.0	0.2	97.9	0.1
Gadiformes	Gadiformes	22	3.7	2.4	65.7	2.4	65.2	2.4
	Merluccius productus	72	12.0	9.7	80.4	10.1	84.2	9.9

Appendix 10. Male Lingcod gut contents listed with dietary metrics. There were 45 types of prey items from 660 stomachs.

Prey Group	Prey Item	# Stomachs	%O	%N	%PN	%W	%PW	%PSIRI
Crustacea & Gastropoda	**Unidentified Crustacea**	1	0.2	*	25.0	*	12.6	*
	Eucarida	1	0.2	0.2	100.0	0.2	100.0	0.2
	Decapoda	1	0.2	0.1	33.3	*	0.4	*
	Pleuroncodes planipes	12	1.8	1.2	64.5	1.6	89.0	1.4
	Brachyura	2	0.3	0.1	41.7	*	1.8	0.1
	Caridea	6	0.9	0.4	47.2	0.4	42.9	0.4
	Heptacarpus	1	0.2	0.1	50.0	0.1	64.3	0.1
	Crangon	1	0.2	*	25.0	0.1	97.4	0.1
	Paguroidea	1	0.2	0.1	33.3	*	3.7	*
	Lithodidae	1	0.2	*	25.0	*	3.0	*
	Paguridae	1	0.2	0.2	100.0	0.2	100.0	0.2
	Pagurus	2	0.3	0.1	18.8	0.2	55.5	0.1
	Unidentified Gastropoda	8	1.2	0.6	52.1	0.2	18.1	0.4
	Trichotropis cancellata	3	0.5	0.1	27.8	0.1	30.9	0.1
	Anabathridae	1	0.2	0.1	50.0	0.1	33.3	0.1
	Columbellidae	1	0.2	0.2	100.0	0.2	100.0	0.2
	Littorinidae	1	0.2	*	2.1	*	1.1	*
	Littorina plena	1	0.2	0.1	50.0	*	25.0	0.1
	Muricidae	2	0.3	0.1	36.8	*	10.6	0.1
	Ocenebra	1	0.2	0.1	75.0	0.1	92.3	0.1
	Rissoidae	1	0.2	*	16.7	*	10.7	*
	Trochidae	3	0.5	*	10.2	*	3.7	*
Cephalopoda	Cephalopoda	7	1.1	0.7	61.9	0.8	77.0	0.7
	Octopodidae	254	38.5	28.9	75.2	25.6	66.6	27.3
	Octopus dofleini	9	1.4	1.1	83.3	1.4	99.9	1.2
	Loligo opalescens	24	3.6	1.7	47.7	1.3	35.9	1.5
Unidentified Teleostei	Unidentified Teleostei	390	59.1	46.3	78.3	46.8	79.2	46.5
	Fish egg mass	8	1.2	0.4	35.6	0.5	41.0	0.5
Scorpaenidae	Scorpaenidae	11	1.7	1.3	78.4	1.3	77.8	1.3
	Sebastes spp.	87	13.2	9.5	71.8	10.9	82.3	10.2
	Sebastes jordani	1	0.2	0.2	100.0	0.2	100.0	0.2
	Sebastes melanops	1	0.2	0.2	100.0	0.2	100.0	0.2
	Sebastes semicinctus	1	0.2	0.1	42.9	0.1	54.7	0.1
Demersal Fishes	Cottidae	7	1.1	0.6	57.1	0.9	82.6	0.7
	Leptocottus armatus	3	0.5	0.3	56.0	0.2	53.0	0.2
	Hexagrammidae	2	0.3	0.2	75.0	0.2	58.5	0.2
	Ammodytes personatus	4	0.6	0.4	60.4	0.6	98.6	0.5
	Ophiidae	1	0.2	0.2	100.0	0.2	100.0	0.2
Semi-Pelagic Fishes	*Scomber japonicus*	11	1.7	1.0	60.9	1.0	61.7	1.0
	Clupeidae	1	0.2	0.2	100.0	0.2	100.0	0.2
	Clupea pallasii	2	0.3	0.2	62.5	0.2	55.7	0.2
Pleuronectiformes	Pleuronectiformes	15	2.3	1.3	57.8	1.9	81.6	1.6
	Citharichthys sordidus	1	0.2	0.2	100.0	0.2	100.0	0.2
Gadiformes	Gadiformes	4	0.6	0.5	75.0	0.6	99.6	0.5
	Merluccius productus	10	1.5	1.1	70.8	1.5	97.0	1.3