**Title (87/120 characters w/spaces):** Ocean condition and prey availability determine harbor seal trophic position during the past century

**Running Title (40 letters):**

**Authors:** Megan L. Feddern1, Gordon W. Holtgrieve1, Eric J. Ward2

1. University of Washington, School of Aquatic and Fishery Sciences, 1122 NE Boat Street, Seattle, WA 98105

2. Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112

**Corresponding Author:** Megan L. Feddern, 603-651-6802, mfeddern@uw.edu

*Page Count: 32 of 30*

**Abstract (350 words)**

**Keywords (6-12)**

**Introduction**

Climatic and anthropogenic changes are reshaping ecosystems, presenting new challenges for ecosystem-based management. Food web structure is regulated by availability of resources (bottom-up control) and the presence of top predators (top-down control). Anthropogenic and environmental drivers can alter resource availability and predator abundance and thus can reshape the structure and composition of marine ecosystems by changing predation pressure, competition for resources, and interaction strength (Goñi 1998, Kordas et al. 2011). Understanding the relative importance of these forms of food web regulation has long been a focal point in studying aquatic systems (Carpenter et al. 1985, Hunter et al. 1992, Estes et al. 1998). Physical ocean conditions alter nutrient distribution, light penetration, and community composition at the base of the food web (Strom et al. 2006), which can impact primary productivity and ultimately constrain energy availability and thus abundance at higher trophic levels (Ware and Thomson 2005, Chassot et al. 2010, Moore et al. 2018). Similarly, the removal of top predators from an ecosystem as a result of human activities such as fishing can decrease predation pressure and increase abundance at adjacent trophic levels, an effect that can cascade through the food web and impact abundance at non-adjacent trophic levels (Heithaus et al. 2008, Steneck 2012). Legislative action aimed at promoting top predator abundance by reducing fishing pressure or by-catch can have inverse effects as species recover (Ohlberger et al. 2019). Top-down and bottom-up control are often studied as independent mechanisms, however large scale changes in nutrient availability (Rykaczewski and Dunne 2010), primary productivity (Bopp et al. 2013), and top predator abundance over the past century (Magera et al. 2013) means many food webs are experiencing shifts in both mechanisms of regulation in tandem, making it challenging to identify dominant drivers structuring abundance and manage for change.

Ecosystems in coastal Washington and the Salish Sea have experienced dramatic restructuring over the past century due to declines and subsequent recoveries of marine predators (Jeffries et al. 2003, Ohlberger et al. 2019) and changes in environmental conditions (Mantua et al. 2002, Peterson et al. 2002). Decades of state-financed population control programs of resulted in harbor seals (*Phoca vitulina*) reaching a historic low in the 1970's, with abundance estimated to be approximately 1,000 (Jeffries et al. 2003). Following the cessation of bounties in 1960 and the passage if the Marine Mammal Protection Act in 1972 top-predator abundance increased dramatically. Benefitting from a relatively short life history, generalist diet, and legislation restricting mortality, harbor seal populations increased 10-fold between 1970 and 2003 (Jeffries et al. 2003). This increase in abundance has been characterized as a causal mechanism for declines in economically and ecologically important prey species in the region (Chasco et al. 2017, Nelson et al. 2019), specifically, Chinook salmon (*Oncorhynchus tshawytscha*) which have been listed as endangered in the region (WDFW 2017). While increases in marine mammal abundance has been a primary change in the ecosystem, dramatic changes in physical oceanic conditions have occurred simultaneously, which have a potential for altering the food web and harbor seal foraging strategies.

The recovery of harbor seals in the Salish Sea and coastal Washington region presents challenges, as management strategies for economically and culturally significant protected prey (i.e., Chinook salmon) and competitors (i.e., southern resident killer whales) require significant tradeoffs with protected harbor seals (Chasco et al. 2017). Informed management decisions require a comprehensive understanding of harbor seal interactions with the ecosystem and the environment in order to avoid unexpected outcomes and unrealized expectations for stakeholders. For example, harbor seals are generalist predators which feed opportunistically on a variety of available prey sources and are capable of prey switching in response to prey availability and intraspecific competition (Ostfeld and Keesing 2000, Thomas et al. 2011, Thomas et al. 2017). While increases in harbor seal abundance and declines in Chinook salmon abundance are a primary ecological change in the system since the 1970s, the Salish Sea and coastal Washington has also experienced changes in ocean condition (Khangaonkar et al. 2019), climate regimes (Mantua and Hare 2002, Corwith and Wheeler 2002), anthropogenic nitrogen inputs (Mohamedali et al. 2011, Feddern et al. 2021), and abundances of other important prey species such as Pacific herring (*Clupea pallasii*, Siple and Francis 2016). As a result, it is unlikely harbor seal foraging strategies have been constant throughout the past decade and predation pressure exerted by the harbor seal population has likely been dynamic. Additionally, harbor seal density has a stronger relationship in Chinook salmon productivity compared to other management strategies such as hatchery releases, and depredation is rarely incorporated into stock assessments (Nelson et al. 2019). Thus, it is important to understand how other ecological factors influence harbor seal foraging ecology to justify assumptions of predator-prey interactions and manage for changes in top-down forces in the region.

Understanding the future of ecosystem function in coastal Washington and the Salish Sea in response to human decisions, environmental change, and predator recoveries requires datasets that span multiple environmental, ecological, and anthropogenic contexts. Historic datasets are able to provide this information and are particularly useful for understanding ecosystem dynamics in the absence of anthropogenic pressure and ecological responses to climatic shifts. However, historic data and methods for analyzing these data are limited, which presents a challenge for understanding ecosystem interactions and anticipating outcomes of management decisions. For example, harbor seal population estimates were only consistently collected at multiple haul out sites starting in 1983 (Jeffries et al 2003) and only modern estimates of harbor seal diets in the region exist in the published record[[1]](#footnote-1) (Lance and Jeffries 2007). Robust data does not extend prior to declines in Chinook salmon populations in 1970s, prior to the 1977 regime shift of the Pacific Decadal Oscillation, or prior to implementation of the marine mammal protection act in 1972. A longer time series of data for harbor seal foraging ecology is thus necessary for teasing apart multiple drivers of ecosystem interactions in the region to accurately understand the dynamics of predator-prey interactions.

Measuring trophic position can be a useful proxy for major changes in foraging strategies and ecological interactions. For a generalist predator trophic position represents a weighted average of consumed and assimilated prey sources (Martínez del Rio et al. 2009). Major changes in foraging strategies should be reflected in predator trophic position if they represent prey switching between distinct trophic levels. For example, prey switching between adult salmon and herring would be represented in harbor seal trophic position but switching between juvenile salmon and herring would not. When trophic position data are available in long time series and combined with prey abundances and environmental time series, drivers of changes in food web interactions can be identified. Combining these datasets with trophic position of top predators can help identify bottom up forces influencing the system, and in turn, can characterize how top down pressure (i.e., harbor seal foraging) changes in response to prey availability and ocean condition.

Reconstructing time series of trophic position requires archival specimens and controlling for changes in the isotopic signature of primary producers caused by nitrogen cycling (McCarthy and McMahon 2016). Compound specific stable isotope analysis of individual amino acids provides the necessary means of control for reconstructing historical ecological data. Source amino acids (i.e., phenylalanine, lysine, methionine) exhibit minimal trophic discrimination and thus are a proxy for the isotopic signature of primary producers at the base of the food web, in contrast to trophic amino acids (i.e., alanine, glutamic acid, valine, proline) which demonstrate strong trophic enrichment (McCarthy and McMahon 2016). When combined, this approach allows for reconstruction of historical trophic dynamics where characterizing the isotopic baseline of past ecosystems may not be possible (McMahon et al. 2019).

Here we examine a century of harbor seal trophic position data in coastal Washington and the Salish Sea. The objective of this work is to identify how physical ocean condition, prey availability, and location impact the role of harbors seals as marine predators through bottom-up control of their trophic ecology. We anticipate environmental factors and spatial location will alter harbor seal trophic position reflecting changes predation pressure on Chinook salmon and other important prey species. We assume a correlation between trophic position and prey species is the result of increased consumption of that species. Additionally, we aim to establish a multi-amino acid framework for measuring trophic position and compare these results to a single amino acid analysis that is typically applied in compound-specific stable isotope analysis studies.

**Methods**

*Sample collection and analysis*

Samples were obtained using methods described in Feddern et al. (2020). Briefly, harbor seal bone was obtained from specimens curated four museum institutions (the Burke Museum, the Slater Museum, the Royal British Columbia Museum, the Smithsonian Institute) and the National Marine Mammal Laboratory (NOAA) (*Supplementary Table*). Sampling targeted adult specimens to avoid dietary differences between adults and juveniles and prioritized long-term temporal coverage in two main regions: coastal Washington and the Salish Sea (which included 18 specimens from British Columbia). Specimens with sex and age metadata were also prioritized but not available for most specimens. A total of 153 specimens were sampled representing 1928-2014.

*Trophic position calculation*

Bone collagen was decalcified, acid hydrolyzed, derivatized and analyzed for compound-specific stable isotope (δ15N) analysis (CSIA) of 12 individual amino acids (*SI Appendix 1*). δ15N was measured as:

Collagen samples were measured in triplicate with a laboratory standard containing a 12 amino acid mixture of known isotopic composition. Previous controlled feeding studies have determined the trophic discrimination factor (TDF) for harbor seals is substantially lower than the conventional literature value of 7.6‰ (Germain et al. 2013) and thus applying a harbor seal specific trophic discrimination factor is more ecologically realistic (McMahon et al. 2015). Therefore, trophic position was calculated using a harbor seal specific trophic discrimination factor, described by McMahon et al. (2015) as a "multi-TDF" approach, using the following equation:

where *TDF(Tr-Phe) Average*is the difference between given trophic amino acid - phenylalanine of an average consumer derived from Nielsen et al. (2015). *TDF(Tr-Phe) harbor seal* represents the harbor seal specific trophic discrimination factor for a given trophic amino acid - phenylalanine pair calculated from Germain et al. (2013) controlled feeding study data (Table 1) and β is the δ15N difference between a specific trophic amino acid and phenylalanine of primary producers. Multiple parameterizations of the multi-TDF trophic position calculation were considered (*SI Table S1*) using species and taxa specific values, and average across species, trophic discrimination factor.

Application of a multi-TDF approach has led to consistent underestimates of trophic position compared to known feeding ecology (McMahon et al 2015, McMahon et al. 2019, Germain et al. 2015) despite its more realistic representation of metabolic pathways and improved accuracy (*SI Figure S1*). Harbor seals are expected to exhibit a trophic position ranging from approximately 3.5 to 5 and only 12%-66% of data fell within this range (*SI Figure S1*). Primary producers utilize C4 photosynthesis pathways such as sea grasses and some macrophytes (i.e., *Ulva spp.* Xu et al. 2012) and have substantially lower discrimination between trophic amino acids and phenyalanine (Vander Zanden et al. 2013, Choi et al. 2017) (Table 1). Thus, if C4 photosynthesis pathways are utilized in marine food webs and trophic position calculations assume only C3 pathways, trophic position will be consistently underestimated. Given the abundance of seagrasses in coastal Washington and the Salish Sea (Shelton et al. 2017) and food web coupling in these coastal environments (Howe and Simenstad 2015) it is expected C4 primary producers contribute to Salish Sea and coastal Washington food webs in which harbor seals forage (Feddern et al. 2021). Therefore, we applied a two-source mixing model using carbon stable isotope data similar to Choi et al (2017):

Where *δ 13CHarbor Seal* is the mean observed δ13C value for Washington harbor seals *δ 13CSeagrass* is the C4 carbon stable isotope end member (-9.3‰) and *δ 13CDiatoms* is the C3 carbon stable isotope end member (-19.4‰) derived from Howe and Simenstad (2015). *%C4* is the relative contribution of C4 plants to the food web in which harbor seals forage. This assumes the trophic enrichment of 13Cis generally negligible (0–1‰, Deniro and Epstein 1978). A weighted β that incorporates both C4 and C3 photosynthesis pathways in marine environments was then derived by:

Where *βC3, Tr* is β the for an individual trophic amino acid for aquatic phytoplankton (Nielsen et al. 2015; Table 1) and *βC4, Tr* is β the for an individual trophic amino acid for sea grass which utilize exclusively C4 photosynthesis pathway (Vander Zanden et al. 2013;Table 1). Trophic position calculations were more ecologically realistic from applying βw when compared to applying a *βC3, Tr* (*SI Figures 1 & 2*). Therefore, harbor seal trophic position was calculated using the most ecologically accurate and parsimonious equation:

*Identifying trends in harbor seal trophic position*

Generalized additive models (GAMs) were fit to trophic position by year using a smoothed term for year and forward selection of the following covariates

Previous studies have found sex specific differences in the stable isotope values of bulk tissue which has been attributed to differences in nearshore verse offshore foraging strategies (Bjorkland et al. 2015). Additionally, prey switching is common as juveniles pinnipeds grow to adults (Zhao et al. 2004). We tested the significance of sex and length in harbor seal trophic position to understand whether this trend was reflective of long-term relationships in harbor seal trophic position. Only a subset of the samples included sex and length metadata and therefore separate length and sex specific analyses were fit to the data. Two standard linear models (equation 3) with an interaction effect between trophic amino acid as a factor and 1) sex as a factor and 2) length as a continuous covariate were fit to both Salish Sea and coastal WA to test whether trophic position varies with length and sex, and whether these trends are consistent between amino acids. The standard linear model took the following structure:

where *y* represents harbor seal trophic position calculated from phenylalanine and a trophic amino acid *Tr*, ***X*** is a matrix of bottom-up drivers for a given model, ***β*** is a vector of covariates (sex, length, year, location), and *a* is the intercept.

*Quantifying bottom-up drivers of foraging*

We were interested in two categories of bottom-up drivers of harbor seal trophic ecology: ocean condition and prey availability. Therefore, potential explanatory variables of harbor seal trophic position encompassed a range of environmental and ecological time series (Table 2). A total of 15 explanatory variables were selected based on the length of the time series and evidence of ecological importance in the region; selected time series were divided *a priori* into the two categories of interest, ocean condition and prey availability. All time series were standardized around a mean of 0 and standard deviation of 1. For each bottom-up driver category, a series of candidate models were fit to the data including all possible combinations of covariates; a null model and location only model were also included. Location (Salish Sea or coastal Washington) was included as a factor in all candidate models except the null model. Due to the known relationship between Pacific hake and Pacific herring (hake depend on herring for >20% of their diet, Surma et al. 2018) an interaction effect between hake and herring was also tested. Similarly, due to the correlation between the multivariate El Niño Southern Oscillation index and the Pacific Decadal Oscillation (PDO), and summer and spring upwelling, only one of these covariates were included in each model. Inclusion of times series covariates in the model with the most support is indicative of ecological parameters that alter harbor seal foraging ecology. Additionally, magnitude and sign of the coefficients for included covariates can be interpreted as the degree of trophic change either between species, life stages of species, or groups of species, induced by a given covariate.

To identify the most important explanatory variables of ocean condition and prey availability on harbor seal trophic ecology, two sets of candidate models were fit using a multi amino acid (glutamic acid, alanine, proline, valine) hierarchical model. The best model for both of these approaches was selected using Akaike information criterion with a correction for small sample size (AICc). The hierarchical linear model took the following structure:

where *y* represents harbor seal trophic position from year *t* and *Tr* represents four different trophic amino acids used to calculate trophic position included as a random effect. ***X*** is a matrix of continuous bottom-up drivers in year *t*. ***β*** is a vector of predicted effects (coefficients) of bottom-up drivers included in the model (Table 2) on harbor seal trophic position, and *a* is the predicted trophic position when all included bottom-up drivers are at an average value (represented by 0) in the coastal region of Washington. A 1, 2, and 3-year lag was applied to harbor seal trophic position and each lag was modelled using the same candidate model set separately. The 1-year lag accounts for the tissue turnover time of bone collagen and thus corresponds to ‘year-0’ or the conditions present in the non-lagged covariate data. The 2-year and 3-year lags account for a 1-year and 2-year delay in the response of harbor seal trophic position to ecological and ocean conditions after accounting for tissue turnover time. Models will be referred to as ‘year-n’ in reference to their lag. To avoid collinearity between covariates no more than three covariates were included in each model. To validate collinearity was not problematic in the models with the most support, matrix scatterplots and variance inflation factors (VIF) were used from the usdm package (Naimi 2014) in R (R Development Core Team, 2013).

*Identifying trends through time*

To understand any changes through time to harbor seal foraging ecology over the past 100 years that were not explained by the tested covariates, the residuals for the best ocean condition-prey model was plotted by year with a smooth term fit to the residuals through time using a generalized additive model with a k term of 5. This plot was compared to the raw time series of harbor seal trophic position data to understand trends through time that are unexplained by the covariates included in this analysis.

**Results**

*Patterns in harbor trophic position*

Trends in harbor seal trophic position through time were different between the Salish Sea and coastal Washington (Figure 2). The time series of the glutamic acid trophic position in coastal Washington had a significant trend through time (Figure 2b) which increased from 1948-1968 and remained relatively constant following 1975. Trophic position calculated from alanine and proline showed similar trends, although the alanine trophic position trend was not significant (Figure 2a). In contrast harbor seal trophic position in the Salish Sea has been relatively stable over the past century, but the trophic position calculated from valine showed a substantial decline since 1968 which was not observed in trophic position calculations derived from any other amino acids. Mean harbor seal trophic position estimates were similar across trophic amino acids however some were more variable than others. The standard deviation of trophic position was higher for proline (4.6 ± 0.7, mean ± 1SD), and valine (3.7 ± 0.8) and included more ecologically unrealistic values compared to glutamic acid (4.5 ± 0.4) and alanine (3.9 ± 0.4). Trophic position calculated from aspartic acid (4.1 ± 1.0) had the highest standard deviation and also demonstrated an unusual trend through time compared to other amino acid trophic position calculations (Figure 2).

There were no significant differences in trophic position between male and female harbor seals in either Salish Sea (Figure 3A) or coastal Washington (Figure 3B) and this relationship was consistent across amino acids. Similarly, trophic position did not change based on harbor seal length (Figure 4). Interestingly, the exception to this finding was trophic position calculated by proline which showed a significant decline with size suggesting harbor seals forage at lower trophic levels compared to smaller harbor seals. Mean harbor seal trophic position calculated from proline for seal ranging from 150 - 180 cm in standard was 0.6 lower than harbors seals that were less than 120 cm of standard length (Figure 4). Trophic position calculated from alanine, aspartic acid and valine also showed negative trends with size although the trend was not significant. In contrast trophic position calculated from glutamic acid was positive although this trend was also not significant.

*Bottom-up forces on harbor seal trophic position*

Summer upwelling, sea surface temperature and El Niño Southern Oscillation (ENSO) all impact harbor seal trophic position but on different temporal scales. The best environmental models (Figure 5) for year-0 included location (Salish Sera verse Coastal Washington) as a factor and summer upwelling (Figure 5A), the year-1 model included summer sea surface temperature (Figure 5B), and the year-2 model included upwelling and ENSO (Figure 5C). Summer upwelling exhibited an immediate impact on harbor seal trophic position, where upwelling resulted in the consumption of lower trophic level species during the same year (Figure 5A). However, two years following there was a positive relationship between trophic position (Figure 5C) and upwelling indicating upwelling has both immediate and delayed effects on trophic position that result in different trophic shifts depending on the timescale. Summer sea surface temperature also exhibited a delayed impact, where harbor seals foraged lower in the food web the year following summers with higher than average sea surface temperatures (Figure 5B). The coefficients for year-0 summer upwelling (-0.016, Figure 5A) and year-2 summer upwelling (0.04, Figure 5C) were low indicating a small, albeit significant, impact of upwelling on harbor seal trophic position compared to year-1 sea surface temperature (-0.20, Figure 5B) and year-2 ENSO (-0.11, Figure 5C). Location had the highest effect on trophic position with a coefficient of ~ -0.3 for all three models (Figure 5).

Location, abundance of salmon smolts, and hake and herring spawning biomass, were correlated with harbor seal trophic position in Washington. Harbor seals in the Salish Sea fed approximately 0.2 trophic levels lower than coastal Washington harbor seals (Figure 6). Hake biomass and harbor seal trophic position were positively correlated in the year-0 model (Figure 6A). In contrast, the hake biomass in the year-2 model was negatively correlated with harbor seal trophic position (Figure 6C), thus, harbor seals are feeding lower in the food web two years after hake spawning biomass is high. In the year-2 model harbor seal trophic position was also positively correlated to Pacific herring spawning biomass (Figure 6C). Chinook salmon smolt production (which included hatchery releases and wild production of Chinook salmon; *SI Table S3*) was included in both the year-1 (Figure 6B) and year-2 (Figure 6C) models and was positively correlated with harbor seal trophic position. The correlation coefficient between harbor seal trophic position and smolt production was higher on the year-1 model (0.14, Figure 6B) compared to the year-2 model (0.08, Figure 6C).

**Discussion**

Harbor seal trophic position over the past century has been stable despite major changes climate and food webs (Figure 2). While there are no major temporal trends in harbor seal trophic position our hierarchical modeling shows correlations between harbor seal trophic position, and ocean conditions and prey availability, indicating harbor seals do alter their foraging strategies in response to ecosystem changes (Figures 5 & 6). Harbor seal generalist foraging strategies appear to compensate for ecological changes. Assuming the correlation between trophic position and prey species is the result of increased consumption of that species, our results show that harbor seal consumption of Chinook salmon, Pacific herring, and hake is density dependent. This means that high abundance of these prey sources results in greater predation on these prey sources. Similarly, location, upwelling, sea surface temperature and ENSO, alter harbor seal trophic ecology. These results indicates total abundance of harbor seals is not the only factor influencing prey consumption. Consideration for density dependent consumption, location and environmental condition may be important to predict predation pressure on threatened prey species.

Harbor seals in Washington do not have distinct trophic ecology based on size (Figure 3) or sex (Figure 4). Bjorkland et al. (2015) did not observe sex or size (weight) based differences in bulk 15N values in harbor seals in the San Juan Islands in the Salish Sea between 2007 and 2008. Our results agree with this finding and with similar studies of other Pacific pinniped species (Drago et al. 2009, Dehn et al. 2007). While both males and females harbor seals have a similar trophic position it is possible sex and size-based differences in foraging strategies within a similar trophic position exist (Bjorkland et al. 2015, Wilson et al. 2014). Additionally, this study focused on adult harbor seals and changes in trophic position between juveniles, sub adults and adults are possible based on previous pinniped studies (Zhao et al. 2004). Regardless, our results show long-term consistencies in the trophic niche exploited by both male and female harbor seals regardless of adult size in Washington.

Environmental conditions impact abundance of fish species in coastal Washington (Reum et al. 2011, Greene et al. 2015). Harbor seals respond to this bottom up force by adjusting their relative consumption of prey species resulting in trophic position change in response to environmental conditions. More specifically, harbor seals consume more low trophic level species in years of above average summer upwelling and summer sea surface temperature (Figure 5). However, harbor seals respond to these environmental conditions on different temporal scales. Reum et al. (2011) found age-0 Pacific herring abundance in Puget Sound is positively correlated with annual upwelling in the Strait of Georgia. This increase in abundance of low trophic level, juvenile, fish could explain the negative correlation between harbor seal trophic position and upwelling in year-0 (Figure 5A). Similarly, this could explain the positive correlation between trophic position and upwelling in year-2, as this age class of juveniles grows to age-2 fish and continue to be consumed by harbor seals, there is a trophic shift. In addition, Salish Sea predators and fish species are correlated to sea surface temperature but responses in reproductive success (Smith et al. 2017) or abundance (Duguid et al. 2019) are often delayed by a year or more. This temporal delay was also observed in harbor seal trophic position in response to both sea surface temperature and ENSO. This result highlights the importance of considering delayed responses of consumers when predicting ecological responses to environmental conditions.

Pacific hake and Pacific herring are frequently documented as common prey sources in Washington harbor seal diet (Orr et al. 2004, London et al. 2002, Lance et al. 2012). Female Pacific hake reach sexual maturity at 4-5 years at which point they are approximately 60 cm in length (Smith et al. 1990). When spawning biomass is high, harbor seals take advantage of the of this high-trophic level prey source as indicated by the positive correlation between hake and trophic position in year-0 (Figure 6A). In contrast, harbor seal trophic position is negatively correlated with hake spawning biomass in year-2 (Figure 5C). The likely explanation for this trophic shift is that above average spawning biomass leads to above average recruitment in the following years. As a result, smaller 2-year old fish are (which are only 30-35 cm in length, Smith et al. 1990) are available and consumed by harbor seals. Thus, harbor seals take advantage of adult hake in years of high spawning biomass and then forage on juvenile fish which are a fraction of their adult size and lower in the food web in the following years (Figure 6).

In contrast to the correlation between trophic position and hake, harbor seals do not exhibit am immediate change (year-0) in trophic position in response to herring spawning biomass and instead exhibit a response two years later (year-2, Figure 6C). Harbor seals are known to preferentially consume juveniles during herring spawning season and adult herring during the non-spawning season and generally spend more time in herring areas during the non-spawning season (Thomas et al. 2014). Additionally, the relative abundance of adult to juvenile herring in harbor seal diet varies between years (Lance et al. 2012). It is possible that herring spawning biomass from two years ago (year-2) provides a better proxy for adult herring availability for predation than current spawning biomass estimates. Herring grow dramatically in the first 2 years of life (Hay et al. 2008) and do not reach sexual maturity until 2-3 years (Barton and Wespestad 1980). If 2-year old fish are an important component to harbor seal foraging this could explain the positive correlation between trophic position and herring spawning biomass in year-2 (Figure 6). Alternatively, this result may be due to covariation between a third variable. For example, upwelling and harbor seal trophic position were correlated in the year-2 and upwelling is known to impact herring abundance (Reum et al. 2011). Similarly, herring are an important component of hake diet (Schweigert et al. 2010) and herring from 2 years ago (year-2) may covary with current hake abundance (year-0) resulting in the positive correlation. However, the coefficient of year-2 herring is 0.21 which is substantially higher than the coefficient for year-0 hake (0.11) and year-2 upwelling (0.04). Thus, covariation with these two variables does not seem to be the only factor contributing to the correlation between harbor seal trophic position and year-2 herring, and direct consumption of herring by harbor seals is likely a contributing factor

A combined index of hatchery Chinook smolt production and wild Chinook production offer the best index of salmon availability to harbor seals. Escapement counts of individual salmon species were not correlated with harbor seal trophic position. Salmon that have ‘escaped’ to freshwater have already been predated on and thus these numbers may not reflect the availability of salmon to harbor seals prior to predation. The correlation between harbor seal trophic position and smolt production indicate harbor seals do take advantage of increased salmon abundance. Surprisingly, year-0 abundance is not correlated with trophic position (Figure 6A) and year-1 and year-2 abundance is positively correlated with trophic position (Figure 6B & C). This suggests that harbor seal trophic position is not dependent on out migrating smolts, which would likely result in a negative correlation with year-0 abundance. Instead, year-1 and year-2 smolt abundance is determining the abundance of 1-ocean (salmon that have spent one year in the ocean) and 2-ocean (salmon that have spent 2 years in the ocean) fish which are then predated on by harbor seals.

Previous work has documented juvenile salmon in harbor seal diets (Steingass 2017, Lance and Jeffries 2007, Lance et al. 2012, Wright et al. 2007). While our results do not show that harbor seal trophic ecology responds to year-0 smolt abundance, it is likely harbor seals do consume out migrating smolts. If the biomass of out migrating smolts consumed by harbors seals is low relative to the total biomass of harbor seal diet, or the biomass consumed by harbor seals is not dependent on the abundance of out migrating smolts, a change in trophic position would not be expected. Even if the total biomass of Chinook smolts is low, the total number of smolts consumed may be high (Chasco et al. 2019) and thus an important component of salmon survival. Additionally, the smolt abundance in this study was specific to Washington Chinook salmon due to the length of time series compared to data available for other species in the region. It is possible that harbor seal trophic position could correlate with a metric of total smolt abundance of all species for year-0 if harbor seals are not selective on juvenile salmon species consumed. This is an especially important consideration given the known importance of pink salmon (*Oncorhynchus gorbuscha*) to harbor seal diet in the region (Lance et al. 2012). Similarly, inclusion of a broader spatial scope of smolts not specific to Washington (i.e., British Columbia) could be important. Regardless, this analysis ocean-1 and ocean-2 Chinook salmon may be an important component to at sea survival of Washington Chinook.

High specialization in harbor seal diet sites has been documented in the region (Wilson et al. 2014, Lance et al. 2012). Thus, it is unsurprising that our results indicated substantial trophic differences between the Salish Sea and coastal Washington harbor seals, with Salish Sea harbor seal foraging 0.3 trophic levels lower than their coastal Washington counterparts (Figures 5 & 6). Our sampling prioritized creating a long-term dataset rather than a spatially exhaustive one and as a result the dataset is limited in its ability to discern smaller scale spatial patterns that are known to exist even between haul out sites (Wilson et al. 2014). Regardless of this limitation, our results show that both long-term spatial specialization and common long-term patterns in harbor seal trophic ecology in response to prey availability and environmental conditions exists within the region.

CSSIA offers improved characterization of trophic ecology of top predators over long time scales compared to traditional bulk methods. Bulk stable isotope analysis of trophic position is limited in its ability to discern between changes in trophic ecology and changes in the isotopic signature of primary producers unless both are sampled simultaneously. CSSIA allows for internal standardization of the stable isotope signature of primary producers through source amino acids (McClelland and Montoya 2002, Chikaraishi et al. 2009). The nitrogen stable isotope signature of primary producers is known to change based on the relative abundance of nitrogen sources and their isotopic signatures (McMahon et al. 2015) which very in response to environmental conditions (Sherwood et al. 2011, Sherwood et al. 2014). Over the past century the isotopic signature of nitrogen of source amino acids has changed in the northeast Pacific in response to oceanic conditions and climate change (Feddern et al. 2021, de la Vega 2020). Nonetheless, like bulk stable isotope analysis, CSIAA is sensitive to the parameterization of trophic position equation (McMahon et al. 2019, Germain et al. 2013; *SI Figures S2 and S3*). Thus the utility and reliability of CSIAA for trophic position studies requires careful considerations of the trophic discrimination factors and beta values applied. Additionally, application of a multi-amino acid framework improved model certainty (*SI Appendix 4*, Nielsen et al. 2015). We recommend using a multi-trophic discrimination factor approach with taxa specific trophic discrimination factors and system specific betas when appropriate.

Management of predators that consume threatened, economically important prey species such as harbor seals requires extensive management tradeoffs (Marshall et al 2015). Harbor seals demonstrate drastic variations in trophic ecology in response to location, prey availability, and ocean condition. Our results also show the response of trophic position (and assumed predation) change is often delayed on the order of 1-2 years in response to ecological conditions. Currently, estimates of total biomass consumed that treats harbor seal predation pressure as static through time (Chasco et al. 2015). Based on our results and others (Wilson et al. 2014, Lance et al. 2012) this is likely inaccurate as seasonality, spatial location and individual behavior impact harbor seal predation. This variability if foraging ecology should be carefully considered when assessing tradeoffs of harbor seal management decisions to ensure realized expectations for stakeholders. Spatially distinct management strategies that are frequently reevaluated will likely be important strategies for managing harbor seal prey considering their dynamic foraging strategies.

**Acknowledgements**

We would like to extend our deepest gratitude to our museum collaborators for permitting sampling and coordinating logistics. Specifically, we thank Jeff Bradley and Sharlene Santana of the UW Burke Museum, Peter Wimberger and Gary Shugart of the Slater Museum, Link Olson and Aren Gunderson of the Museum of the North, Robert Delong of the National Marine Mammal Laboratory, Lesley Kennes and Gavin Hanke of the Royal BC Museum, and Darrin Lunde and John Ososky of the Smithsonian Institute. We thank Megan Stachura and Tom Royer for assistance with environmental datasets, and Chris Harvey and Jens Nielsen for helpful discussions and support. Hyejoo Ro and Karrin Leazer assisted in lab work. Mark Haught and Terry Rolfe assisted with GC/C/IRMS methods development, maintenance, and troubleshooting. This publication was funded in part by grants from Washington Sea Grant, University of Washington, pursuant to National Oceanic and Atmospheric Administration Award No. NA18OAR4170095 and NA19OAR4170360. This publication is partially funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement NA15OAR4320063, Contribution No. 2020-1116. Additional funding was provided by an internal grant from the Northwest Fisheries Science Center. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies.

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**Tables**

**Table 1:** Trophic amino acid specific parameter values for β and trophic discrimination factors (TDF) to test parameterization of trophic position calculations using multiple TDFs and β values (Supplementary Material Appendix 1, Table S1, Figures S2 & S3).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Trophic Amino Acid | βAq  Nielsen et al. 2015 | βSeagrass  Vander Zanden et al. 2013 | βW  This study | TEFHS  Germain et al. 2013 | TEFPhyto  Chikaraishi et al. 2009 | TEFAve  Nielsen et al. 2015 |
| Glutamic acid (Glu) | 2.9 | -8.7 | -3.9 | 3.4 | 7.6 | 6.6 |
| Alanine (Ala) | 2.8 | -8.0 | -3.6 | 2.5 | 5.6 | 6.8 |
| Aspartic Acid (Asp) | 1.8 | -7.3 | -4.2 | 3.5 | 5.4\*  Nielsen et al. 2015 | 5.4\* |
| Valine (Val) | 3.4 | -6.8 | -2.6 | 7.5 | 4.2 | 4.6 |
| Proline (Pro) | 2.7 | -7.7\*  Not reported used average of other AAs |  | 5.5 | 5.0 | 5.0 |

**Table 2:** Covariates used to test bottom-up drivers of harbor seal trophic position. Dataset details are included in *SI Tables S2 & S3*.

|  |  |
| --- | --- |
| Ocean Condition Covariates | Food web Covariates |
| Multivariate El Niño Index (MEI) | Pacific hake spawning biomass  (*Merluccius productus*) |
| Pacific Decadal Oscillation (PDO) | Pacific herring spawning biomass  (*Clupea pallasii*) |
| Columbia River discharge (high flow months) | Chinook salmon escapement  (*Oncorhynchus tshawytscha*) |
| Mean summer sea surface temperature (SST) | Coho salmon escapement  (*Oncorhynchus kisutch*) |
| Mean summer upwelling index | Chum salmon escapement  (*Oncorhynchus keta*) |
| Mean spring upwelling index | Chinook salmon smolts (combined wild and hatchery production) |
|  | Harbor seal abundance  (*Phoca vitulina*) |

**Figures**

**Figure 1:** Spatial and temporal distribution of harbor seal specimens where a) shows the locations specimens were collected in the Salish Sea (yellow) and coastal Washington (blue) and b) and c) show the year of specimen collection and total number of specimens for each year from 1928-2014 in the Salish Sea and coastal Washington respectively.

**Figure 2:** Time series of harbor seal trophic position in a) coastal Washington and b) the Salish Sea for five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) calculated using the source amino acid phenylalanine. Color corresponds to trophic amino acid, line shows the fit of a generalized additive model with a smoothed term by year and a k of 6. \* denotes a significant smoothed term.

**Figure 3**: Sex specific trophic position for male (M) and female (F) harbor seals pooled over the past century and calculated using five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) for a) Salish Sea and b) coastal Washington specimens.

**Figure 4:**  Relationship between harbor seal size (standard length, cm) and trophic position calculated using five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline). The line shows the fit of a generalized additive model with a smoothed term by year and a k of 6 and \* denotes a significant smoothed term.

**Figure 5**: The covariates of the best environmental hierarchical models using a) 1-, and b) 2-year lags. Y axis denotes the coefficient for each covariate, black points are fixed effects and colored points are random effects.

**Figure 6**: The covariates of the best food web hierarchical models using 1-, 2-, and 3-year lags. Y axis denotes the coefficient for each covariate, black points are fixed effects and colored points are random effects. Models with a 1-year lag account for tissue turnover time of collagen and represent an immediate impact of the given covariate, model with a 2-year lag or higher represent a delayed effect. Hake and herring both represent spawning biomass, smolts represent both hatchery releases and estimated wild production (*SI Table*)

**Figure 7**: Conceptual diagram representing the mechanisms of prey abundance on harbor seal trophic position on multiple time scales (year-0, year-1, year-2). Solid arrows represent direct effect on harbor seal trophic position and signs indicate the direction of the effect, dashed lines represent indirect effects contributing to the direct effect. Boxes represent coefficients supported in the best models from Figure 6.

**Figure 1**

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**Figure 2**

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**Figure 3**

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**Figure 4**

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**Figure 5**

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**Figure 6**

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**Figure 7**

1. These authors acknowledge traditional knowledge of historic harbor seal diets may exist [↑](#footnote-ref-1)