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

**Running Title (40 letters):**

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[Articles in Ecology are hard to get. They really want them to be definitive pieces of work on a particular topic. I suspect tis will be seen as cool new work with high interest, but not definitive on the topic. The editors are pushing for Reports over Articles and I think they will want this to be a Report. Currently you are about 10 pages over. At a minimum you would need to drop a couple figures plus shorten the text by maybe ¼. Not impossible, but not simple either.]

**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) (needs a citation). 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).

,environmental

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). Management 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.

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).

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 driven by X, Y and Z (Mantua et al. 2002, Peterson et al. 2002). Decades of state-financed population control programs resulted in harbor seals (*Phoca vitulina*) reaching a historic low in the 1970's, with an estimated abundance of approximately 1,000 individuals (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). The dramatically increased abundance of this top predator has been implicated in the 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 are 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 and prey species populations have occurred simultaneously, which have a potential for altering the food web and harbor seal foraging strategies. 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 the 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). It is therefore 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.

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 abundance is the result of increased or decreased consumption of that species. Additionally, we established a multi-amino acid framework for measuring trophic position that improves upon the traditional single amino acid approach by….

(This paragraph should all be in the past tense. Always in past tense when talking about the study itself.).

**Methods**

*Sample collection and analysis*

Samples were obtained using methods described in Feddern et al. (2020). Briefly, harbor seal bone was obtained from 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 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, length, age data were also prioritized. A total of 153 specimens were sampled with field collection dates ranging 1928-2014.

*Trophic position determination*

Bone collagen was decalcified, acid hydrolyzed, derivatized and analyzed for compound-specific stable isotope (δ15N) analysis (CSIA) of 12 individual amino acids. Collagen samples were measured in triplicate with a laboratory standard containing a 12 amino acid mixture of known isotopic composition and a linear drift correction was applied. Full analytical details are described in *SI Appendix S1*. 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 a given trophic amino acid and 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 and phenylalanine pair calculated from Germain et al. (2013) controlled feeding study data (Table 1). 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 as well as the average across species.

The *β* parameter in equation 2 differs substantially between primary producers using the C3 vs C4 photosynthetic pathway (Table 1, *SI Appendix S3*). In food webs that assimilate organic matter from both C3 and C4 – including coastal food webs *β* will be intermediate. 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 and *δ 13CDiatoms* is the C3 carbon stable isotope end member (Table 1). *%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 (*Tr*)for aquatic phytoplankton and *βC4, Tr* is *β* the for an individual trophic amino acid (*Tr*)for sea grass which utilize exclusively C4 photosynthesis pathway (Table 1).

*Quantifying bottom-up drivers of foraging*

A total of 15 potential 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 our two categories of interest, ocean condition and prey availability representing our expected primary forcing mechanisms as described above (Table 2). All time series were standardized around a mean of 0 and standard deviation of 1. For each 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 (*Merlucciua productus*) and Pacific herring (*Clupea palasii*) (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. To avoid collinearity, no more than three covariates were included in each model.

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 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. The best model for both of these approaches was selected using Akaike information criterion with a correction for small sample size (AICc).). 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.

A 1-year lag was applied to all harbor seal trophic position estimates to account for the tissue turnover time of bone collagen, where the collagen in a harbor seal collected in year *t* reflects what it ate in year *t-1*. Delayed harbor seal foraging response to ecosystem dynamics was also tested by applying additional 1-year and 2-year lags to trophic position data in addition to the 1-year lagged applied for tissue turnover time. For example, the association between harbor seal trophic position and environmental conditions 2 years before the collection year would indicate that there was a 1-year delay between when the environmental change happened and when the resultant changes propagated through the food web, after accounting for the 1-year tissue turnover time. Models will be referred to in reference to the delayed ecological response as ‘n-delay’. 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 Team, 2020)

**Results**

Summer upwelling, sea surface temperature and El Niño Southern Oscillation (ENSO) all impacted harbor seal trophic position but on different temporal scales. The best environmental models (Figure 5) for the 0-delay models 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 that indicated consumption of lower trophic level species during the same year (after account for tissue turnover; Figure 5A). However, there was also a positive relationship between trophic position and upwelling 2 years prior to collection (Figure 5C) indicating upwelling has both immediate and delayed effects on trophic position. Summer sea surface temperature showed 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 more strongly associated with harbor seal trophic position than environmental drivers. 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 in the Salish Sea and coastal Washington 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, ocean conditions, and prey availability, but not abundance of harbors seal themselves. Harbor seals therefore alter their foraging strategies in response to bottom-up ecosystem changes (Figures 5 & 6) suggesting their generalist foraging strategies can 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 positively related to density of these prey. Similarly, location, upwelling, sea surface temperature and ENSO, alter harbor seal trophic ecology. These results indicate 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 adult 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 as indicted by 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.

[I think somewhere around here you need to have a clear summary of the patterns described in figure seven. You want to somehow give a big-picture overview of how you think the system works. Then you can go into the specifics about year 0 vs year 2 hake, year 1 herring, etc. Lots of details that are presumably building to a bigger lesson. You need to give the bigger lesson first to hook people then take a little time to fill in the details.]

Multiple studies have shown that environmental conditions such as X, Y ad Z impact abundance of coastal Washington fishes (Reum et al. 2011, Greene et al. 2015). This work, however, shows that top predators (harbor seals) can have delayed responses to this bottom up force in terms of the trophic position. Harbors seals adjusted their relative consumption of prey species in line with changing prey abundance and environmental conditions, but with 1 and 2 year lags. 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 have been 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 vary 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. [I would end here and move the next paragraph up in the Discussion, possibly even the first paragraph.]

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 (UW), pursuant to National Oceanic and Atmospheric Administration Award No. NA18OAR4170095 and NA19OAR4170360. This publication is Contribution No. 2020-1116 with additional funding by the Northwest Fisheries Science Center via the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement NA15OAR4320063. The H. Mason Keeler Endowed Professorship in the UW School of Aquatic and Fishery Sciences provided additional support to Holtgrieve. 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, while 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. [↑](#footnote-ref-1)