**Title (89/120 characters w/spaces):** Climate regimes determine harbor seal trophic ecology in Washington over the past century

**Running Title (40 letters):**

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**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 (Figure?? 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. 2020), 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 (citation), 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, productivity, 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. 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. 2020, 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 with utilize C4 photosynthesis pathways such as sea grasses and some macrophytes (i.e., *Ulva spp.* Xu et al. 2012) 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. 2020,). 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:

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 (citation). Additionally, prey switching is common as juveniles grow to adults (citation). 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 analysis 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.

*Quantifying bottom-up drivers of foraging*

We were interested in three categories of bottom-up drivers of harbor seal trophic ecology: ocean condition, productivity, 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 each of the three categories of interest, ocean condition, productivity 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 prey on herring citation?), an interaction effect between hake and herring was also included in all models that contained both hake and herring time series. Similarly, due to th e correlation between the multivariate ENSO index (MEI) and Pacific Decadal Oscillation (PDO) only one of these covariates were included in each model. Inclusion of times series 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 prey switching either between species or life stages 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 (*Supplement*) 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 standard linear model took the following structure:

where *y* represents harbor seal trophic position calculated from glutamic acid and phenylalanine, ***X*** is a matrix of bottom-up drivers for a given model, **β** is a vector of predicted effects of bottom-up drivers included in the model (described in *Supplementary Tables 1-3*) 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 hierarchical linear model took the following structure:

where *j* represents four different trophic amino acids used to calculate trophic position included as a random effect and all other parameters are represented the same as equation 3. 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).

To better understand how prey availability and ocean condition impact harbor seal foraging ecology in tandem, a combined ocean condition - prey availability model was also fit to the data. All times series that were included in the most supported models for prey availability and ocean condition were included in the candidate model set (n = 23) and tested in all possible combinations. The goal of this model was to identify annually monitored predictors that influence harbor seal trophic position and that could be useful for time variant estimates of predation pressure. Thus the isotopic data included in the productivity models was excluded as it is not currently a component of ecological monitoring and management programs such as integrated ecosystem assessments.

*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.

*Assessment of multi-amino acid framework*

Sensitivity 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 glutamic acid 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, however 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 and sea surface temperature both impact harbor seal trophic position but on different temporal scales. The best environmental models (Figure 5) included location (Salish Sera verse Coastal Washington) as and summer upwelling with a 1-year lag (Figure 5A) and summer sea surface temperature with a 2-year lag (Figure 5B). 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. In contrast, summer sea surface temperature exhibited a delayed impact, where harbor seals foraged lower in the food web the following year after summers with higher than average sea surface temperatures. The coefficient for summer upwelling was low (-0.016) indicating a small, albeit significant, impact of upwelling on harbor seal trophic position compared to sea surface temperature (-0.20). Location had the highest effect on trophic position with a coefficient of ~ -0.3 for both models. Increasing the lag to 3 years for environmental models led to increased model uncertainty, thus only 1-year and 2-year lagged models are reported here.

**-** No change through time indicates harbor seal foraging strategies able to compensate for dramatic changes in resources without altering foraging niche

-Dynamics that operate on more trophic level/community wide scales that may alter multiple species at the same time are a better predictor of harbor seal foraging abundance than individual prey species

-forward selection is bias towards type II error, but for the sake of this exercise we believe it is justified.

-Food web results represent a prey species that is both abundant in harbor seal diet and has experienced large scale changes in the system

-Sex does not appear to influence trophic position. While coastal harbor seals may exhibit different foraging strategies based on sex. This is contradictory to previous studies. Weight may be a better predictor than length but given the nature of this data was not possible to analyze. Or previous studies may have identified a more local phenomenon.

-Location is important, and variability may be the most important component of

**Results**

Models showed support for covariates over the null model or location only model. Similar results for GLU and multi AA approaches, but multi AA approach had more model certainty. When possible, the hierarchical model likely will provide improved model fitting particularly with covariates. Multi AA approach will be limited based on availability of trophic enrichment factors for AAs other than Glu. Its ability to improve model fit will depend on availability of TEFs and quality of chromatography.

**Discussion**

). Most trophic position estimates (76%, *SI Figure S2*) ranged from 3.5-5, which are ecologically realistic based on previous diet studies (Jeffries).

-decrease in length—could be slower turnover times?

Previous research has presented compelling evidence that harbor seals negatively impact Chinook salmon populations. Next steps in management involve decisions regarding culling, similar to stellar sea lions in the Columbia River. However most culling of mammals requires drastic, maintained reductions in predator numbers, and few culling programs have demonstrated changes in predator numbers (Bowen and Lidgard 2012). In order to ensure realized expectations for stakeholders, it is important to consider the broader ecological context of predators. Harbor seals demonstrate drastic variations in foraging ecology in response to location, prey availability, and environmental change. This variation should be embraced to produced effective management strategies. Estimates of total biomass consumed that treats harbor seal predation pressure as static through time are likely inaccurate as we observed differences as high as XXX.

Seasonality and spatial variance as well. Spatially distinct managment strategies may be good

-Other important prey species that were not considered? Ie walleye pollock and sand lance (Austen papere on herring)

-paragraph on age specific predation

- when prey are abundant, harbor seals forage lower in the food web potentially targeting trophic levels that have less of an energetic cost. When prey are less abundant there appears to be less trophic discrimination.

1) Trophic response to prey availability and environmental conditions

2) Applications of MULTI AA frameworks

3) recs for reconstructing SI time series

4) conclusions

**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*.

**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 pf 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 food web hierarchical models using 1-, and 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**: Explanatory plot

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