**Title (120/120 characters w/spaces):** Harbor seal trophic position exhibits delayed responses to ocean condition and prey availability during the past century

**Running Title (32 letters):** Delayed harbor seal trophic response

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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 (197 of 200 words)**

Marine predators often exhibit delayed responses to changes in their environment. Understanding how predators respond to prey abundance and environmental change is important for effective management decisions. Here, we utilize a century of stable isotope data derived from museum skull specimens of harbor seals to determine how this marine predator has responded to ecological change over the past century. We applied compound specific stable isotope analysis of individual amino acids to derive trophic position estimates of 150 harbor seal specimens. The relationships between harbor seal trophic position, ocean condition and prey abundance, was analyzed using hierarchical modelling applying a multi-amino acid framework and applying 1-, 2-, and 3- year lags. We determined harbors seals exhibit a delayed response to both ocean conditions (upwelling, sea surface, el nino) and prey availability (Pacific hake, Pacific herring and Chinook salmon). However, the magnitude and direction of the trophic response to ecological changes depended on the temporal delay and harbor seal trophic position responded to some changes on multiple temporal scales. These results highlight the importance of considering dynamic responses of predators to their environment as multiple ecological factors are often changing simultaneously and predators respond on multiple temporal scales.

**Keywords (6-12)**

**Introduction**

Food web structure is primarily regulated by availability of resources (bottom-up control) and the presence of top predators (top-down control) (Hunter and Price 1992). Physical ocean conditions alter nutrient distribution, light penetration, and community composition at the base of the food web, which can impact primary production 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). Thus, predator abundance 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 and Price 1992, Estes et al. 1998).

Measuring trophic position can be a useful proxy for major changes in foraging strategies and ecological interactions. 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 (Chassot et al. 2010), 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 ecosystems. 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 and juvenile life stages of a species, or a consuming a greater proportion of a low trophic level species, would be represented in predator trophic position. Long times series of predator trophic position can be combined with indices of prey abundances and environmental conditions to characterize how top-down pressure (predator trophic ecology) changes in response to bottom-up forces (environmental condition and prey availability).

Understanding ecosystem response to top-down and bottom-up forces requires datasets that span multiple environmental, ecological, and anthropogenic contexts. Historic datasets can serve this purpose and are particularly useful for understanding ecosystem dynamics in the absence of anthropogenic pressure and ecological responses to climatic shifts. Reconstructing time series of trophic position requires archival specimens and controlling for changes in the isotopic signature of primary producers caused by nitrogen cycling (McMahon and McCarthy 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 (McMahon and McCarthy 2016). When combined, this approach allows for reconstruction of historical trophic dynamics when 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). 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). Simultaneously, the region has also experienced changes in dissolved oxygen and nitrogen inputs (Mohamedali et al. 2011), climate regimes (Mantua and Hare 2002, Corwith and Wheeler 2002) and abundances of other important prey species such as Pacific herring (*Clupea pallasii*, Siple and Francis 2016). 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.

Here we examined 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 anticipated environmental factors and spatial location will alter harbor seal trophic position reflecting changes predation pressure on Chinook salmon and other important prey species. We assumed 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 precision and ecological accuracy compared to the traditional single amino acid approach.

**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 XXX*). 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, and 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**

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.

*Delayed trophic position response to environmental conditions*

Multiple studies have shown that ocean conditions such as sea surface temperature, upwelling, and discharge impact abundance and recruitment of coastal Washington fishes (Reum et al. 2011, Greene et al. 2015). For some species of seabirds in the region, breeding success also responds to ocean conditions but exhibits a temporally lagged response (Duguid et al. 2019). This work shows trophic position of top predators (harbor seals) can also have delayed responses to bottom up forcing of ocean conditions with 1- and 2-year lags. More specifically, harbor seals consume a greater proportion of low trophic level species in years of above average summer upwelling, summer sea surface temperature, and multivariate ENSO index (Figure 5) but respond to these environmental conditions on different temporal scales. Reum et al. (2011) found age-0 Pacific herring abundance in Puget Sound is also positively correlated with annual upwelling in the Strait of Georgia. Consumption of a greater proportion of these low trophic level, juvenile, fishes, by harbor seals could explain the negative correlation between 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.

*Delayed trophic position response to prey abundance*

Harbor seal trophic position responds to the abundance of multiple prey species and the magnitude and direction of the response depends on both the individual species and temporal delay. Pacific hake and Pacific herring have been frequently documented as common prey sources in Washington harbor seal diet (Thomas et al. 2011, Lance et al. 2012). For some species of hake, trophic level can differ by as much at 0.6 trophic levels between individuals of different size classes (Itembu et al 2012). In years when Pacific hake spawning biomass is high, harbor seal trophic position increases, indicating harbor seals are opportunistically feeding on large, sexually mature adults. Harbor seal trophic position also exhibits a delayed response to hake spawning biomass, feeding lower in the food web in the two years following high spawning biomass of Pacific hake, indicating a greater consumption of juvenile, low trophic level, fish. Similar to Pacific hake, harbor seal trophic position exhibits a delayed response to herring spawning biomass. The relative abundance of adult to juvenile herring in harbor seal diet varies between years (Lance et al. 2012). 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. 2011). Our results are in agreement with the findings, indicating a trophic shift in response to spawning biomass, which is likely a result of a density dependent response of adult:juvenile herring in harbor seal diet. Consumption of a greater proportion of adult herring following years of strong recruitment could explain this trophic dynamic. Alternatively, this result may be due to covariation between a third variable. For example, upwelling and hake spawning biomass were also correlated to harbor seal trophic position with a 2-year delay and are known to impact herring abundance (Reum et al. 2011, Schweigert et al. 2010).

A combined index of hatchery Chinook smolt production and wild Chinook production offer the best index of salmon availability to harbor seals. The relationship between harbor seal trophic position and smolt production indicates harbor seals do take advantage of increased salmon abundance however, year-0 abundance was not correlated with trophic position. This suggests that harbor seal trophic position is not dependent on the abundance out migrating smolts, which would 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. This finding is contrary to previous work documenting juvenile salmon in harbor seal diets (Thomas et al. 2017, Lance et al. 2012). It is likely harbor seals do consume out migrating smolts but this consumption is not reflected in trophic position. If the biomass of out migrating smolts consumed by harbors seals is low relative to the total biomass of harbor seal diet, or the smolt biomass consumed by harbor seals is relatively constant despite the abundance of out migrating smolts, a change in trophic position would not be expected. 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 shows ocean-1 and ocean-2 Chinook salmon are important to harbor seal trophic position and predation on these age classes may be an important component for at sea survival of Washington Chinook.

*Application of multi-amino acid and weighted beta trophic position calculations*

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 (Feddern et al. 2021, 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.

**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.

**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 5**

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**Figure 6**

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**Figure 7**