**Title (105/120 characters w/spaces):** Delayed trophic response of harbor seals to ocean condition and prey availability during the past century

**Running Title (35 letters):** Delayed trophic response of harbor seals

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**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 of a multi-amino acid framework and applying 1-, 2-, and 3- year temporal lags. We determined harbors seals exhibit a delayed response to both ocean conditions (upwelling, sea surface, ENSO) 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 lag and harbor seal trophic position responded to ecological change 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)**

*Stable isotope, trophic position, harbor seal, amino acid, Washington, Salish Sea, Chinook salmon*

**Introduction**

Food web structure is primarily regulated by availability of resources (bottom-up control) and the presence of top predators (top-down control). 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). 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).

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 prey, or a consuming a greater proportion of a low trophic level prey, 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 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 by applying species specific trophic discrimination factor and a system specific beta value compared to universal values applied in with a 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) (Appendix S2: Table S1). 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 Appendix S1: Section 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 TDF is more ecologically realistic (McMahon et al. 2015). Therefore, trophic position was calculated using a harbor seal specific TDF, 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 (Appendix S1: Table S2). *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 (Appendix S1: Table S2). 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 (Appendix S1: 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 (Appendix S1: Table S2). 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 (Appendix S1: Table S2). *%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 (Appendix S1: Table S2).

*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 (Appendix S1: Tables S3 & S4). 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 (Appendix S1: Tables S2&S3) 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. Time (year, Appendix S1: Section S4 $ Fig. S6), sex and size (Appendix S1: Section S3, Fig. S4 & S5), and seasonality (month, Appendix S1: Fig. S1), were also considered as covariates but no significant trends were identified and thus these parameters were not included in the hierarchical modeling.

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 physiological delay from 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 2-year and 3-year lags to trophic position data, these models represent a 1-year and 2-year ecological delay while also accounting for the 1-year physiological delay 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. To validate collinearity was not problematic in the models with the most support, matrix scatterplots and variance inflation factors (vif) were used from the car package (Fox and Weisberg 2019) in R (R Development Core 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 (Fig. 2 a-c) for physiological delay model included location (Salish Sera verse Coastal Washington) as a factor and summer upwelling (Fig. 2c), the 1-year ecological delay model included summer sea surface temperature (Fig. 2b), and the 2-year ecological delay model included upwelling and ENSO (Fig. 2a). 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; Fig. 2c). However, there was also a positive relationship between trophic position and upwelling 2 years prior to collection (Fig. 2a) 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 (Fig. 2b). The coefficients for summer upwelling (-0.016, Figure 2c) in the physiological delay model and summer upwelling (0.04, Fig. 2a) in the 2-year ecological delay model were low indicating a small, albeit significant, impact of upwelling on harbor seal trophic position compared sea surface temperature (-0.20, Fig. 2b) and ENSO (-0.11, Fig. 2a). Location had the highest effect on trophic position with a coefficient of ~ -0.3 for all three models (Fig. 2 a-c).

Location, abundance of Chinook salmon smolts, and hake and herring spawning biomass, were strongly associated with harbor seal trophic position. Hake biomass and harbor seal trophic position were positively correlated in the physiological delay model (Fig. 2f). In contrast, the hake biomass in the 2-year ecological delay model was negatively correlated with harbor seal trophic position (Fig. 2d). Thus, harbor seals are feeding lower in the food web two years after hake spawning biomass is high. In the 2-year ecological delay model, harbor seal trophic position was also positively correlated to Pacific herring spawning biomass (Fig. 2d). Chinook salmon smolt production (which included hatchery releases and wild production of Chinook salmon;Appendix S1: Table S3) was included in both the 1-year (Fig. 2e) and 2-year (Fig. 2d) ecological delay 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 1-year delay model (0.14, Fig. 2e) compared to the 2-year delay model (0.08, Fig. 2d).

**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 of 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 reevaluated in the context of changing ecological conditions will likely be important strategies for managing harbor seal prey given 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 (Fig. 2 a-c) 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 the physiological delay model (Fig. 2c). Similarly, this could explain the positive correlation between trophic position and upwelling in 2-year ecological delay model (Fig. 2a), 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 between individuals of different size classes (Iitembu 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 produced by the spawners (Fig. 2g). 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) and harbor seals are known to preferentially consume juveniles during herring spawning season and adult herring during the non-spawning season (Thomas et al. 2011). Our results are in agreement with the findings and indicate a delayed trophic shift in response to herring spawning biomass (Fig. 2 d&g) 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 2 years after a year 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).

A combined index of hatchery Chinook smolt production and wild Chinook production offers the best index of salmon availability to harbor seals. The delayed positive relationship between harbor seal trophic position and smolt production indicates harbor seals do take advantage of increased smolt production as they age to 1-ocean and 2-ocean fish (Fig. 2g). This suggests that harbor seal trophic position is not dependent on the abundance out migrating smolts, which would result in a negative correlation for the physiological delay model. Instead, smolt abundance during the previous two years 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 static 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. It is possible that harbor seal trophic position could correlate with a metric of total smolt abundance of all species of Pacific salmon for the physiological delay model 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). However, data available for other species in the region did not provide enough temporal overlap with the trophic position data and thus were omitted. 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 contribute to harbor seal trophic ecology 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*

Application of a multi-TDF approach has led to consistent underestimates of trophic position compared to known feeding ecology (McMahon et al 2015, McMahon et al. 2019, Germain et al. 2015) despite its more realistic representation of metabolic pathways compared to a single- TDF approach (Appendix S1: Fig. S2 & S3). 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 when applying the calculation described above (Appendix S1: Fig. S2). Primary producers that utilize the C4 photosynthesis pathway such as sea grasses and some macrophytes (i.e., *Ulva spp.*) have substantially lower discrimination between trophic amino acids and phenyalanine than C3 producers (Choi et al. 2017) (Appendix S1: Table S2). Thus, if C4 derived organic matter is 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 and food web coupling in these coastal environments (Howe and Simenstad 2015) it is expected C4 primary producers contribute to Salish Sea and coastal Washington food webs in which harbor seals forage (Feddern et al. 2021).

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 (Appendix S1: Section S6, 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.

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**References**

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience10: 634-639.

Chasco, B. E., I. C. Kaplan, A. Thomas, A. Acevedo-Gutierrez, D. Noren, M. J. Ford, M. B. Hanson, J. Scordino, S. Jeffries, S. Pearson, K. Marshall, and E. J. Ward. 2017. Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. Canadian Journal of Aquatic and Fishery Sciences 74: 1173-1194.

Chassot, E., S. Bonhommeau, N. K. Dulvy, F. Mélin, R. Watson, D. Gascuel, and O. Le Pape. 2010. Global marine primary production constrains fishery catches. Ecology Letters13: 495-505.

Chikaraishi, Y., N. O. Ogawa, Y. Kashiyama, Y. Takano, H. Suga, A. Tomitani, H. Miyashita, H. Kitazato, and N. Ohkouchi. 2009. Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnology and Oceanography Methods 7: 740-750.

Choi, B., H. Sun-Yong, J. S. Lee, Y. Chikaraishi, N. Ohkouchi, and K. Shin. 2017. Trophic interaction among organisms in a seagrass meadow ecosystem as revealed by bulk δ13C and amino acid δ15N analyses. Limnology and Oceanography62: 1426-1435.

Corwith, H. L., and P. A. Wheeler. 2002. El Niño related variations in nutrient and chlorophyll distributions off Oregon. Progress in Oceanography54: 361-380.

de la Vega, C., C. Mahaffey, R. E. Tuerena, D. J. Yurkowski, S. H. Ferguson, G. B. Stenson, E. S. Nordøy, T. Haug, M. Biuw, S. Smout, J. Hopkins, A. Tagliabue, and R. M. Jeffreys. 2020. Arctic seals as tracers of environmental and ecological change. Limnology and Oceanography Letters 6: 24-32.

Duguid, W. D. P., J. L. Boldt, L. Chalifour, C. M. Greene, M. Galbraith, D. Hay, D. Lowry D., S. McKinnell, C. M. Neville, J. Qualley, T. Sandell, M. Thompson, M. Trudel, K. Young, amd F. Juanes. 2019. Historical fluctuations and recent observations of Northern Anchovy *Engraulis mordax* in the Salish Sea. Deep Sea Research II159: 22-41.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282: 473-476.

Feddern, M. L., G. W. Holtgrieve, and E. J. Ward. 2021. Stable isotope signatures in archival harbor seal bone link food web-assimilated carbon and nitrogen to a century of environmental change. Global Change Biology00: 1–15.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression, Third edition. Sage, Thousand Oaks, CA.

Germain, L. R., P. L. Koch, J. Harvey, and M. D. McCarthy. 2013. Nitrogen isotope fractionation in amino acids from harbor seals: implications for compound-specific trophic position calculations. Marine Ecology Progress Series 482: 265-277.

Greene, C., L. Kuehne, C. Rice, K. Fresh, and D. Penttila. 2015. Forty years of change in forage fish and jellyfish abundance across greater Puget Sound, Washington (USA): anthropogenic and climate associations. Marine Ecology Progress Series 525: 153-170.

Goñi, R. 1998. Ecosystem effects of marine fisheries: an overview. Ocean and Coastal Management 40: 37-64.

Howe, E. R., and C. A. Simenstad C.A. 2015. Using stable isotopes to discern mechanisms of connectivity in estuarine detritus-based food webs. Marine Ecology Progress Series 518:13-29.

Heithaus, M. R., A. Frid, A. J. Wirsing, B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution 23: 202-210.

Hunter, M. D., and Price P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724-732.

Iitembu, J. A., T. W. Miller, K. Ohmori, A. Kanime, and S. Wells. 2012. Comparison of ontogenic trophic shift in two hake species, *Merluccius capensis* and *Merluccius paradoxus*, from the Northern Benguela Current ecosystem (Namibia) using stable isotope analysis. Fisheries Oceanography21: 215-225.

Jeffries, S. J., H. R. Huber, J. Calambikidis, and J. Laake. 2003. Trends and status of harbor seals in Washington State: 1978-1999. Journal of Wildlife Management 67: 208-219.

Kordas, R. L., C. D. G. Harley, and M. I. Connor. 2011. Community ecology in a warming world: the influence of temperature on interspecific interactions in marine systems. Journal of Experimental Marine Biology and Ecology 400: 218-226.

Lance, M. M., W. Chang, S. J. Jeffries, S. F. Pearson, and A. Acevedo-Gutiérrez. 2012. Harbor seal diet in northern Puget Sound: implications for the recovery of depressed fish stocks. Marine Ecology Progress Series 464: 257-271.

Magera, A. M., J. E. Mills Flemming, K. Kaschner, L. B. Christensen, and H. K. Lotze. 2013. Recovery trends in marine mammal populations. PLoS One8: e77908.

Marshall, K. N., A. C. Stier, J. F. Samhouri, R. P. Kelly, and E. J. Ward. 2015. Conservation challenges of predator recovery. Conservation Letters9: 70-78.

Martínez del Rio, C., N. Wolf, S. A. Carleton, and L. Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews 84: 91-111.

Mantua, N. J., and S. R. Hare. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58: 35-44.

McClelland, J. W., and J. P. Montoya. 2002. Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. Ecology83: 2173-2180.

McMahon, K. W., M. D. McCarthy, O. A. Sherwood, T. Larsen, and T. P. Guilderson. 2015. Millennial-scale plankton regime shifts in the subtropical North Pacific Ocean. Science 350: 1530-1533.

McMahon, K. W., C. I. Michelson, T. Hart, M. D. McCarthy, W. P. Patterson, and M. J. Polito. 2019. Divergent trophic responses of sympatric penguin species to historic anthropogenic exploitation and recent climate change. PNAS 116: 25721-25727.

McMahon, K. W., and M. D. McCarthy. 2016. Embracing variability in amino acid δ15N fractionation: mechanisms, implication, and applications for trophic ecology. Ecosphere 7: e01511.

Moore, J. K., W. Fu, F. Primeau, G. L. Britten, K. Lindsay, M. Long, S. C. Doney, N. Mahowald, F. Hoffman, and J. T. Randerson. 2018. Sustained climate warming drives declining marine biological productivity. Science359: 1139-1143.

Mohamedali, T., M. Roberts, B. S. Sackmann, and A. Kolosseus. 2011. Puget Sound dissolved oxygen model: nutrient load summary for 1999–2008. Publication no. 11-03-057, Washington State Department of Ecology, Olympia, Washington.

Nelson, B. W., C. J. Walters, A. W. Trites, and M. K. McAllister. 2018. Wild Chinook salmon productivity is negatively related to seal density and not related to hatchery releases in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 76: 447-462.

Nielsen, J. M., B. N. Popp, and M. Winder. 2015. Meta-analysis of amino acid stable nitrogen isotope ratios for estimating trophic position in marine organisms. Oecologia178: 631-642.

Ohlberger, J., D. E. Schindler, E. J. Ward, T. E. Walsworth, and T. E. Essington. 2019. Resurgence of an apex predator and the decline in prey body size. PNAS 116: 26682-26689.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Reum, J. C., T. E. Essington, C. M. Greene, C. A. Rice, and K. L. Fresh. 2011. Multiscale influence of climate on estuarine populations of forage fish: the role of coastal upwelling, freshwater flow and temperature. Marine Ecology Progress Series 425: 203-215.

Rykaczewski, R. R., and J. P. Dunne J.P. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. Geophysical Research Letters37: L21606.

Schweigert, J. F., J. L. Boldt, L. Flostrand, and J. S. Cleary J.S. 2010. A review of factors limiting recovery of Pacific herring stocks in Canada. ICES Journal of Marine Science 67: 1903-1913.

Siple, M. C., and T. B. Francis. 2016. Population diversity in Pacific herring of the Puget Sound, USA. Oecologia 180: 111-125.

Sherwood, O. A., M. F. Lehmann, C. J. Schubert, D. B. Scott, and M. D. McCarthy. 2011. Nutrient regime shift in the western North Atlantic indicated by compound-specific δ15N of deep-sea gorgonian corals. PNAS 108: 1011-1015.

Smith, R. S., L. M. Weldon, J. L. Hayward, and S. M. Henson. 2017. Time lags associated with effects of oceanic conditions on seabird breeding in the Salish Sea region of the northern California Current system. Marine Ornithology 45: 39-42.

Steneck, R. S. 2012. Apex predators and trophic cascades in large marine ecosystems: learning from serendipity. PNAS109: 7953-7954.

Thomas, A. C., M. M. Lance, S. J. Jeffries, B. G. Miner, and A. Acevedo-Gutiérrez. 2011. Harbor seal foraging response to a seasonal resource pulse, spawning Pacific herring. Marine Ecology Progress Series441: 225-239.

Thomas, A. C., B. W. Nelson, M. M. Lance, B. E. Deagle, and A. W. Trites. 2017. Harbour seals target juvenile salmon of conservation concern. Canadian Journal of Fisheries and Aquatic Sciences 74: 907-921.

Ware, D. M., and R. E. Thomson. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science 308: 1280-1284.

Washington Department of Fish & Wildlife and Puget Sound Indian Tribes. 2017. Comprehensive Management Plan for Puget Sound Chinook: Harvest Management Component. Northwest Indian Fisheries Commission, Olympia, WA. 247 pages.

Wilson, K., M. Lance, S. Jeffries, and A. Acevedo-Gutiérrez. 2014. Fine-scale variability in harbor seal foraging behavior. PLoS One 9: e92838.

**Figures Captions**

**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**: The covariates of the best ocean condition (a-c) and prey availability (d-f) hierarchical models. Y axis denotes the coefficient for each covariate (colored points; magnitude of trophic level change in response to the covariate); black points are fixed effects and grey points are random effects (amino acid). Models represent multiple time scales of trophic position response to ecological conditions, a physiological delay only models (c & f; tissue turnover, 1-year lag); a 1-year ecological delay in addition to the physiological delay (b & e; 2-year lag) and a 2-year ecological delay in addition to the physiological delay (a & d; 3-year lag). Panel g) is a conceptual diagram representing the mechanisms of prey abundance on harbor seal trophic position on multiple time scales. Solid arrows represent direct effect on harbor seal trophic position dashed lines represent indirect effects contributing to the direct effect. Boxes represent coefficients supported in the best models from panels d-f and signs indicate the direction of the effect based on coefficient estimates.

**Figure 1**

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**Figure 2**

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