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

**Running Title (35 letters):** Delayed predator trophic response

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

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

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

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

*Page Count: 29 of 30 (article)*

**Abstract (187 of 200 words)**

Understanding the ecological response of predators to environmental change at multiple temporal scales can elucidate critical predator-prey dynamics, thereby facilitating effective ecosystem management decisions. We performed compound-specific nitrogen stable isotope analysis (CSIA) of amino acids on 150 harbor seal museum skull specimens to determine how this marine predator has responded to ecosystem change over the past century. 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 identified delayed responses of harbor seals to both physical ocean conditions (upwelling, sea surface, discharge) 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. For example, harbor seal trophic position was positively associated with current herring spawning biomass, but had a 2- year delayed response to Chinook smolt production. These results highlight the importance of considering dynamic responses of predators to their environment as multiple ecological factors are often changing simultaneously and predator response occurs at multiple temporal scales.

**Keywords (6-12)**

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

**Introduction**

The regulation of food web structure by resources (bottom-up control) and the presence of top predators (top-down control) (Carpenter et al. 1985, Hunter and Price 1992, Estes et al. 1998) is fundamental for understanding food web responses to environmental, ecological, and anthropogenic change. Communities are continuously experiencing both biotic and abiotic disturbances (Paine et al. 1998) and the ability for food webs to dynamically respond to these changes is crucial for ecosystem stability (Ghedini et al. 2015). In marine food webs, physical ocean conditions 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 alter abundance in both adjacent and non-adjacent trophic levels (Heithaus et al. 2008, Steneck 2012). 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 multiple mechanisms of regulation in tandem, making it challenging to identify dominant drivers structuring ecosystems.

How marine predators respond to multiple types of bottom-up drivers (i.e., ocean condition, prey availability), and the different temporal scales over which they respond, is crucial for understanding community stability and resistance to change. Marine predators can serve as ecosystem sentinels by exhibiting responses to ecological disturbances (bottom-up control), shaping marine food webs (top-down control), and indicating anthropogenic impacts to food webs (Hazen et al. 2019). Typically, superior sentinels are both sensitive and timely in their response to ecological change (Hazen et al. 2019). However, delayed predator responses to environmental perturbations are prevalent in marine system, as impacts do not immediately propagate through the food web (Duguid et al. 2019, Smith et al. 2017). In addition, there is evidence that climate warming and other anthropogenic impacts can shift communities from bottom-up to top-down controlled (Kratina et al. 2012) systems. Furthermore, the balance of top-down verse bottom-up effects on food webs in response to resource perturbations is determined by a top-predators ability to exploit subsidies (McCary et al. 2021).

Historical marine predator data that spans multiple environmental, ecological, and anthropogenic contexts are particularly useful for identifying predator responses to ecosystem drivers. Compound-specific stable isotope analysis (CSIA) of amino acid nitrogen serves as a useful tracer of predator response to ecological and environmental change and can derive retrospective trophic position estimates from museum specimens (McMahon et al. 2019, Feddern et al. 2020). Source amino acids (i.e., phenylalanine, lysine, methionine) exhibit minimal trophic discrimination (the difference in 15N/14N between trophic and source amino acids in consumers from a trophic transfer) and thus are a proxy for the isotopic signature of primary producers at the base of the food web. In contrast, trophic amino acids (i.e., alanine, glutamic acid, valine, proline) demonstrate trophic enrichment (McMahon and McCarthy 2016) that varies for individual amino acids. Combined, this approach allows for reconstruction of historic trophic position estimates when characterizing the isotopic baseline of past ecosystems may not be possible (McMahon et al. 2019). Thus, CSIA is well suited to identify drivers of food web dynamics when analyzed with historic indices of ocean condition and prey availability.

Reconstructing time series of predator trophic position requires careful consideration of physiological and ecological parameters that contribute to stable isotope signatures. First, taxa exhibit different trophic enrichment factors based on excretion pathways, diet type (omnivory, herbivory, carnivory), and growth (Nielsen et al. 2015). Second, the nitrogen production pathway of vascular (i.e., seagrasses) verse nonvascular (i.e., marine diatoms) primary producers impart distinct stable isotope fractionation factors (*β*) as inorganic sources of nitrogen are converted to tissues (Vander Zanden et al. 2013). Assumptions about the relative contributions of vascular versus nonvascular plants can impact trophic position estimates (Choi et al. 2017). Finally, there is a delay between the time a prey source is consumed and when that prey source has been fully assimilated into consumer tissues referred to as the ‘tissue turnover time’ that are both tissue-specific and amino acid-specific. Turnover times must be considered when comparing trophic position data to ocean condition and prey availability covariates, as the consumer response to an ecological change will not be immediately observable.

Nearshore coastal ecosystems provide a model system to assess long-term changes of food web drivers using archival museum specimens of a marine predator by applying CSIA. 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 dramatic increase in 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*). Chinook salmon are listed as endangered in the region (WDFW 2017) and are an important prey species for the endangered southern resident Orca (Marshall et al. 2015). Simultaneously, the region has also experienced changes in nutrients (Mohamedali et al. 2011), climate regimes (Corwith and Wheeler 2002, Mantua and Hare 2002,) and abundances of other important prey species such as Pacific herring (*Clupea pallasii*, Siple and Francis 2016).

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 the time scales at which physical ocean conditions and prey availability exert bottom-up control on marine predator trophic ecology. 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 (McMahon et al. 2019, Nielsen et al. 2015). We also include a system specific *β* value compared to universal values, and apply temporal lags to account for both physiological and ecological delays in consumer response.

**Methods**

*Sample collection and analysis*

Samples were obtained using methods described in Feddern et al. (2021). 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 but this information was not available for all sampled specimens. 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 nitrogen CSIA (δ15N) analysis 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, *δ15Ni* is the measured stable isotope composition of a trophic amino acid *i* in a sample and *δ15No* is the stable isotope composition of a source amino acid *o* in a sample. represents the total trophic enrichment that has occurred throughout the food web. *TDF(i-o)j* is the trophic discrimination factor between trophic amino acid *i* and source amino acid *o* of a specific consumer *j* (in this study either harbor seals) which occurs when consumer *j* assimilates prey. is the mean difference of enrichment between a specific trophic amino acid *i* and source amino acid *o* for primary producers that occurs when primary producers assimilate inorganic nitrogen (Nielsen et al. 2015; Table 1). represents trophic discrimination that occurs at other trophic levels in the food web, and is calculated from the mean difference between trophic amino acid *i* and source amino acid *o* across all consumers described in Nielsen et al. (2015).

The *β* parameter differs substantially between vascular and nonvascular primary producers (Appendix S1: Table S2). In food webs that assimilate organic matter from both vascular and nonvascular plants, including some nearshore food webs, *β* will be intermediate. Instead of applying a value that is averaged across primary producers (), we applied a two-source mixing model using carbon stable isotope data similar to Choi et al (2017). This generates a *β* that is weighted (*βW(i-o)* ) based on the contributions of vascular relative to nonvascular plants specific to the Washington nearshore ecosystem by first calculating the percent contribution of vascular plants to the food web:

where, *δ 13CConsumer* is the mean observed δ13C value for Washington harbor seals *δ 13CV* is the carbon stable isotope end member for vascular plants, *v* (derived from seagrasses) and *δ 13CN* is the carbon stable isotope end member for nonvascular plants, *n* (derived from marine diatoms) (Appendix S1: Table S2). *%V* is the percent contribution of vascular 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). *βW(i-o)* was then derived by:

where, *βN,(i-o)* is the enrichment between an individual trophic amino acid *i* and source amino acid *o* for aquatic phytoplankton and *βV,(i-o)* represents the trophic enrichment of seagrass which are vascular plants (Appendix S1: Table S2).

*Quantifying bottom-up drivers of foraging*

To identify the most important explanatory variables of ocean condition and prey availability on predator trophic ecology, two sets of candidate models were fit using a multi-amino acid (glutamic acid, aspartic acid, alanine, proline, valine) hierarchical model. 15 putative explanatory variables were selected based on the length of the time series and divided *a priori* into our two categories of interest, ocean condition and prey availability, representing our expected primary forcing mechanisms described above (Appendix S1: Tables S3 & S4). Candidate models were fit to the trophic position and covariate data, and the candidate model set included a null and location only model (Appendix 1:Tables S4 & S5). 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. All time series were standardized around a mean of 0 and standard deviation of 1. To avoid collinearity, no more than three covariates were included in an individual model.

Nielsen et al. (2015) determined using multiple amino acids to estimate trophic position improves precision. Therefore, we used multiple trophic amino acids *i* (alanine, glutamic acid, valine and proline) and one source amino acid *o* (phenylalanine) to calculate trophic position. These amino acids were chosen based on: their prevalence in previous studies to derive parameters for equation 2, tissue turnover time relative to the source amino acid, phenylalanine, and their concentrations in bone collagen. The hierarchical linear model took the following structure:

where *y* represents harbor seal trophic position from year *t* and *i* represents four different trophic amino acids (factor) 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. *l* is the temporal delay (or lag) between a change in bottom up drivers and when that change is reflected in harbor seal bone collagen*.* This delay can be due to both physiological (tissue turnover) or ecological effects (rate of propagation through the food web). Time (year, Appendix S1: Section S4, Fig. S6), sex, size (Appendix S1: Section S3, Fig. S4 & S5), and seasonality (month, Appendix S1: Fig. S1), were also considered as predictors of trophic position but no significant associations were identified and thus these parameters were not included in the hierarchical modeling (Appendix S1: Section S3). The best performing model for both of these approaches was selected using Akaike information criterion with a correction for small sample size (AICc). Inclusion of predictors 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 predictors can be interpreted as the degree of trophic change induced by consuming different species, life stages of species, or groups of species, caused by a given predictor.

A 1-year lag (*l)* 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 the individual ate in the previous 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 in addition to 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**

Inclusion of multiple trophic enrichment factors (Appendix 1: Section S2), multiple trophic amino acids, and a system specific *β* value in the trophic position equation improved trophic position estimates (Appendix 1: Figures S2 & S3) compared to a single trophic enrichment factor, *βN*, and using only the canonical trophic amino acid, glutamic acid (Appendix 1: Section S6). Harbor seals are known to consume both adult and juvenile hake, Pacific herring, and Pacific salmon, thus a trophic position of 3.5 – 5 would be considered ecologically realistic based on known foraging strategies. 76% of observations were considered ecologically realistic when applying a system specific *β*, harbor seal specific trophic discrimination factor and including glutamic acid, valine, alanine, aspartic acid (Appendix 1:Figures S2.2). This parameterization offered substantial improvement over other parameterizations of the trophic position equation and was more parsimonious than similarly performing equations (Appendix 1: Figures S2.4). However, aspartic acid was more variable than other trophic amino acids in all parameterizations and thus was omitted from the hierarchical modelling analysis (Appendix 1: Section S2).

*Drivers of predator trophic position*

Among the physical variables tested, summer upwelling, sea surface temperature and Columbia River discharge during high flow months all impacted harbor seal trophic position but on different temporal scales. A single best model (∆AICc < 2) was identified for ocean condition at all three temporal lags (Appendix 1: Table S7-S9). All three best ocean condition models supported the inclusion of a single covariate (Fig. 2a). The best physiological delay model (Fig. 2a, green circle) included location (Salish Sea versus coastal Washington) as a factor and a negative coefficient for summer upwelling. The 1-year ecological delay model (Fig. 2a, blue square) included a negative coefficient for summer sea surface temperature. Columbia River discharge during high flow months was included in the best 2-year ecological delay model (Fig 2a, pink diamond) and had the highest impact on harbor seal trophic position with a coefficient of 0.4. Summer upwelling exhibited an immediate impact on harbor seal trophic position that resulted in overall lower trophic position during the same year (after accounting for tissue turnover; Fig. 2c). 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 (-0.2, Fig. 2b). The coefficients for summer upwelling (-0.016, Figure 2a) in the physiological delay model was low indicating a small, albeit significant, impact of upwelling on harbor seal trophic position compared sea surface temperature (-0.20, Fig. 2b) and Columbia River discharge (0.4, Fig. 2a). Location also had high coefficient of ~ -0.3 which was similar across all three best models, demonstrating harbor seals in the Salish Sea feed lower in the food web than their coastal Washington counterparts.

Location, Chinook salmon abundance, and hake and herring spawning biomass, were the biological variables strongly associated with harbor seal trophic position. The physiological delay model and the 1-year ecological delay model had high model certainty with only one best model (Appendix 1:Tables S10 & S11). Chinook salmon escapement and herring spawning biomass were correlated to trophic position in the physiological delay model (Fig. 2b, green circles). In contrast, hake spawning biomass in the 1-year ecological delay model was positively correlated with harbor seal trophic position (Fig. 2b, blue square). Thus, harbor seals are feeding higher in the food web one year after hake spawning biomass is high. In the 2-year ecological delay model, harbor seal trophic position was also positively correlated to Chinook salmon smolt production (Fig. 2b, pink diamond). Chinook salmon smolt production (which included hatchery releases and wild production of Chinook salmon;Appendix S1: Table S3) was positively correlated with harbor seal trophic position indicating harbor seals feed higher in the food web two years after a year of above average smolt production. However, there was model uncertainty for the 2-year ecological delay model and six models had ∆AICc < 2 including the location only model. Regardless, Chinook salmon smolt production was included in the top 3 models and had a total AICc weight (sum of AICc weight for all candidate models that included Chinook salmon smolts) of 0.52 across the entire candidate model set.

**Discussion**

Harbor seals occupy different trophic positions depending on ecological conditions and exhibit delayed trophic responses to ecological perturbations. We found that both ocean conditions and prey availability impact predator trophic ecology, however, the magnitude and time scale in which predators exhibit at trophic response to these bottom-up drivers varied. In fact, some of the most influential drivers of predator trophic position (i.e., freshwater discharge) had a multi-year delay in predator trophic response. Therefore, some effects of ecosystem change on nearshore marine predators will not be immediately observable based on our results and others (Smith et al. 2017). Following years with extreme ocean conditions, ecological responses will continue to manifest for multiple years into the future as impacts propagate through the food web. Furthermore, changes in ocean conditions can alter top-down pressure on the community in subsequent years, as generalist top predators shift their trophic ecology in response to their environment.

*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 nearshore fishes (Reum et al. 2011, Greene et al. 2015) in coastal Washington. 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 up to a 2-year delay. More specifically, harbor seals consume a greater proportion of low trophic level species in years of above average summer upwelling and summer sea surface temperature (Fig. 2a) 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. 2a).

*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. Similar to Pacific hake, harbor seal trophic position exhibits a positive relationship with 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 agree with this finding and indicate a delayed trophic shift in response to herring spawning biomass (Fig. 2b) which is likely a result of a density dependent response of adult herring in harbor seal diet. Consumption of a greater proportion of adult herring in years when spawning biomass is high explains this result. Alternatively, this result may be due to covariation between a third variable. For example, upwelling was also correlated to harbor seal trophic position in the physiological delay model and is known to impact herring abundance (Reum et al. 2011).

A combined index of hatchery Chinook smolt production and wild Chinook smolt production offers the best predictor of salmon availability to harbor seals. The delayed positive relationship between harbor seal trophic position and smolt production indicates harbor seals may take advantage of increased smolt production as they age to 1-ocean (salmon that have spent 1 year in the ocean) and 2-ocean fish (salmon that have spent 2 years in the ocean) (Fig. 2 b & c). This suggests that harbor seal trophic position is not dependent on the abundance of out migrating smolts, which should result in a negative correlation for the physiological delay model. Instead, smolt abundance during the previous two years is determining the abundance of 2-ocean fish which are then predated on by harbor seals likely as they return to nearshore areas to spawn. There is strong evidence that harbor seals do consume out migrating smolts (Thomas et al. 2017, Lance et al. 2012) but this consumption is not reflected in our trophic position estimate. 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 net 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 a relevant 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 indicates 2-ocean 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.

Management of predators that consume threatened, economically important prey species such as harbor seals requires extensive tradeoffs (Marshall et al 2015). Harbor seals demonstrate large variations in trophic ecology in response to location, prey availability, and ocean condition which indicates they could exert dynamic top-down effects on the community in which they forage. 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, model estimates of total biomass of Chinook salmon consumed by harbor seals is assumed to be 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 predator 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 for managing harbor seal prey given their dynamic foraging strategies.

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

CSIA offers improved characterization of trophic ecology of top predators over long time scales compared to traditional bulk methods by providing 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).

CSIA is a powerful tool for reconstructing historical ecological data and consideration for system specific dynamics, and ecological and physiological variability will improve retrospective analyses. Despite its benefits CSIA is sensitive to the parameterization of trophic position equation (McMahon et al. 2019, Germain et al. 2013; SI Figures S2 and S3). 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). Thus, the utility and reliability of CSIA for trophic position studies requires careful considerations of the trophic discrimination factors and *β* values applied. 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). Phenylalanine in vascular primary producers such as sea grasses is depleted in 15N relative to trophic amino acids whereas non-vascular primary producers are enriched (Choi et al. 2017) (Appendix S1: Table S2). Thus, if nitrogen derived from vascular plants is utilized in marine food webs and trophic position calculations assume only non-vascular pathways, trophic position will be consistently underestimated. Given the abundance of seagrasses in coastal Washington and the Salish Sea and the evidence of food web coupling in these coastal environments (Howe and Simenstad 2015) it is expected vascular primary producers contribute to Salish Sea and coastal Washington food webs (Feddern et al. 2021). Our application of a multi-amino acid framework and weighted *β* parameterization significantly reduced model uncertainty (Appendix S1: Section S6, Nielsen et al. 2015). We therefore recommend using a multi-trophic discrimination factor approach with taxa specific trophic discrimination factors and system specific *β* when evidence of vascular plant contributions to the food web deem appropriate.

**Conclusions**

The regulation of food web structure by resources is foundational for understanding ecosystem response to perturbations. Based on our findings, nearshore marine predators exhibit a trophic response to ecological change on multiple temporal scales, as different perturbations propagate through the food web at different rates. More research is needed to investigate the degree to which top predator trophic position change can serve as an indicator of top-down control on the community, which undoubtedly depends on food web structure of a given system (i.e., degree of omnivory, connectance). Regardless, delayed predator dynamics are not limited to marine or nearshore environments, although the temporal scales for delayed trophic responses for other predators and systems warrants investigation.

Immediate predator response to ecosystem change is an important component for using marine predators as sentinels in for management (Hazen et al. 2019) but anticipating delayed responses of predators may be equally fruitful in predicting long-term change to climate extremes. Through top-down forces predators influence abundance at both adjacent and non-adjacent trophic levels (Estes et al. 1998). As such, changes to predator trophic ecology can have consequences throughout the food web that are not immediately realized especially following environmental perturbations. Impacts of the 2014-2016 marine heatwave in the Gulf of Alaska (the longest lasting event of the past decade) are still being observed and some ecological responses have persisted for up to 5 years (Suryan et al. 2021). The usefulness of marine predator data as an ecological indicator for management is not limited to immediate responses. Delayed responses may be equally important for anticipating long-term ecological consequences in response to future climate perturbations, especially as extreme climate events become more frequent and severe.

**Acknowledgements**

We extend our gratitude to our museum collaborators for permitting sampling and coordinating logistics. We thank 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 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 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.

**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.

Ghedini, G., B. D. Russell, and S. D. Conell. 2015. Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. Ecology Letters 18: 182-187.

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

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.

Hazen, E. L., B. Abrahms, S. Brodie, G. Carroll, M. G. Jacox, M. S. Savoca, K. L. Scales, W. J. Sydeman, and S. J. Bograd. 2019. Front Ecol Environ 17: 565-574.

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.

Kratina, P., H. S. Greig, P. L. Thompson, T. S. A. Carvalho-Pereira, and J. B. Shurin. 2012. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. Ecology 93: 1421-1430.

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.

McCary, M. A., J. S. Phillips, T. Ramiadantsoa, L. A. Nell, A. R. McCormick, and J. S. Botsch. 2021. Transient top-down and bottom-up effects of resources pulsed to multiple trophic levels. Ecology 102: e03197.

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.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1: 535-545.

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.

Vander Zanden, H. B., K. E. Arthur, A. B. Bolten, B. N. Popp, C. J. Lagueux, E. Harrison, C. L. Campbell, and K. A. Bjorndal. 2013. Trophic ecology of green turtle breeding population. Marine Ecology Progress Series 476: 237-249.

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 (n) for each year from 1928-2014 in the Salish Sea and coastal Washington respectively.

**Figure 2**: The covariates of the best ocean condition (a) and prey availability (b) hierarchical models. Y axis denotes the coefficient for each covariate (magnitude of trophic level change in response to the covariate). Models represent multiple time scales of trophic position response to ecological conditions, a physiological delay only models (green; tissue turnover, 1-year lag); a 1-year ecological delay in addition to the physiological delay (blue; 2-year lag) and a 2-year ecological delay in addition to the physiological delay (pink; 3-year lag). Panels c-e are 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 a & b and signs indicate the direction of the effect on trophic position based on coefficient estimates.

**Figure 1**

****

**Figure 2**

