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Delayed trophic response of a marine predator to ocean condition and prey availability during the past century

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Complete List of Authors:	Feddern, Megan; University of Alaska Fairbanks College of Fisheries and Ocean Sciences Holtgrieve, Gordon; University of Washington, School of Aquatic and Fishery Sciences Ward, Eric; Northwest Fisheries Science Center, Conservation Biology
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1 **Title:** Delayed trophic response of a marine predator to ocean condition and prey availability
2 during the past century

3 **Running Title:** Delayed predator trophic response

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

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

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

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

10

11 **Open Research Statement:** (3) Harbor seal stable isotope data are provided as private-for-peer
12 review on a repository [available here](#). Upon publication data will become public with a
13 permanent doi hosted through Dryad. (2) Some data are already published and publicly and the
14 sources are described in the supplementary material.

15

16 **Abstract**

17 Understanding the response of predators to ecological change at multiple temporal scales
18 can elucidate critical predator-prey dynamics that would otherwise go unrecognized. We
19 performed compound-specific nitrogen stable isotope analysis (CSIA) of amino acids on 153
20 harbor seal museum skull specimens to determine how trophic position of this marine predator
21 has responded to ecosystem change over the past century. The relationships between harbor seal
22 trophic position, ocean condition, and prey abundance, were analyzed using hierarchical
23 modelling of a multi-amino acid framework and applying 1-, 2-, and 3- year temporal lags. We
24 identified delayed responses of harbor seal trophic position to both physical ocean conditions
25 (upwelling, sea surface temperature, freshwater discharge) and prey availability (Pacific hake,
26 Pacific herring and Chinook salmon). However, the magnitude and direction of the trophic
27 position response to ecological changes depended on the temporal delay. For example, harbor
28 seal trophic position was negatively associated with summer upwelling, but had a 1- year
29 delayed response to summer sea surface temperature, indicating some predator responses to
30 ecosystem change are not immediately observable. These results highlight the importance of
31 considering dynamic responses of predators to their environment as multiple ecological factors
32 are often changing simultaneously and can take years to propagate up the food.

33 **Keywords**

34 *Stable isotope, trophic position, harbor seal, amino acid, Washington, Salish Sea, Chinook*
35 *salmon, Phoca vitulina, Pacific herring, Columbia River, sea surface temperature*

36 **Introduction**

37 The regulation of food web structure by resources (bottom-up control) is fundamental for
38 understanding food web responses to environmental, ecological, and anthropogenic change
39 (Carpenter et al. 1985, Hunter and Price 1992, Estes et al. 1998). Ecological communities are
40 continuously experiencing both biotic and abiotic disturbances (Paine et al. 1998) and the ability
41 of food webs to dynamically respond to these changes is crucial for ecosystem stability (Ghedini
42 et al. 2015). In marine food webs, physical ocean conditions can impact primary production and
43 ultimately constrain energy availability and thus biomass at higher trophic levels (Ware and
44 Thomson 2005, Chassot et al. 2010, Moore et al. 2018). Large-scale changes in nutrient
45 availability (Rykaczewski and Dunne 2010), primary productivity (Chassot et al. 2010), and top
46 predator abundance over the past century (Magera et al. 2013) means many food webs are
47 experiencing shifts in multiple mechanisms of regulation in tandem. However, impacts of
48 ecological change do not immediately propagate through the complete food web (Duguid et al.
49 2019, Smith et al. 2017) making it challenging to identify dominant drivers structuring food
50 webs over the long term.

51 Historical marine predator data that span multiple environmental, ecological, and
52 anthropogenic contexts are useful for identifying time scales over which predators respond to
53 ecosystem drivers. Compound-specific stable isotope analysis (CSIA) of amino acid nitrogen can
54 serve as a tracer of historical predator response to ecological and environmental change by
55 deriving retrospective trophic position estimates from museum specimens (McMahon et al. 2019,
56 Feddern et al. 2021). Source amino acids (i.e., phenylalanine, lysine, methionine) exhibit
57 minimal trophic discrimination (the difference in $^{15}\text{N}/^{14}\text{N}$ between trophic and source amino
58 acids in consumers from a trophic transfer) and thus are a proxy for the nitrogen stable isotope

59 signature of primary producers at the base of the food web. In contrast, trophic amino acids (i.e.,
60 alanine, glutamic acid, valine, proline) demonstrate trophic enrichment (McMahon and
61 McCarthy 2016) that varies for individual amino acids. Combined, this approach allows for
62 reconstruction of historic trophic position estimates under changing environmental conditions
63 when characterizing the isotopic baseline of past ecosystems may not be possible (McMahon et
64 al. 2019). Thus, CSIA is well suited to identify long-term drivers of food web dynamics when
65 analyzed with historic indices of ocean condition and prey availability.

66 Reconstructing time series of predator trophic position requires careful consideration of
67 physiological and ecological parameters that contribute to stable isotope values. First, taxa
68 exhibit different trophic enrichment factors based on excretion pathways, diet type (omnivory,
69 herbivory, carnivory), and growth (Nielsen et al. 2015). Second, the nitrogen production pathway
70 of vascular (i.e., seagrasses) versus nonvascular (i.e., marine diatoms) primary producers impart
71 distinct stable isotope fractionation factors (referred to as β) as inorganic sources of nitrogen are
72 converted to tissues (Ramirez et al. 2021). Assumptions about the relative contributions of
73 vascular versus nonvascular plants can therefore impact trophic position estimates (Choi et al.
74 2017). Finally, there is a delay between the time a prey source is consumed and when that prey
75 source has been assimilated by (and thus measurable in) consumer tissues (Martinez del Rio and
76 Carleton 2012). Rate of assimilation must be considered when comparing trophic position data to
77 ocean condition and prey availability covariates, as the consumer response to an ecological
78 change will not be immediately observable in consumer tissues.

79 Nearshore coastal ecosystems provide a model system to assess long-term changes of
80 food web drivers using archival museum specimens of a marine predator by applying CSIA.
81 Food webs of coastal Washington and the Salish Sea have experienced dramatic restructuring

82 over the past century due to declines and subsequent recoveries of marine predators (Jefferson et
83 al. 2021, Ohlberger et al. 2019). Decades of state-financed population control programs resulted
84 in harbor seals (*Phoca vitulina*) reaching a historic low in the 1970's, with an estimated
85 abundance of approximately 1,000 individuals (Jefferson et al. 2021). Following the cessation of
86 bounties in 1960 and the passage of the Marine Mammal Protection Act in 1972, harbor seal
87 populations increased 10-fold between 1970 and 2003 (Jefferson et al. 2021) due to legislation
88 restricting mortality. The increase in abundance of this top predator has been implicated in the
89 declines in economically and ecologically important prey species in the region (Chasco et al.
90 2017, Nelson et al. 2019), specifically, Chinook salmon (*Oncorhynchus tshawytscha*). Chinook
91 salmon are listed as endangered in the region and are an important prey species for the
92 endangered southern resident orca (Marshall et al. 2015). Simultaneously, the region has also
93 experienced changes in nutrients (Mohamedali et al. 2011), climate regimes (Corwith and
94 Wheeler 2002, Mantua and Hare 2002) and abundances of other important prey species such as
95 Pacific herring (Siple and Francis 2016).

96 Harbor seals are a useful predator to trace ecosystem drivers in Washington. Harbor seals
97 are generalist, opportunistic, predators known to forage on species with recent abundance
98 changes, specifically Pacific salmon (*Oncorhynchus spp.*) and Pacific herring (*Clupea pallasii*).
99 In addition, Pacific hake (*Merluccius productus*) make up a large portion of their diet along with
100 other forage fish and gadid species (Lance et al. 2012). Harbor seals have high site fidelity and
101 home ranges up to 100 km (Hardee 2008). Coastal Washington and Washington inland waters
102 (Salish Sea) are comprised of genetically distinct harbor seal stocks (Jefferson et al. 2021).

103 Here we examined a century of harbor seal trophic position data in coastal Washington
104 and the Salish Sea. The objective of this work is to identify the time scales at which physical

105 ocean conditions and prey availability exert bottom-up control on marine food webs as indicated
106 by predator trophic position. We assumed a correlation between trophic position and prey species
107 abundance is the result of increased or decreased consumption of that species. Similarly, we
108 assume a correlation between trophic position and ocean condition indicates an environmentally
109 induced change in food web structure the alters harbor seal prey availability. In conducting this
110 work, we established a multi-amino acid framework for measuring trophic position that improves
111 ecological accuracy by applying a species-specific trophic discrimination factor (McMahon et al.
112 2019). We also included a system specific β rather than a universal value, and applied temporal
113 lags to account for both physiological and ecological delays in consumer response.

114 Methods

115 *Sample collection and analysis*

116 Samples were obtained using methods described in Feddern et al. (2021). Briefly, harbor
117 seal bone was obtained from four museum institutions (the Burke Museum, the Slater Museum,
118 the Royal British Columbia Museum, and the Smithsonian Institute) and the National Marine
119 Mammal Laboratory (NOAA) (Appendix S2: Table S1). A total of 153 specimens were sampled
120 with field collection dates ranging 1928-2014 (Figure 1). Specimens were treated by maceration
121 in warm water and stored in acid free boxes. Only adult specimens were sampled and specimens
122 were divided into two main regions based on genetic stock delineations and expected foraging
123 ranges: coastal Washington and the Salish Sea (which included 18 specimens from British
124 Columbia). Specimens that provided long term temporal coverage and included sex, length, age,
125 and month of collection data were prioritized but this information was not available for all
126 sampled specimens. Museum specimens were primarily salvaged from beaches. While cause of

127 death was usually unknown, most adult strandings in the region are the result of trauma (i.e.,
128 fishing entanglements, boat strikes) or infectious disease (Ashley et al. 2020).

129 *Trophic position determination*

130 Bone collagen was decalcified, acid hydrolyzed, derivatized, and analyzed for nitrogen
131 CSIA ($\delta^{15}\text{N}$) of 12 individual amino acids. Collagen samples were measured in triplicate with a
132 laboratory standard containing a 12 amino acid mixture of known stable isotope value and a
133 linear drift correction was applied. Full analytical details are described in Appendix S1: Section
134 S1. Previous controlled feeding studies have determined the trophic enrichment factor (TEF) for
135 harbor seals is substantially lower than the conventional literature value of 7.6‰ (Germain et al.
136 2013) and thus applying a harbor seal-specific TEF is more accurate (McMahon and McCarthy
137 2016). Therefore, trophic position was calculated using a harbor seal-specific "multi-TEF"
138 approach, using the following equation:

$$139 \quad 1. \text{ Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - TEF_{(i-o), j} - \beta_{(i-o), N}}{\overline{TEF}_{(i-o)}} \right) + 2,$$

140 where $\delta^{15}\text{N}_i$ is the measured stable isotope value of a trophic amino acid i in a sample and $\delta^{15}\text{N}_o$
141 is the stable isotope value of a source amino acid o in a sample. $\delta^{15}\text{N}_{(i-o)}$ represents the total
142 trophic enrichment that has occurred throughout the food web measurable from predator tissues.
143 $TEF_{(i-o), j}$ is the trophic enrichment factor between trophic amino acid i and source amino acid o of
144 a specific consumer j (in this study, harbor seals) which occurs when consumer j assimilates
145 prey. $\beta_{(i-o), N}$ is the difference in enrichment between a specific trophic amino acid i and source
146 amino acid o for non-vascular primary producers N that occurs when primary producers
147 assimilate inorganic nitrogen (Nielsen et al. 2015; Appendix S1: Table S2). $\overline{TEF}_{(i-o)}$ represents
148 the mean trophic enrichment that occurs at other trophic levels in the food web, and is calculated

149 from the mean difference between trophic amino acid i and source amino acid o across all
150 consumers described in Nielsen et al. (2015).

151 β differs substantially between vascular and nonvascular primary producers (Ramirez et
152 al. 2021; Appendix S1: Table S2). In food webs that assimilate organic matter from both vascular
153 and nonvascular plants, including many nearshore food webs, β will be intermediate. In addition
154 to testing a value that represents nonvascular primary producers exclusively ($\beta_{(i-o), N}$), we also
155 applied a two-source mixing model using harbor seal carbon stable isotope data similar to Choi
156 et al. (2017). This generates a β that is weighted ($\beta_{(i-o), NV}$) based on the contributions of both
157 vascular and nonvascular plants specific to the Washington nearshore ecosystem by first
158 calculating the percent contribution of vascular plants to the food web:

159

$$2. \%V = \frac{\delta^{13}C_H - \delta^{13}C_N}{\delta^{13}C_V - \delta^{13}C_N} / 100,$$

160 where $\delta^{13}C_H$ is the mean observed $\delta^{13}C$ value for Washington harbor seals; $\delta^{13}C_V$ is the carbon
161 stable isotope end member for vascular plants, v (-9.5 ‰, derived from seagrasses *Zostera spp.*);
162 and $\delta^{13}C_N$ is the carbon stable isotope end member for nonvascular plants, n (-19.5 ‰, derived
163 from phytoplankton). Carbon end members were specific to the Washington nearshore
164 ecosystems (Howe and Simenstad 2015). $\%V$ is the percent contribution of vascular plants to the
165 food web in which harbor seals forage. This assumes the trophic enrichment of ^{13}C is generally
166 negligible (0–1‰, Deniro and Epstein 1978). $\beta_{(i-o), NV}$ was then derived by:

167

$$3. \beta_{(i-o), NV} = (\beta_{(i-o), V} * \%C4) + (\beta_{(i-o), N} * (1 - \%V)),$$

168 where $\beta_{(i-o), N}$ is the enrichment between an individual trophic amino acid i and source amino acid
169 o for aquatic phytoplankton and $\beta_{(i-o), V}$ represents the trophic enrichment of seagrass which are
170 vascular plants (Appendix S1: Table S2).

171 *Quantifying bottom-up drivers of trophic position*

172 To identify the most important explanatory variables of ocean condition and prey
173 availability on predator trophic position, we fit two sets of candidate models using a multi-amino
174 acid (glutamic acid, aspartic acid, alanine, proline, valine) hierarchical model. We selected 12
175 putative explanatory variables based on the length of the time series and divided them *a priori*
176 into our two categories of interest, ocean condition and prey availability, representing our
177 expected primary forcing mechanisms (Appendix S1: Tables S3 & S4). We fit the candidate
178 models to trophic position and covariate data, and the candidate model set included a null and
179 location-only model (Appendix S1: Tables S5 & S6). Location (Salish Sea or coastal
180 Washington) was included as a factor in all candidate models except the null model. Due to the
181 correlation between the multivariate El Niño Southern Oscillation index and the Pacific Decadal
182 Oscillation only one of these covariates were included in a single model. All timeseries were
183 standardized around a mean of 0 and standard deviation of 1. To avoid collinearity, no more than
184 four covariates (including location) were included in an individual model.

185 Nielsen et al. (2015) determined that the use of multiple amino acids improves estimates
186 of trophic position. Therefore, we used multiple trophic amino acids i (alanine, glutamic acid,
187 valine and proline) and one source amino acid o (phenylalanine) to calculate trophic position.
188 We selected amino acids based on: their prevalence in previous studies to derive parameters for
189 equation 2; tissue turnover time relative to the source amino acid, phenylalanine; and their
190 concentrations in bone collagen. The hierarchical linear model took the following structure:

$$191 \quad 4. \quad y_t = \alpha_k + \beta X_{t-d} + \epsilon,$$

192 where y represents harbor seal trophic position from year t and k represents four different trophic
193 amino acids (factors) used to calculate trophic position included as a random effect. X is a matrix
194 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 S3 & S4) on harbor seal trophic position, and α is the random effect representing predicted trophic position when all included bottom-up drivers are at an average value (represented by 0) in the coastal region of Washington for each trophic amino acid k . The variable d is the temporal lag between a change in bottom-up drivers and when that change is reflected in harbor seal bone collagen. This lag can be due to both physiological (isotope incorporation rate) 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 month of collection (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 models for both of these approaches were selected using Akaike's Information Criterion (Akaike 1973) with a correction for small sample size (AIC_c). Inclusion of predictors in the model with the most support is indicative of ecological parameters that alter harbor seal foraging ecology or food web dynamics. Additionally, magnitude and sign of the coefficients for included predictors can be interpreted as the degree of trophic position change induced by consuming different species, life stages of species, or groups of species, caused by a given predictor.

A change in dietary stable isotope composition is reflected in bone collagen after approximately 1 year (Hobson and Clark 1992, Newsome et al. 2006, Riofrío-Lazo and Auriolles-Gamboa 2013). This means the stable isotope composition of bone collagen is time averaged over approximately the last year of the harbor seal's life. Therefore, the last month of a harbor seal's life should have minimal influence on the stable isotope composition of bone collagen and as a result we assume cause of death does not impact trophic position (Appendix S1: Text S7). A

218 1-year lag (d) was applied to all harbor seal trophic position estimates to account for the
219 physiological delay from stable isotope incorporation rate of bone collagen, where the collagen
220 in a harbor seal collected in year t reflects what the individual ate in the previous year, $t-1$.
221 Delayed harbor seal foraging response to ecosystem dynamics was also tested by applying
222 additional 2-year and 3-year lags to trophic position data; these models represent a 1-year and 2-
223 year ecological delay in addition to the 1-year physiological delay. For example, the association
224 between harbor seal trophic position and environmental conditions 2 years before the collection
225 year would indicate that there was a 1-year delay between when the environmental condition
226 changed and when the resultant changes propagated through the food web, after accounting for
227 1-year for the isotopes to be incorporated into bone collagen. To confirm there was no
228 collinearity in predictors in the models with most support ($\Delta AIC_c < 2$), we consulted matrix
229 scatterplots and calculated variance inflation factors. All analyses were conducted in R (R
230 Development Core Team, 2020).

231 **Results**

232 *Drivers of predator trophic position*

233 Among the physical variables tested, summer upwelling, sea surface temperature and
234 Columbia River discharge during high flow months all impacted harbor seal trophic position but
235 on different temporal scales. There was model selection uncertainty at all three temporal lags
236 (Appendix S1: Table S7-S9) but covariates and their coefficient estimates were consistent across
237 the most supported models ($\Delta AIC_c < 2$) (Fig. 2). There were five physiological delay models
238 (Fig. 2c) with substantial support ($\Delta AIC_c < 2$) all of which included location (Salish Sea versus
239 coastal Washington) as a factor with a coefficient of -0.29 (95% CI [-0.40, -0.19]) and a negative
240 coefficient for summer upwelling (-0.04[-0.07, -0.02]). There were four models with substantial

support for the 1-year ecological delay (Fig. 2b) all of which included a negative coefficient for summer sea surface temperature (-0.2 [-0.28, -0.11]) and a positive coefficient for spring upwelling (0.03 [0.0, 0.05]). Columbia River discharge during high flow months was included in the five 2-year ecological delay models with the most support (Fig 2a) and had the highest impact on harbor seal trophic position with a coefficient of 0.4 [0.22, 0.57]. All other coefficients did not differ substantially from 0 (Figure 2). 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 [-0.28, -0.11], Fig. 2). The coefficients for upwelling (Fig. 2a-c) in all models were small compared to sea surface temperature (Fig. 2b) and Columbia River discharge (Fig. 2a). Location had an ecologically significant coefficient of ~ -0.3 [-0.40, -0.19]) which was similar across all supported models at all three lags, 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. Similar to the ocean condition analysis, there was model selection uncertainty but covariates and their coefficients were similar across supported models (Appendix S1: Tables S10-S12, Figure 3). Chinook smolt production (0.08 [0.02, 0.16]), and hake (0.13 [0.05, 0.21]) and herring spawning biomass (-0.06 [-0.14, 0.02]) were correlated with harbor seal trophic position in the two physiological delay models with substantial support ($\Delta AIC_c < 2$) but the effect of herring spawning biomass on harbor seal trophic position was not significantly different from 0 (Fig. 2f). Hake spawning

264 biomass and Chinook salmon escapement were included in three out of four 1-year ecological
265 delay models with substantial support (Fig. 2f) and both were included in the best model.
266 Chinook salmon smolt production (combined index of hatchery releases and wild production of
267 Chinook salmon) was included in all four models with substantial support at the same lag (Fig.
268 2f). Both Chinook salmon smolt production (0.12 [0.06, 0.20]) and hake spawning biomass (0.06
269 [-0.0, 0.14]) in the 1-year ecological delay model were positively correlated with harbor seal
270 trophic position (Fig. 2f). Thus, harbor seals fed higher in the food web one year after hake
271 spawning biomass and Chinook salmon smolt production was high (Fig. 3). In contrast, Chinook
272 escapement counts were negatively correlated at the same time lag (-0.07 [-0.14,0.0]). Covariates
273 and the magnitude and direction of their coefficients were similar in the 2-year ecological delay
274 model (Fig. 2d) compared to the 1-year ecological delay model (Fig. 2e) but only three models
275 had substantial support (Fig. 2d).

276 *Parameterization of the trophic position equation*

277 Inclusion of multiple trophic enrichment factors (Appendix S1: Section S2), multiple
278 trophic amino acids, and a system-specific β in the trophic position equation improved trophic
279 position estimates (Appendix S1: Figures S2 & S3) compared to the more commonly applied
280 single trophic enrichment factor, nonvascular β parameter, and using only the canonical trophic
281 amino acid, glutamic acid (Appendix S1: Section S6). Based on known foraging patterns a
282 trophic position of 3.5 – 5 would be considered ecologically realistic for harbor seals (Germain et
283 al. 2012). Seventy-six % of observations were considered ecologically realistic when applying a
284 system-specific $\beta_{(i-o),NV}$, harbor seal-specific trophic enrichment factor, and including the amino
285 acids glutamic acid, valine, alanine, aspartic acid, and proline (Appendix S1: Figures S3.2). This
286 parameterization offered a substantial improvement over other parameterizations of the trophic

287 position equation, which ranged from 15% to 80% of observations being ecologically realistic,
288 and was more parsimonious than similarly performing equations (Appendix S1: Figures S2.4).
289 However, aspartic acid was more variable than other trophic amino acids in all parameterizations
290 and thus was omitted from the hierarchical modelling analysis (Appendix S1: Section S6).

291 Discussion

292 Harbor seals vary in trophic position depending on ecological conditions and exhibit
293 delayed trophic responses to ecological perturbations. We found that both ocean conditions and
294 prey availability impact predator trophic position, however, the magnitude and time scale at
295 which predators exhibited trophic position responses to these bottom-up drivers varied. In fact,
296 some of the most influential drivers of predator trophic position (i.e., freshwater discharge) had a
297 multi-year delay in predator trophic position. Some effects of ecosystem change on nearshore
298 marine predators will not be immediately observable based on our results and others (Smith et al.
299 2017). Furthermore, changes in ocean conditions can alter top-down pressure on the ecological
300 community in subsequent years, as generalist top predators shift their trophic ecology in response
301 to their environment. Our data did not include observations of recent extreme marine heatwave
302 events but our results show delayed, linear, predator responses to environmental shifts.

303 Anticipating delayed ecological responses to environmental conditions is important given
304 environmental perturbations are becoming more common and severe in the northeast Pacific
305 Ocean (Suryan et al. 2021) and ecological impacts will not always be immediately observable.

306 *Delayed trophic position response to environmental conditions*

307 Multiple studies have shown that ocean conditions such as sea surface temperature,
308 upwelling, and freshwater discharge impact abundance and recruitment of nearshore fishes in
309 coastal Washington (Reum et al. 2011, Greene et al. 2015, Duguid et al. 2019). Our results show

310 trophic position of top predators (harbor seals) also respond to bottom-up forcing of ocean
311 conditions with up to a 2-year delay. Abiotic factors in the region alter resources, primary
312 productivity, and prey availability that propagates through the entire coastal Washington food
313 web (Ware and Thomson 2005, Feddern et al. 2021). Reum et al. (2011) found age-0 Pacific
314 herring abundance in Puget Sound is positively correlated with annual upwelling in the Strait of
315 Georgia. This increase in abundance of low trophic level, juvenile, fish could explain the
316 correlation between harbor seal trophic position and upwelling (Figure 2C). In addition,
317 reproductive success of Salish Sea predators (Smith et al. 2017) and fish species (Duguid et al.
318 2019) have been correlated to sea surface temperature and, like harbor seal trophic position
319 (Figure 2B), the responses to sea surface temperature are delayed by a year. Freshwater
320 discharge introduces terrestrial derived nutrients to nearshore environments and in the case of
321 large river plumes can influence upwelling. In Washington, freshwater derived nutrients have
322 been associated with increases in primary production and fish abundance at multiple trophic
323 levels (Ware and Thomson 2005; Kudela et al. 2008). Based on our results and others, abiotic
324 factors associated with freshwater discharge alters resources that eventually propagate through
325 the food web and can impact predator trophic position.

326 *Delayed trophic position response to prey abundance*

327 Harbor seal trophic position responds to the abundance of multiple prey species and the
328 magnitude and direction of the response depends on both the individual species and temporal
329 delay. Pacific hake and Pacific herring have frequently been documented as common prey
330 sources in Washington harbor seal diet (Thomas et al. 2011, Lance et al. 2012). For some species
331 of hake, trophic level can differ by as much as 0.6 among individuals of different size classes
332 (Itembu et al. 2012). In years when Pacific hake spawning biomass is high, and the years

333 following high spawning biomass, harbor seal trophic position increases, indicating harbor seals
334 are opportunistically feeding on large, adult-stage hake (Fig. 3d). This agrees with previous
335 harbor seal scat studies in the region, which have shown that Pacific hake are a major component
336 of harbor seal diet but the relative abundance varies between years. The relative abundance of
337 adult to juvenile herring in harbor seal diet also varies between years (Lance et al. 2012) and
338 harbor seals are known to preferentially consume juveniles during the herring spawning season
339 and adult herring during the non-spawning season (Thomas et al. 2011). Our results agree with
340 these findings and indicate a trophic position shift in response to herring spawning biomass (Fig.
341 2c), which is likely a result of increased juvenile consumption during the spawning season.
342 Alternatively, this result may be due to covariation with a third variable. For example, upwelling
343 was also correlated to harbor seal trophic position in the physiological delay model and is known
344 to impact herring abundance (Reum et al. 2011).

345 Harbor seals opportunistically consume more low-trophic level juvenile salmon when
346 they are abundant which occurs in the two years after high spawner abundance (Fig. 3).
347 Escapement counts represent the number of adult salmon that return to freshwater to spawn after
348 they have been both fished and predated on and serve as a strong predictor of out migrating
349 smolts during the next two years. After hatching, fry and parr reside in freshwater for 12-18
350 months before migrating to estuaries. The 1- and 2- year delayed negative response of harbor
351 seal trophic position to Chinook salmon escapements counts agrees with previous studies
352 documenting harbor seal consumption of out-migrating smolts (Fig. 3d, Thomas et al. 2017,
353 Lance et al. 2012). In contrast, a combined index of hatchery Chinook smolt production and wild
354 Chinook smolt production offers the best predictor of adult salmon availability to harbor seals
355 (Fig. 3). The positive relationship between harbor seal trophic position and smolt production

356 indicates harbor seals are consuming a greater proportion of higher trophic level fish in the years
357 following above average smolt production. Chinook salmon spend 1-7 years in the ocean before
358 returning to freshwater to spawn, and escapement counts only represent the age class of fish that
359 are returning to spawn in a given year. In contrast, smolt production in the current year and
360 during the previous two years provides an index of adult salmon abundance in the ocean that are
361 available to and predated upon by harbor seals (Fig. 3d). Notably, the salmon abundance
362 estimates in this study were specific to Washington Chinook salmon. It is possible that harbor
363 seal trophic position estimates have stronger associations with metrics of total abundance of all
364 species of Pacific salmon if harbor seals do not selectively forage on a specific species. However,
365 data available for other species in the region did not provide enough temporal overlap with the
366 trophic position data and thus were omitted. Regardless, this analysis indicates both adult and
367 juvenile Chinook salmon contribute to harbor seal trophic ecology and predation on both age
368 classes may be an important component for at sea survival of Washington Chinook salmon.

369 Management of predators that consume threatened, economically important, prey species
370 such as harbor seals requires extensive tradeoffs (Marshall et al 2015). Harbor seals demonstrate
371 large variations in trophic position in response to location, prey availability, and ocean condition
372 thus, they exert dynamic top-down effects on the community in which they forage. The balance
373 of top-down versus bottom-up effects on food webs in response to resource perturbations is
374 determined by a top predator's ability to exploit subsidies (McCary et al. 2021). Thus our results
375 also show the response of trophic position (and assumed predation) change is often delayed on
376 the order of 1-2 years in response to ecological conditions. Currently, model estimates of total
377 biomass of Chinook salmon consumed by harbor seals is assumed to be static through time
378 (Chasco et al. 2015). Based on our results and others (Wilson et al. 2014, Lance et al. 2012) this

379 is likely inaccurate as seasonality, spatial location, and individual behavior impact harbor seal
380 predation. This variability in foraging ecology should be carefully considered when assessing
381 tradeoffs of predator management decisions to ensure realized expectations for stakeholders.
382 Spatially distinct management strategies that are reevaluated in the context of changing
383 ecological conditions will likely be important for managing harbor seal prey given their dynamic
384 foraging strategies and trophic responses.

385 *Advances in the application of amino acid based trophic position calculations*

386 CSIA is a powerful tool for reconstructing historical ecological data that requires
387 consideration for system specific dynamics for accurate trophic position estimates. Despite its
388 benefits compared to traditional bulk stable isotope analysis, CSIA is sensitive to the
389 parameterization of the trophic position equation (McMahon et al. 2019, Germain et al. 2013;
390 Appendix S1: Figures S2 and S3). Application of a multi-TEF approach has led to consistent
391 underestimates of trophic position compared to known feeding ecology (McMahon et al 2019,
392 McMahon and McCarthy 2016, Germain et al. 2015) despite its more realistic representation of
393 metabolic pathways compared to a single-TEF approach (Appendix S1: Fig. S2 & S3). Thus, the
394 utility and reliability of CSIA for trophic position studies for retrospective analyses requires
395 careful consideration of the trophic enrichment factors, tissue turnover, and β applied. Harbor
396 seals are expected to exhibit a trophic position ranging from approximately 3.5 to 5 and only
397 12%-66% of data fell within this range when applying $\beta_{(i-o),N}$ (Appendix S1: Fig. S2). Seagrasses
398 are abundant in coastal Washington and the Salish Sea and there is evidence of food web
399 coupling in these coastal environments (Howe and Simenstad 2015). Therefore, vascular primary
400 producers are expected to contribute to these food webs requiring a system specific β value.
401 Variation in vascular plant abundance over time could result in temporal changes to the relative

402 contribution of these primary producers to the food web which would require the application of a
403 time-varying β . We did not find evidence of temporal trends in $\delta^{13}\text{C}$ data in harbor seals (Feddern
404 et al. 2021) which would be expected if seagrass contribution to the food web was time-varying
405 and therefore a temporally static β was appropriate for this study. By applying a system specific
406 β based on expected proportions of primary producer ecophysiology types entering the food web,
407 we significantly improved the realism of our trophic position estimates. We therefore
408 recommend using a multi-trophic enrichment factor approach with taxa specific trophic
409 enrichment factors and system-specific β when there is evidence of vascular plant contributions
410 to the food web.

411 **Conclusions**

412 More research is needed to investigate how top predator trophic position change can
413 serve as an indicator of top-down control on the community, which undoubtedly depends on
414 food web structure of a given system (i.e., degree of omnivory, connectance). Regardless,
415 delayed predator dynamics are not limited to marine or nearshore environments, although the
416 temporal scales for delayed trophic responses for other predators and systems warrants
417 investigation. Anticipating delayed responses may be equally important for identifying long-term
418 ecological consequences in response to future climate perturbations, especially as extreme
419 climate events become frequent and more severe.

420 The regulation of food web structure by resources is foundational for understanding
421 ecosystem response to perturbations. Based on our findings, nearshore marine predators exhibit a
422 trophic position response to ecological change on multiple temporal scales, as different
423 ecological perturbations propagate through the food web at different rates. As such, changes to
424 predator trophic ecology can have consequences throughout the food web that are not

425 immediately realized. Another example of delayed ecological responses to climate extremes is
426 the 2014-2016 marine heatwave in the Gulf of Alaska (the longest lasting event of the past
427 decade) the impacts of which are still being observed and some ecological responses have
428 persisted for up to 5 years (Suryan et al. 2021). Delayed responses of marine predators should be
429 considered when anticipating ecological responses following environmental and ecological
430 change as top-down pressure on the community in subsequent years is likely to change as
431 predators shift their trophic ecology in response to their environment.

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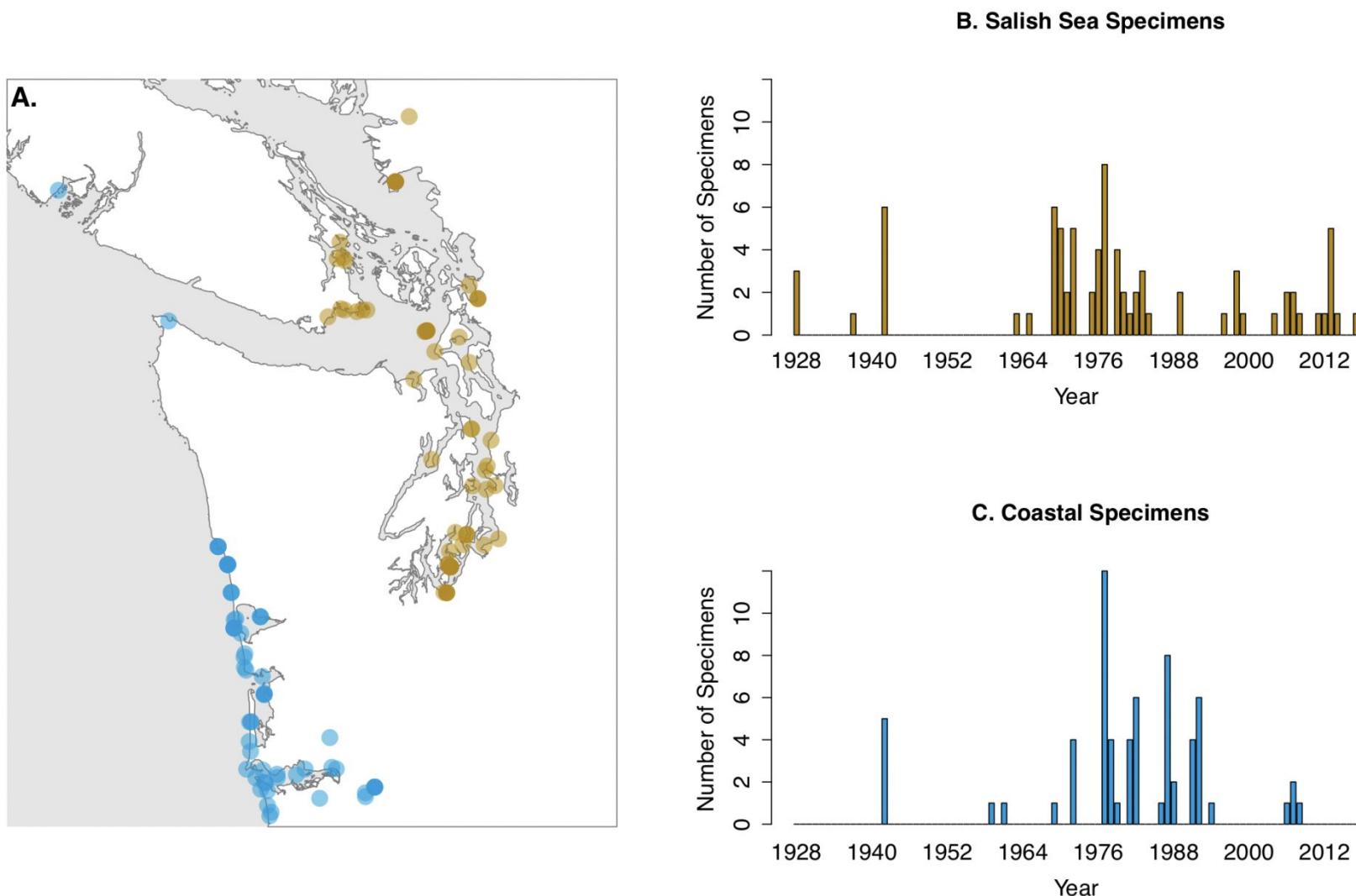
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578 **Figure Captions**

579 **Figure 1:** Spatial distribution of harbor seal specimens (a) collected in the Salish Sea (yellow)
580 and coastal Washington (blue) with the year of specimen collection and total number of
581 specimens (n) for each year from 1928-2014 in the Salish Sea (b) and coastal Washington (c).
582 Darker colors on the map (a) indicate multiple specimens from one location.

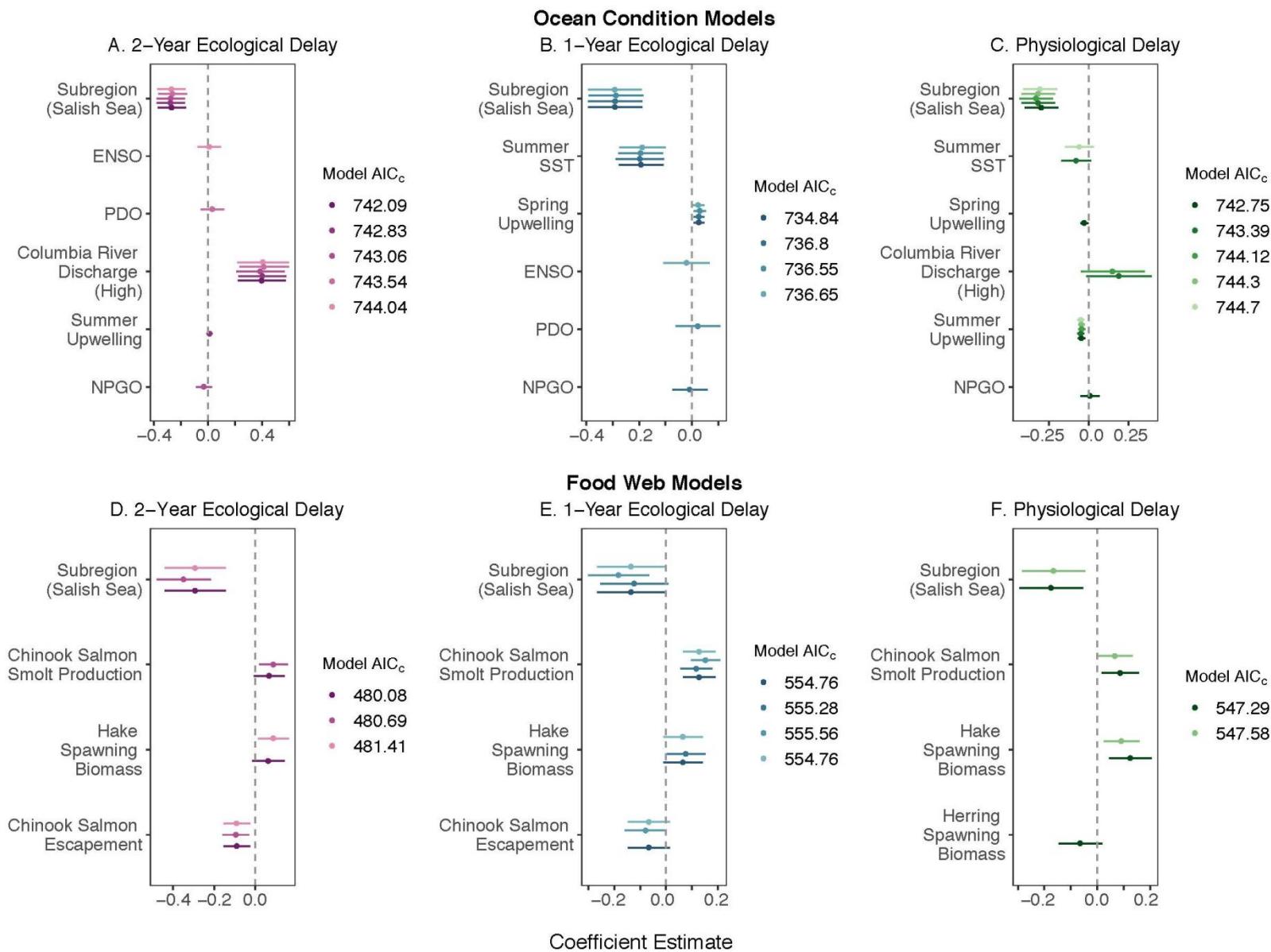
583 **Figure 2:** Coefficient estimates (dots) for the best ocean condition (a-c) and prey availability (d-
584 f) hierarchical models with 95% confidence intervals (whiskers). Y-axis labels describe each
585 covariate for supported models ($\Delta\text{AIC}_c < 2$) and x-axis is the coefficient estimate for each
586 covariate (magnitude of trophic level change in response to the covariate). Colors correspond to
587 the temporal lags applied to the 2-year ecological delay models (pink, a and f), 1-year ecological
588 delay models (blue, b and e) and physiological delay models (green, c and d).

589 **Figure 3:** Conceptual diagram interpreting the mechanism of trophic position response (d) to
590 estimated model coefficients (Fig. 2d-f) included in the best food web models ($\Delta\text{AIC}_c < 2$) for
591 the 2-year ecological delay models (a, pink arrows), 1-year ecological delay models (b, blue
592 arrows) and the physiological delay models (c, green arrows). Solid arrows indicate indirect
593 effects of covariates on harbor seal trophic position, signs indicate the direction of trophic
594 position response based on coefficient estimates, and dashed arrows conceptually represent the
595 mechanism directly impacting harbor seal trophic position.

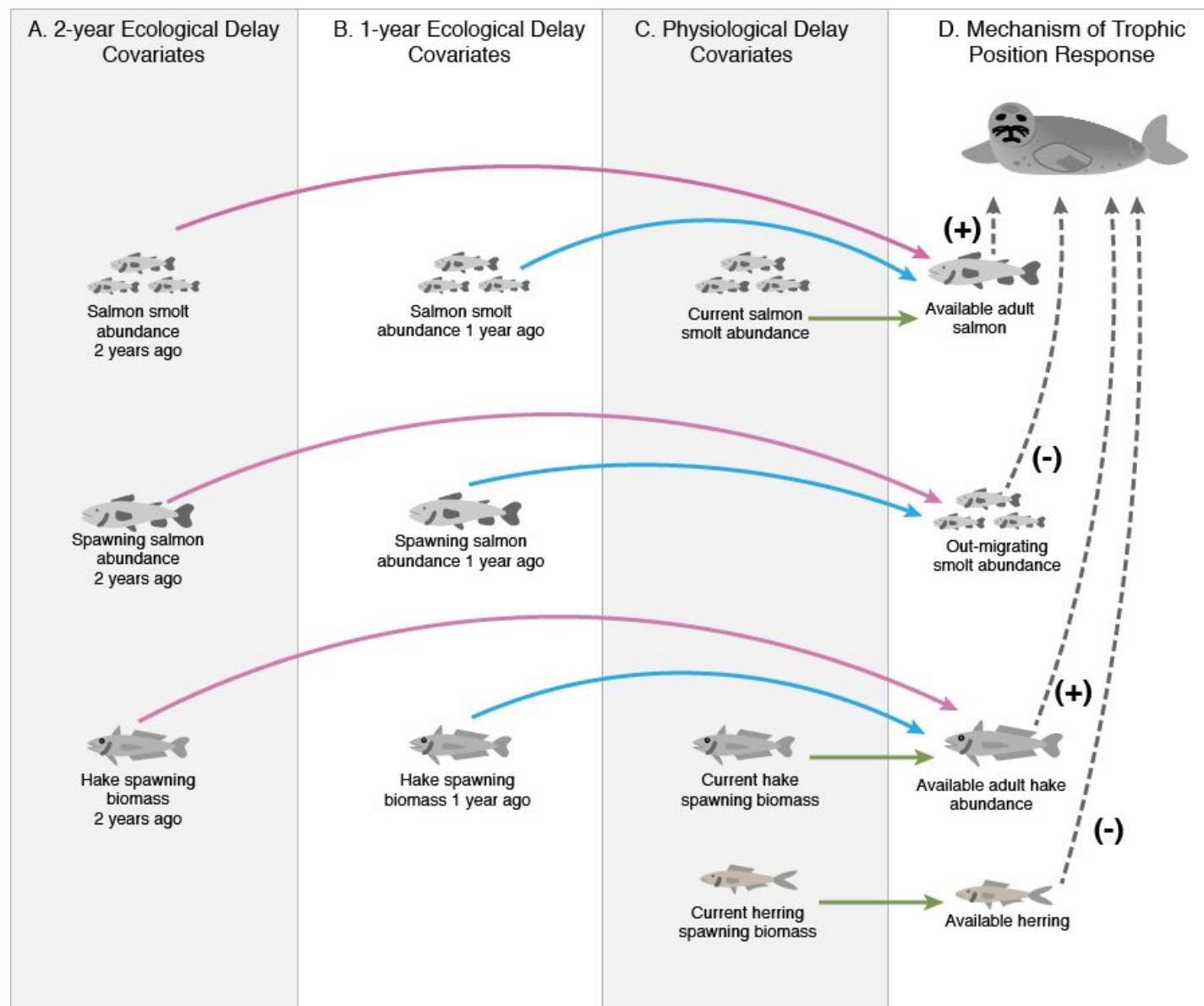
596 **Fig. 1**

597

598 Fig. 2



599 Fig. 3



Supporting Information. Feddern, M.L., G.W. Holtgireve, and E.J. Ward. 2021. Delayed trophic response of a marine predator to ocean condition and prey availability during the past century. *Ecology*.

Section S1. Methods for compound specific stable isotope analysis

Collagen samples have been analyzed for both CSIA and bulk $\delta^{15}\text{N}$ which require 10 mg of purified collagen (100 mg of bone). Preliminary analyses were conducted to determine the highest rate of collagen return from bone sampled from different parts of the skull to minimize destruction. Samples were primarily taken from the internal occipital shelf to maintain external integrity. Bone was decalcified using 0.2 M HCl for 24-72 hours depending on bone thickness, followed by centrifugation and nanopure water rinse. Removal of humic acids was conducted using 0.125 M NaOH for 20 hours. Samples were washed to a neutral pH, then solubilized in 0.01N HCl. Once solubilized samples were blown down under N_2 to prevent isotopic fractionation, and freeze dried. Freeze dried collagen was analyzed for bulk isotopic composition of nitrogen by the UW IsoLab (isolab.ess.washington.edu) using a coupled elemental analyzer-isotope ratio mass spectrometer following the standard protocols of the laboratory. C:N ratios were calculated from this data, which is a measure of the quality for carbon and nitrogen analyses of bone collagen for isotopic analysis. No observations were outside of the acceptable range of 2.7-3.6; indicating there was no substantial loss of glycine or addition of nitrogen due to microbial processing from mortality, decay, curation, and analysis.

$\delta^{15}\text{N}$ of eleven amino acids (alanine, glycine, proline, aspartic acid, leucine, isoleucine, valine, threonine, serine, glutamic acid, phenylalanine) were measured in the UW Facility for Compound-Specific Isotope Analysis of Environmental Samples. Samples were prepared following the procedures developed by Chikaraishi et al. (2007) and protocols by Rachel Jeffrey's lab at University of Liverpool UK which are modifications of that published by Metges et al. (1996) and Popp et al. (2007). Briefly, proteins were hydrolyzed in 6N HCl and purified

using a cation exchange column. 20 µL or norleucine was added as an internal standard. Amino acids were esterified using isopropanol acetyl chloride, and derivatized via acylation with 4:1 toluene: pivaloyl chloride. Samples were brought up in ethyl acetate and analyzed using a coupled gas chromatography-combustion-isotope ratio mass spectrometer system (GC-C-irMA; Thermo Scientific Trace GC + GC IsoLink coupled to a Delta V irMS) in continuous flow mode monitoring masses (m/z) 28 and 29. A 30 m x 0.32 mm x 0.50 µm Agilent Technologies DB-35 capillary column with 35% Phenyl and 65% polysiloxane stationary phase and moderate polarity (Chikaraishi et al. 2010) with an inlet temperature of 260 C, column flow of 2 ml/min and oven ramp of 9 °C min⁻¹. For each run a 12 amino acid external standard with known isotopic composition was injected four times to condition the column followed by sample injections. Samples were injected in triplicate, with the 12 amino acid standard mixture injected every two samples (or six injections). A two-hour column oxidation was performed after 6 samples (25 injections) followed by a 30-minute backflush. δ¹⁵N was measured as:

$$S1. \delta^{15}\text{N} (\text{\% vs. air}) = \left(\frac{(^{15}\text{N}/^{14}\text{N})_{\text{Sample}}}{(^{15}\text{N}/^{14}\text{N})_{\text{Air}}} - 1 \right) * 1000$$

For each machine run, a linear model was fit for each individual amino acid using the following equation:

$$S2. \text{Std}_{aa} = m_{aa}t + b_{aa}$$

Where *m* represents the slope of the precision drift, *t* represents the injection number since last column oxidation, and *Std* represents the δ¹⁵N of an individual amino acid, *aa*, for a standard observation. The data was then corrected using the following equations:

$$S3. D_{aa,t} = \text{Std}_{aa,t} - \text{True}$$

Where $D_{aa,t}$ is the difference between an observed standard $\delta^{15}\text{N}$ ($Std_{aa,t}$) for a given amino acid (aa) at a given injection number (t) and the true $\delta^{15}\text{N}$ for that standard. Then:

$$\text{S4. } \text{Sample}_{\text{corrected, aa, t}} = \text{Sample}_{\text{obs,aa,t}} - D_{aa,t}$$

Where the drift value, $D_{aa,t}$, is subtracted from the sample value for a given amino acid and a given injection to correct the observed sample values for precision drift since last column oxidation. Mean sample corrected values for the triplicate injections were used for all analyses and trophic position calculations. Norleucine had lower precision in standards compared to phenylalanine, therefore no correction using the internal standard was applied. Mean precision for a given aa standard was calculated using the standard deviation of the external standard injections for a given run after drift correction and taking a mean of each run's standard deviation (Table S13). Conditioning injections (first four standard injections) were omitted from this calculation.

Section S2. Accounting for variability in trophic enrichment factors

Trophic enrichment factors are variable based on animal diet (omnivory, carnivory, herbivory), pathways of nitrogen excretion, and trophic level (Nielsen et al. 2015, McMahon et al. 2015) with omnivory, carnivory and higher trophic levels demonstrating the lowest trophic enrichment for most amino acids. Trophic enrichment has ultimately been attributed to diet quality (similarity in tissues between consumer and prey) and mode of nitrogen excretions, although the relative impacts of each is difficult to discern, especially considering most controlled feeding studies include low-trophic level ammonia excretion but not high trophic level species (i.e., adult hake or salmon). In coastal Washington, most trophic transfers are between high diet quality, piscivorous fish (ammonia excretion) with a high-quality transfer between fish and harbor seal (urea excretion). Studies using multiple trophic enrichment factors based on the food web structure and consumption type produce more accurate trophic position estimations especially for higher level consumers (McMahon et al 2015, McMahon et al. 2016, McMahon et al. 2019).

We applied multiple trophic position calculation frameworks for harbor seals to determine the best approach (Tables S1 & S2) by identifying the percentage of data that fell within an ecologically realistic trophic position range for harbor seals. We also applied these approaches to herring, a known harbor seal prey species, with data from Germain et al. 2013. Based on known foraging patterns, we anticipate harbor seals have an average trophic position of 3.5 to 5 and herring will have an average trophic position of 2.5-2.9. Equation 2 produced the most accurate herring trophic position estimates for most amino acids, however valine produced an impossibly low estimate of trophic position. In contrast, equation 3 produced the most accurate results for most amino acids compared to harbor seals, but these estimates were still unrealistically low for some amino acids (proline, valine), which is common for CSIA (Table S1,

McMahon et al. 2016). Additionally, this is not the most ecologically accurate parameterization, as it assumes all trophic transfers are of high prey quality, where there must be at least one herbivorous-low quality trophic transfer in the food web from phytoplankton to zooplankton (parameterization of equation 4, Table S1). It also assumes prey quality (carnivorous) and trophic level of the consumer is more important than nitrogen excretion pathway (urea versus ammonia) for some amino acids but not others. Seemingly, these assumptions impact trophic position estimates from individual trophic amino acids differently which will likely be an important consideration for future studies applying a multi-amino acid framework. It is possible that these reflect biases in conventional trophic position estimates (i.e., stomach content analysis) as proposed by McMahon (2015) or there may be biases in controlled feeding studies. For example, growth rate of individuals in controlled feeding studies may not accurately reflect those in natural ecosystems which may lead to overestimates in trophic enrichment if they are higher in natural systems compared to controlled feeding experiments. This may be plausible in the Washington food web as consumption of juvenile fish is common at multiple trophic levels, and juveniles presumably have higher growth rates than adults.

Section S3. Identifying size and sex-based trends in harbor seal trophic position

Only a subset of the samples included month of collection, sex, and length metadata and therefore separate month, length, and sex specific analyses were fit to the data to test whether they should be considered as predictors for the ocean condition and prey availability data. Standard linear models (equation S5) with: 1) sex as a factor, 2) length as a continuous covariate and 3) month as a continuous covariate were fit to both Salish Sea and coastal WA for each individual trophic amino acid. These models were used to test whether trophic position varies with length and sex, whether these trends are consistent between amino acids, and whether one year was an appropriate approximation for tissue turnover of bone collagen. The standard linear models took the following structure:

$$S5. \mathbf{y}_i = \alpha + \boldsymbol{\beta} \mathbf{X} + \epsilon$$

where y represents harbor seal trophic position calculated from phenylalanine and a trophic amino acid i , \mathbf{X} is a matrix of bottom-up drivers for a given model, $\boldsymbol{\beta}$ is a vector of covariates (sex, length, month, location), and α is the intercept. There were no significant differences in trophic position between male and female harbor seals in either the Salish Sea (Figure S6A) or coastal Washington (Figure S6B); this relationship was consistent across amino acids. Similarly, trophic position did not change based on harbor seal length (Figure S5). Interestingly, the exception to this finding was trophic position calculated by proline, which showed a significant decline with size. Mean harbor seal trophic position calculated from proline for harbor seals ranging from 150 - 180 cm in standard was 0.6 lower than harbors seals that were less than 120 cm of standard length (Figure S5). Trophic position calculated from alanine, aspartic acid and valine also showed negative trends with size, although the trend was not statistically significant, while trophic position calculated from glutamic acid was positive but also not statistically

significant. There was also no observed ‘seasonality’ in harbor seal trophic position (Figure S2) indicating 1-year physiological delay was a reasonable approximation for tissue turnover time of skull bone collagen.

Harbor seals in Washington do not have distinct trophic ecology based on adult size (Figure S5) or sex (Figure S6). Bjorkland et al. (2015) did not observe sex or size (weight) based differences in bulk $\delta^{15}\text{N}$ values in harbor seals in the San Juan Islands in the Salish Sea between 2007 and 2008. Our results agree with this finding and with similar studies of other Pacific pinniped species (Drago et al. 2009, Dehn et al. 2007). While both male and female harbor seals have a similar trophic position, it is possible sex and size-based differences in foraging strategies within a similar trophic position exist (Bjorkland et al. 2015, Wilson et al. 2014). Additionally, this study focused on adult harbor seals and changes in trophic position between juveniles, sub adults and adults are possible as indicated by pinniped studies (Zhao et al. 2004). Regardless, our results show long-term consistencies in the trophic niche exploited by both male and female harbor seals regardless of adult size in Washington.

Section S4. Identifying temporal trends in harbor seal trophic position

To understand any changes through time to harbor seal foraging ecology over the past 100 years that were not explained by the tested environmental and food web covariates (Tables S3 & S4), generalized additive models (GAMs) were fit the residuals for the best ocean condition-prey model with a smooth term by year and a k term of 5. These analyses (Figures S6 & S9) were compared to the raw time series of harbor seal trophic position data (Figure S7) to identify trends through time that are unexplained by the covariates included in this analysis.

Trends in harbor seal trophic position through time were different between the Salish Sea and coastal Washington (Figure S7). The time series of the glutamic acid trophic position in coastal Washington had a significant positive trend through time (Figure S7b) that increased from 1948-1968 and remained relatively constant following 1975. Trophic position calculated from alanine and proline showed similar trends, although the alanine trophic position trend was not statistically significant (Figure S7a). In contrast, harbor seal trophic position in the Salish Sea calculated from glutamic acid, alanine, aspartic acid, and proline has been relatively stable over the past century, but the trophic position calculated from valine showed a significant decline since 1968.

There were no trends through time for the model residuals for any amino acid after accounting for environmental (Figure S8) and food web (Figure S9) conditions at all three time lags. This indicates that prey availability and ocean conditions account for most temporal variation observed in the trophic position time series (Figure S7). However, valine was a notable exception, which demonstrated a decreasing trend through time in model residuals for all of the models with the most support.

Section S5. Methods for Multivariate Autoregressive State-Space (MARSS) Model

A MARSS model was fit to herring stock spawning biomass and harbor seal stock population

size in order to get total population and total biomass estimates for these species for each year.

Harbor seal datasets and herring biomass were collected by stock ($n = 7$ and $n = 20$, respectively)

but did not have observations for every for every year (Figures S12 & S14). Two MARSS

models were fit to the data, one for each species, to estimate population and biomass for each

year for each for each stock (Figures S13 & S15). For both datasets process error (Q) assumed

equal variance and covariance across stocks, and observation error (R) was assumed to be equal

across stocks. U and x_0 were both set to unequal, thus assuming they vary across stocks. Model

states (Figures S13 & S15) were summed across years for total biomass (herring) and population

size (harbor seals) estimates and used as covariates for prey availability models. Harbor seal data

has not been collected since 2000 and we assumed the population has remained constant from

2000-2010.

Section S6. Using multi-trophic amino acid analysis compared to only glutamic acid

Mean harbor seal trophic position estimates were similar across trophic amino acids however some were more variable than others. The standard deviation of trophic position was higher for proline (4.6 ± 0.7 , mean \pm 1SD), and valine (3.7 ± 0.8) and included more ecologically unrealistic values compared to glutamic acid (4.5 ± 0.4) and alanine (3.9 ± 0.4). Trophic position calculated from aspartic acid (4.1 ± 1.0) had the highest standard deviation and also demonstrated a trend through time compared to other amino acid trophic position calculations (Figure S7).

Application of a multi-amino acid trophic position calculation 1) offered a more realistic parameterization of the trophic position equation, 2) improved model certainty and 3) produced similar covariate coefficients compared to a glutamic acid only parameterization (Table S6). Examination of the distribution of trophic position calculations for each individual trophic amino acid shows variability in accuracy and variance for single trophic amino acid calculations (Figures S3 & S4). For example, aspartic acid had a much wider variance compared to other amino acids (Figures S3 & S4) and also produced different trends through time (Figure S7).

It is likely differences in tissue turnover time between individual amino acids and phenylalanine contribute to the variance of the trophic position estimates derived from individual trophic amino acids. Downs et al. (2014) found phenylalanine takes 780 hours to reach 50% turnover in shrimp. This is comparable to glutamic acid, alanine, and valine which take 940, 642, and 942 hours respectively which are substantially lower than aspartic acid which requires 1530 hours. The discrepancy between tissue turnover times between aspartic acid and phenylalanine is likely the cause of the broad distribution for aspartic acid derived trophic position compared to other trophic amino acids, as aspartic acid is incorporating the nitrogen isotope signature over a

substantially larger time period relative to phenylalanine and thus may incorporate more prey switching and/or changes in the isotopic signature of primary producers.

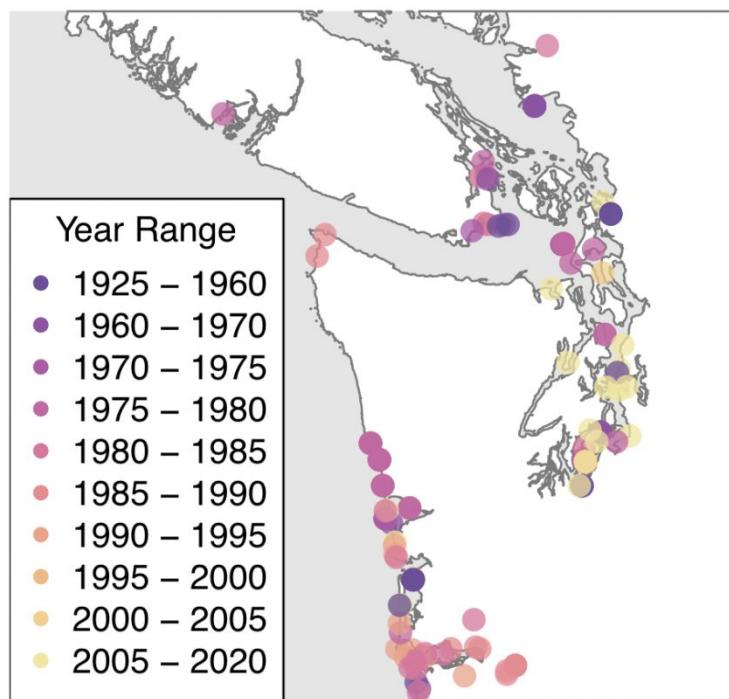
Addition of alanine to the glutamic acid only model resulted in the largest difference in model certainty. A glutamic acid – alanine model supported the same best models for both the environmental and prey models at all time lags. The combined tissue turnover of glutamic acid and alanine of shrimp (791 hours) is very similar to that of phenylalanine (780 hours) ensuring both the trophic and source amino acids were incorporated over a similar time scale (albeit the trophic amino acids were a wider time scale). Benefits of a multi-amino acid trophic position equation may not require four amino acids as previously suggested (Nielsen et al. 2015) but rather carefully selected trophic amino acids to ensure the trophic amino acids are incorporated over a similar time scale as the source amino acids. If tissue turnover times are unable to be approximated, utilizing four trophic amino acids or two source amino acids as suggested by Nielsen et al. (2015) would likely provide the same benefit as fewer, carefully selected amino acids based on tissue turnover times.

Section S7 Tissue turnover time assumption validation

Tissue turnover time of bone collagen in large mammals is not well studied due to the challenges of repeatedly measuring bone in a controlled feeding study. Hobson et al. (1992) found the half-life of carbon in bone collagen of Japanese quails (*Coturnix japonica*) is 170 days. A comparative study of the $\delta^{15}\text{N}$ values in elephant seal bone and tooth dentin found the $\delta^{15}\text{N}$ value in skull (maxilla and mandible) bone collagen was significantly correlated with the previous two years of tooth dentin (Riofrío-Lazo and Aurioles-Gamboa 2013). Another comparative study of northern fur seal (*Callorhinus ursinus*) and California sea lion (*Zalophus californianus*) young-of-year estimated that complete bone collagen turnover takes approximately 8 months (Newsome et al. 2006). Complete bone collagen turnover should be slower in adults than growing young-of-year. Altogether, this indicates that the $\delta^{15}\text{N}$ values in skull bone collagen is time averaged over the past 1 – 2 years of the seals life.

To further test the assumption that stable isotope composition of bone collagen of adult harbor seals reflect the last year of the animals life, month was tested as a smoothed predictor with up to 12 knots for trophic position estimates using a generalized additive model (GAM). Support for a significant smoothing term or trend in the data would identify any seasonality in the data, which would be expected if tissue turnover time is consistently less than a year. There was no support for a smoothing effect by month in generalized additive models of $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{13}\text{C}$ values which would have indicated any seasonal variability in isotope composition and thus a turnover time of less than a year ($p < 0.05$; Appendix S1:Figure S2).

Figure S1: Temporal distribution of sampled harbor seal museum specimens in coastal Washington and the Salish Sea. Colors denotes time period specimens were collected.



View Only

Figure S2: Analysis of seasonality of harbor seal trophic position for five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) calculated using the source amino acid phenylalanine and equation 2 (Table S2; Figure S4.2) with a weighted beta. Color corresponds to trophic amino acid, line shows the fit of a generalized additive model with a smoothed term by month (1 = January, 12 = December) and a k of 12. Smoothed terms were not significant.

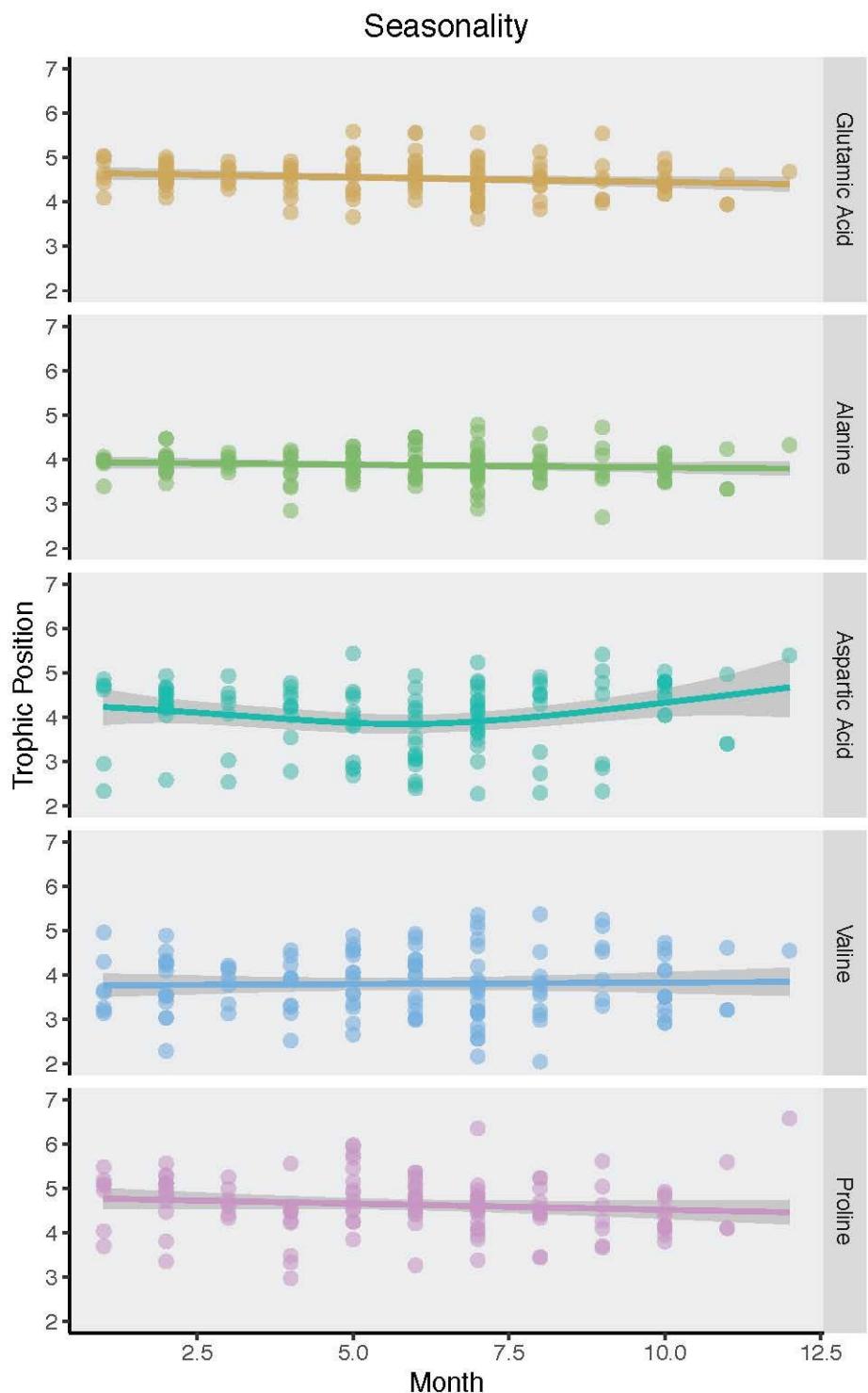


Figure S3: Distributions (density of probability, y-axis) of calculated trophic position (x-axis) for harbor seals in this study. Equations (1-4) refer to Table S1 and parameter values described in Table 1 of the main text. Colors correspond to trophic amino acids (Tr) and the grey box represents ecologically realistic trophic positions for harbor seals if they were to predate 1 trophic position above herring (trophic position of 2.5, minimum expected value) and one trophic position below killer whales (trophic position of 6, maximum). The value within the grey box corresponds to the percentage of observed trophic position values that fell within the ecologically realistic range.

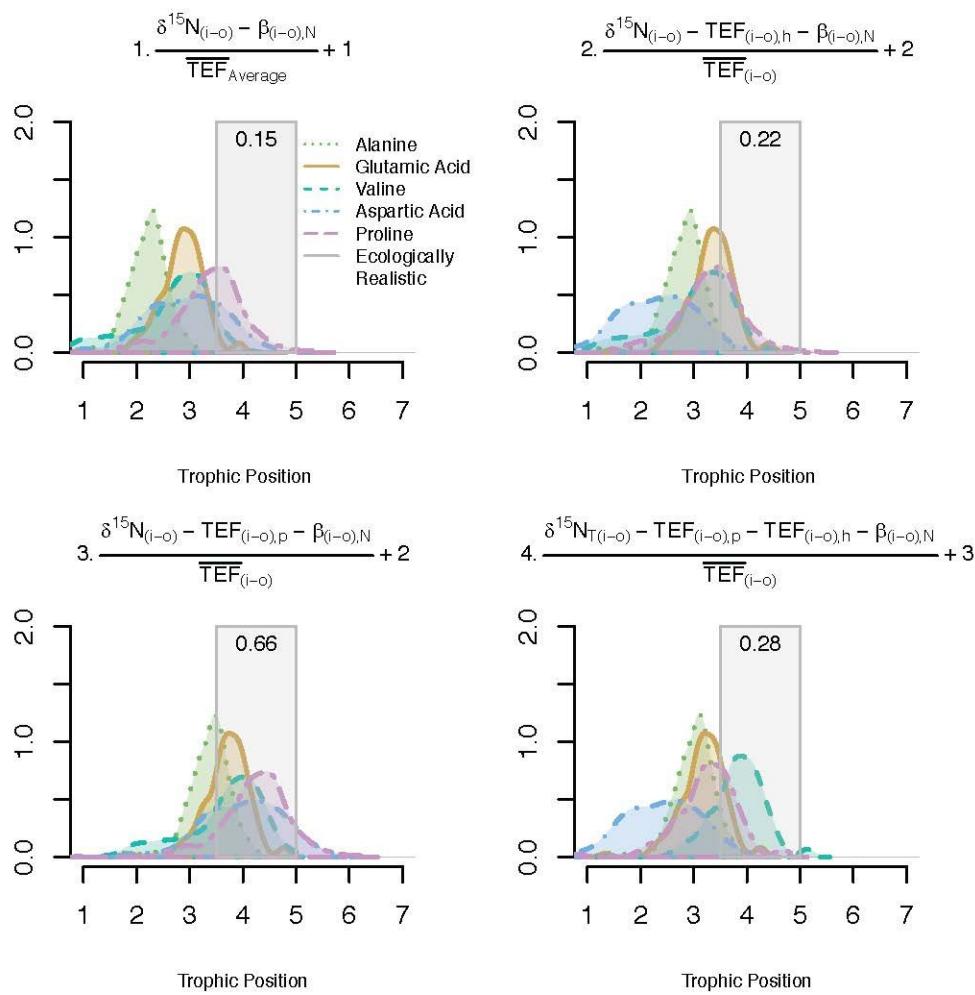


Figure S4: Distributions (density of probability, y-axis) of calculated trophic position (x-axis) for harbor seals in this study applying equations (1-4) in Table S1 with $\beta_{(i-o),NV}$ instead of $\beta_{(i-o),N}$ as described in Table 1 of the main text.

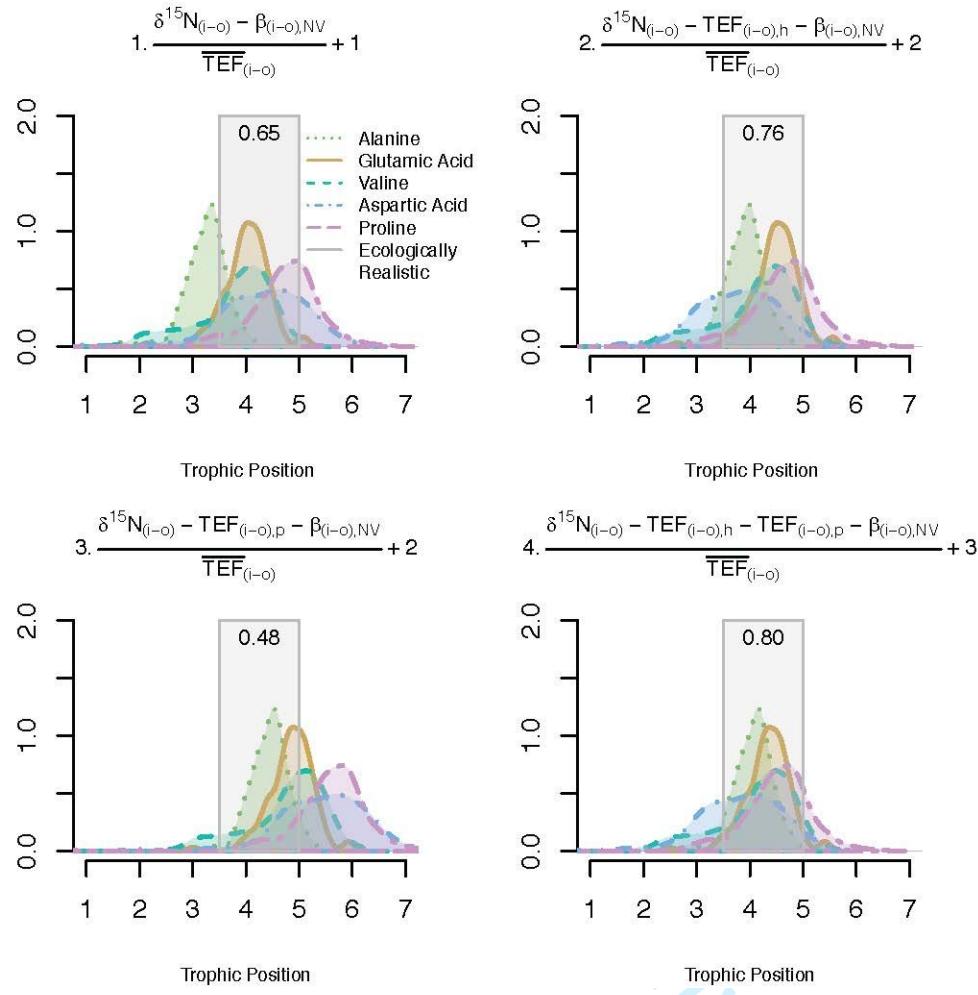


Figure S5: Relationship between harbor seal size (standard length, cm) and trophic position calculated using five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline). The line shows the fit of a generalized additive model with a smoothed term by year and a k of 6 and * denotes a significant smoothed term.

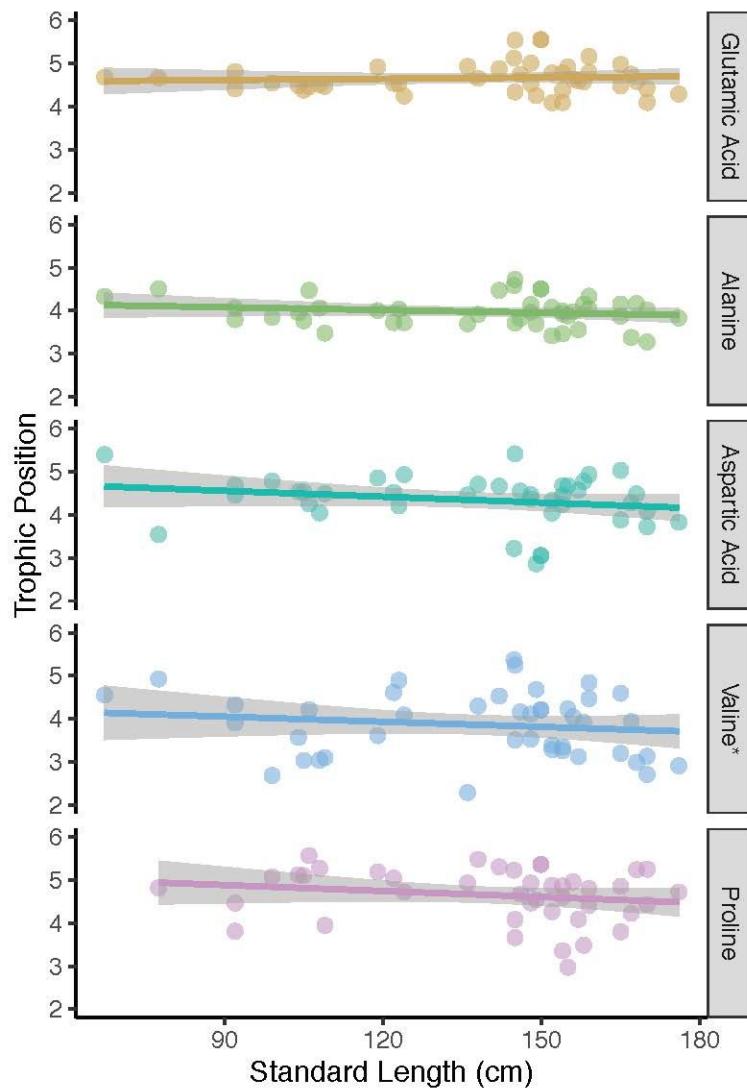


Figure S6: Sex specific trophic position for male (M) and female (F) harbor seals pooled over the past century and calculated using five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) for a) Salish Sea and b) coastal Washington specimens.

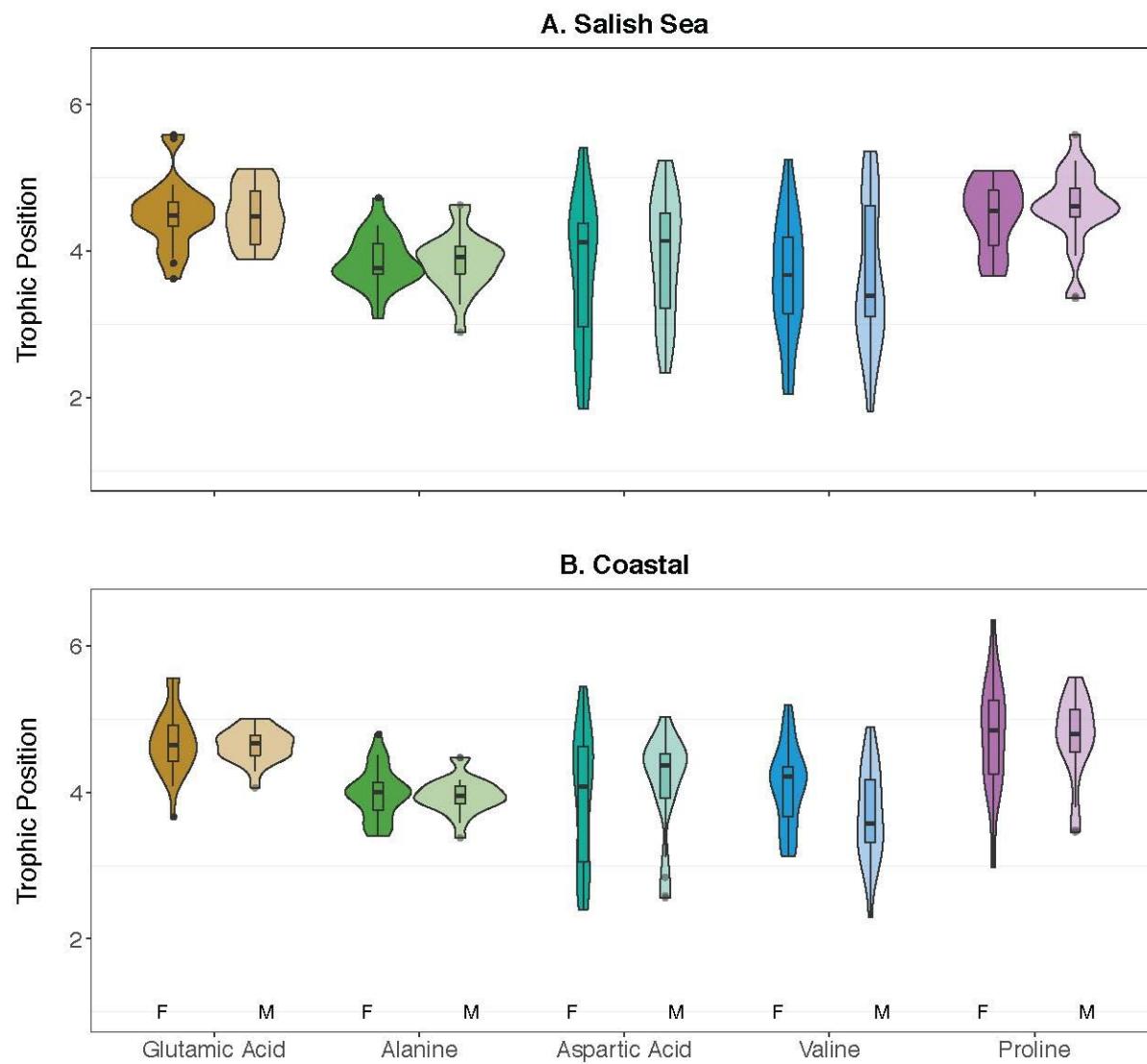


Figure S7: Time series of harbor seal trophic position in a) coastal Washington and b) the Salish Sea for five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) calculated using the source amino acid phenylalanine. Color corresponds to trophic amino acid, while 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.

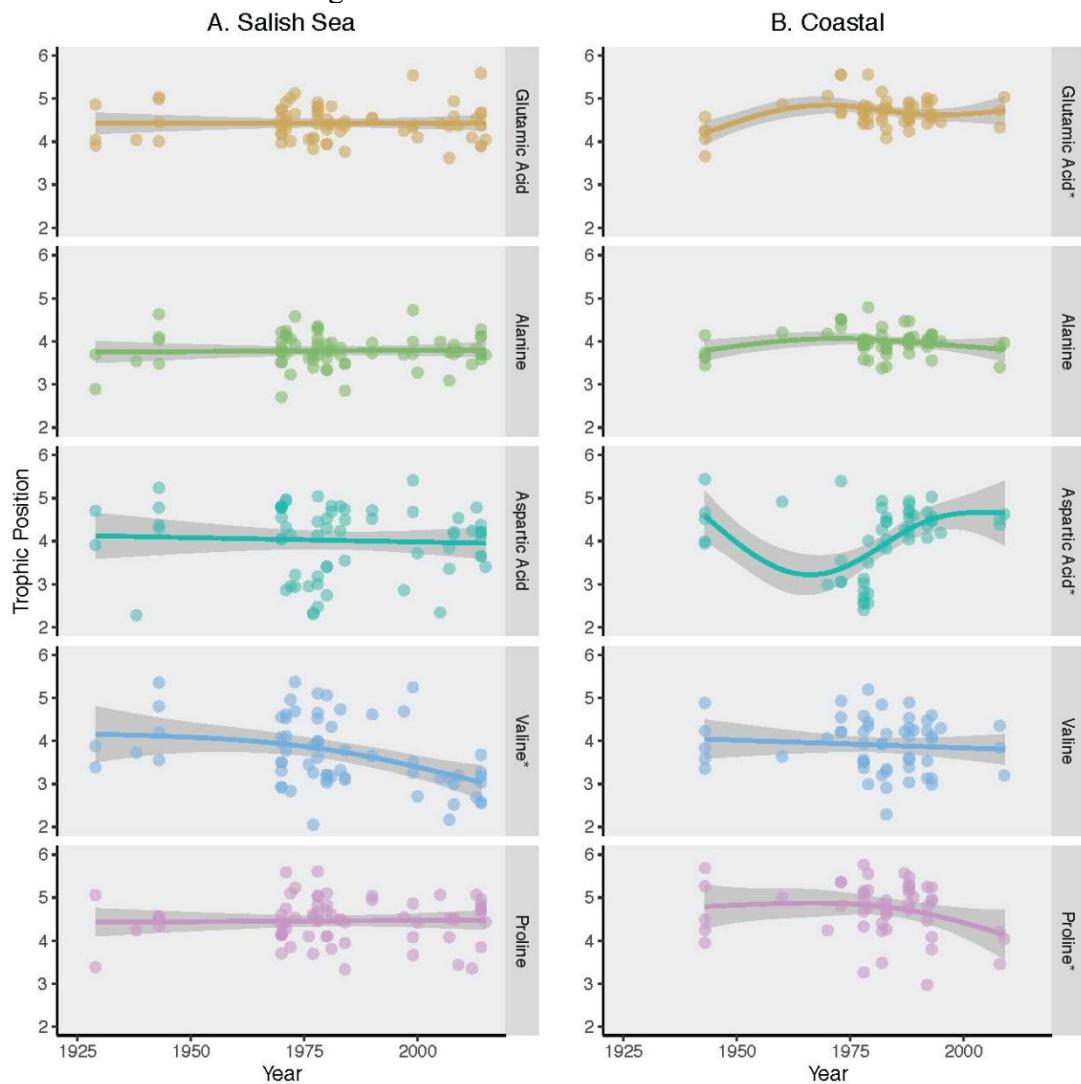


Figure S8: Time series of residuals by year for the three ocean condition models (physiological delay, 1-year ecological delay, 2-year ecological delay) with the most support for the four different trophic amino acids used in the models (glutamic acid, alanine, valine, and proline) with trophic position calculated using the source amino acid phenylalanine. Color corresponds to trophic amino acid, line shows the fit of a generalized additive model with a smoothed term by year and a k of 6. * denotes a significant smoothed term.

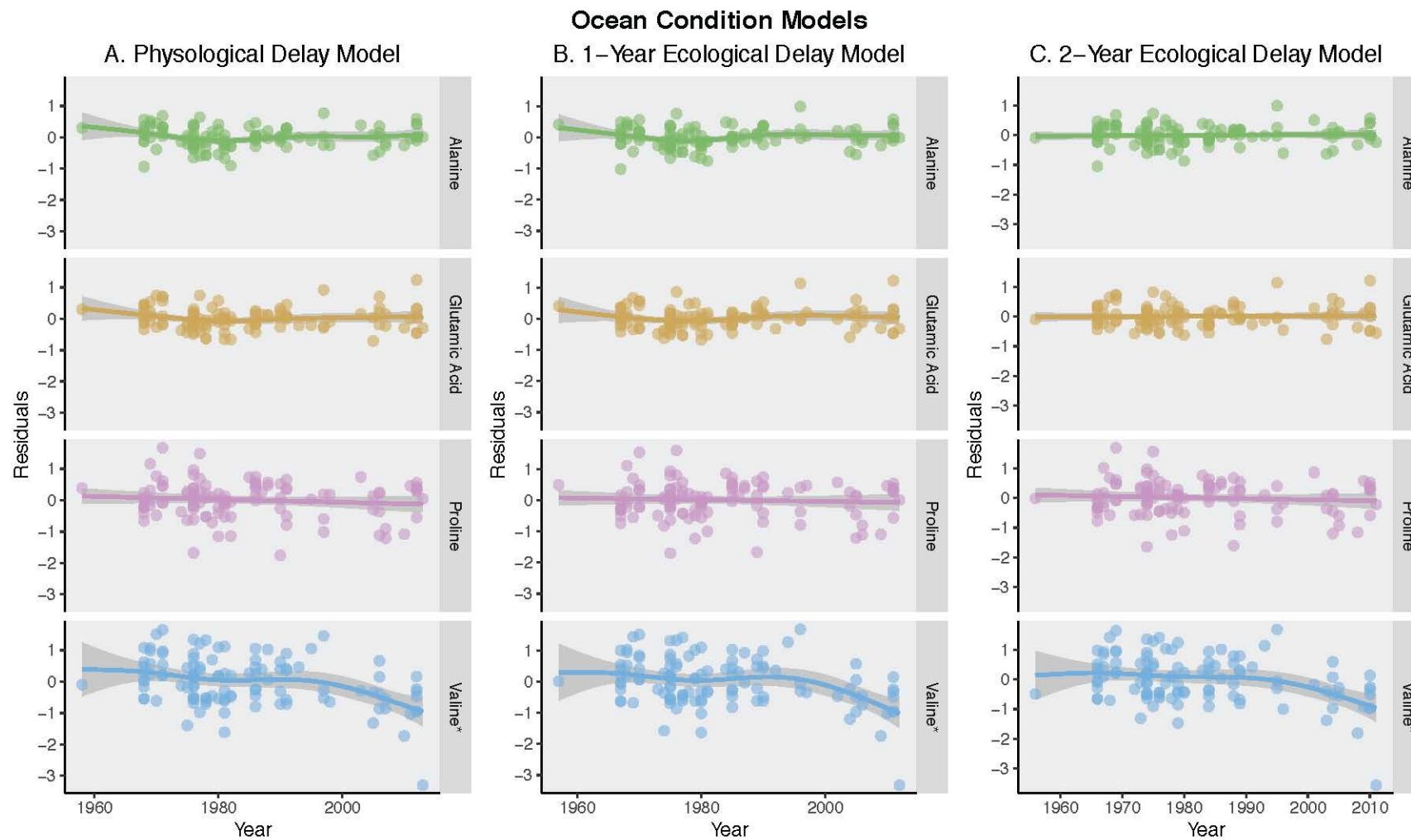


Figure S9: Time series of residuals by year for the three food web models (physiological delay, 1-year ecological delay, 2-year ecological delay) with the most support for the four different trophic amino acids used in the models (glutamic acid, alanine, valine, and proline) with trophic position calculated using the source amino acid phenylalanine. Color corresponds to trophic amino acid, line shows the fit of a generalized additive model with a smoothed term by year and a k of 6. * denotes a significant smoothed term.

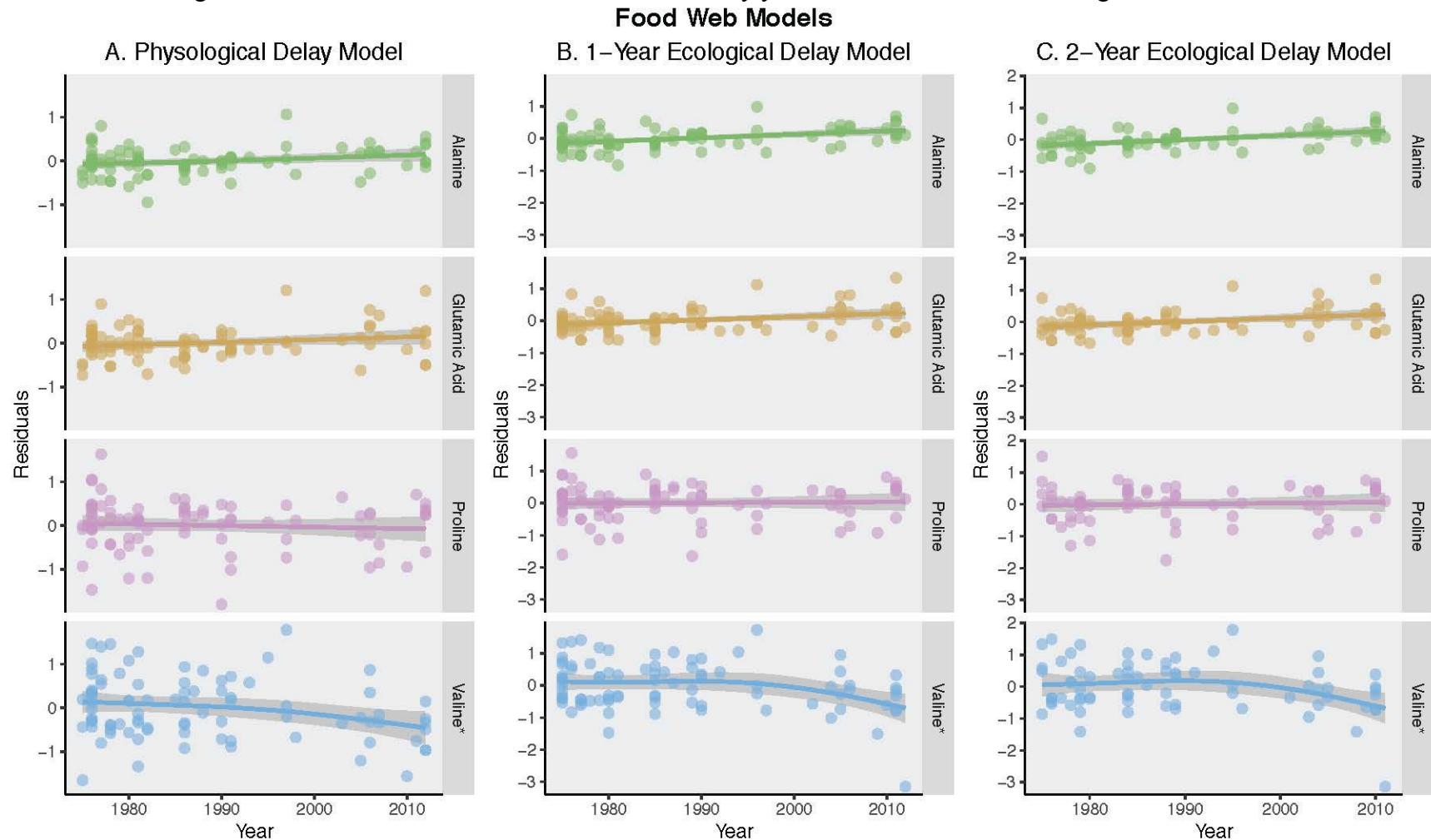


Figure S10: Residual plots for the physiological delay, 1-year ecological delay, and 2-year ecological delay ocean condition models with the most support.

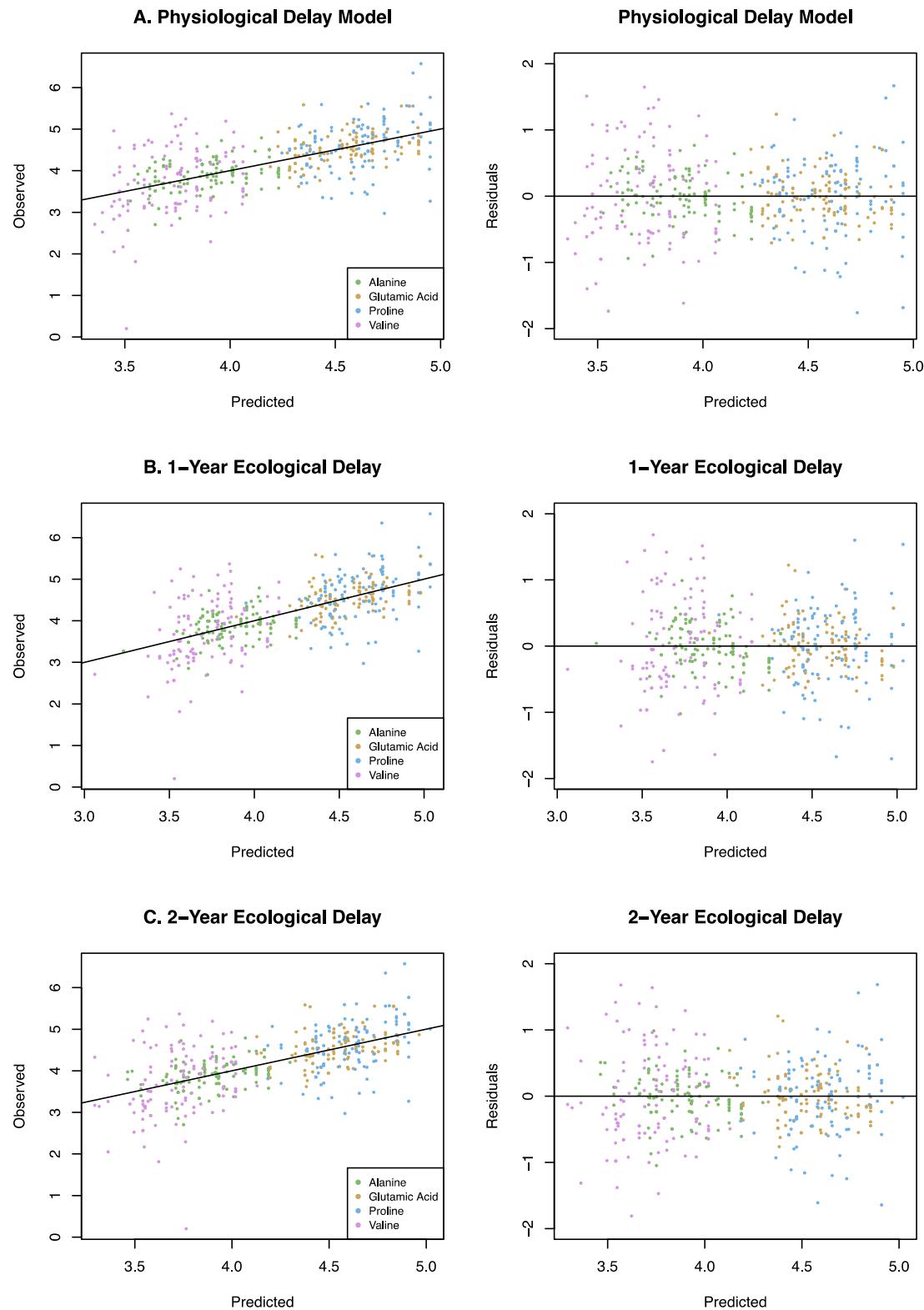


Figure S11: Residual plots for the physiological delay, 1-year ecological delay, and 2-year ecological delay food web models with the most support.

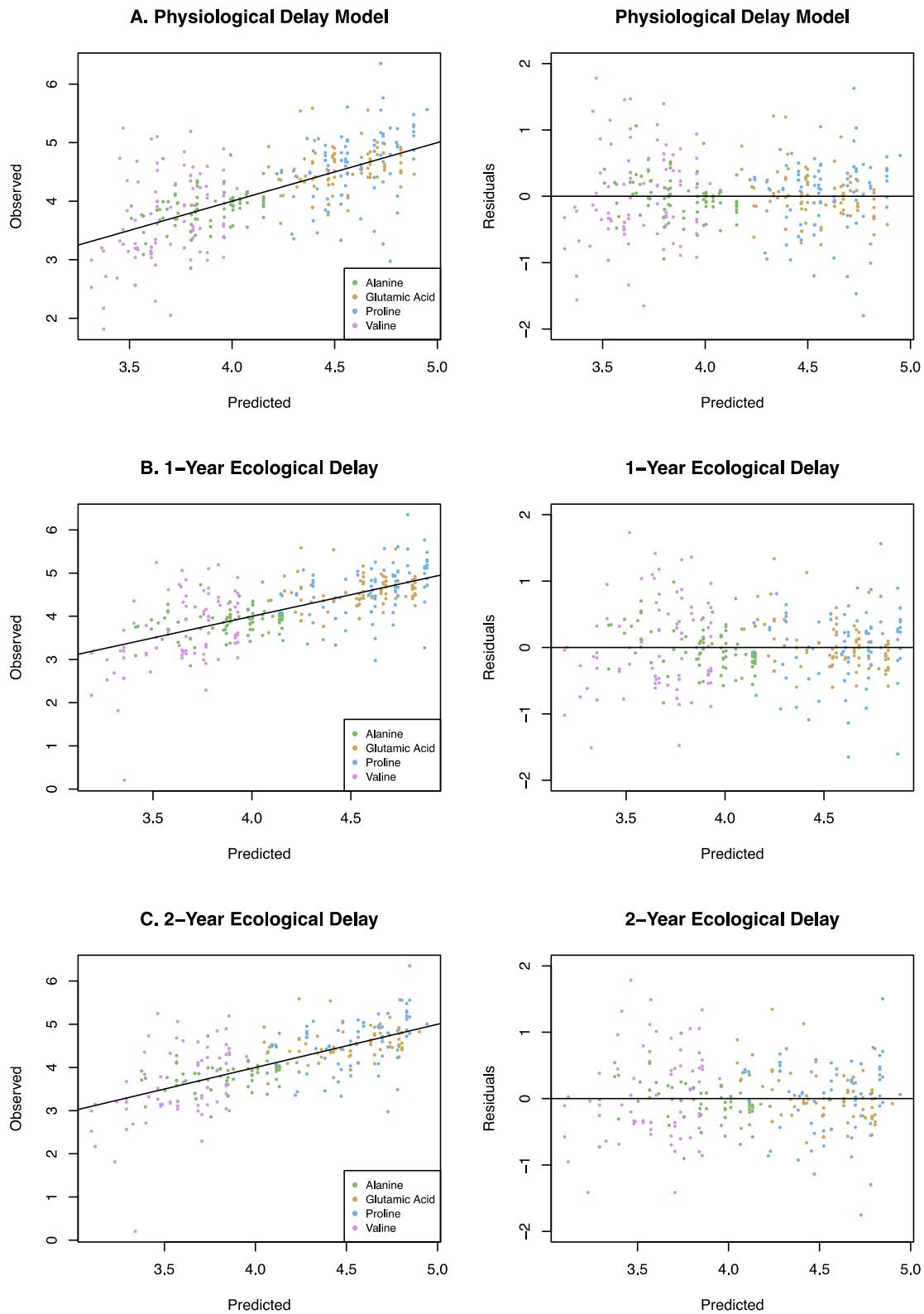


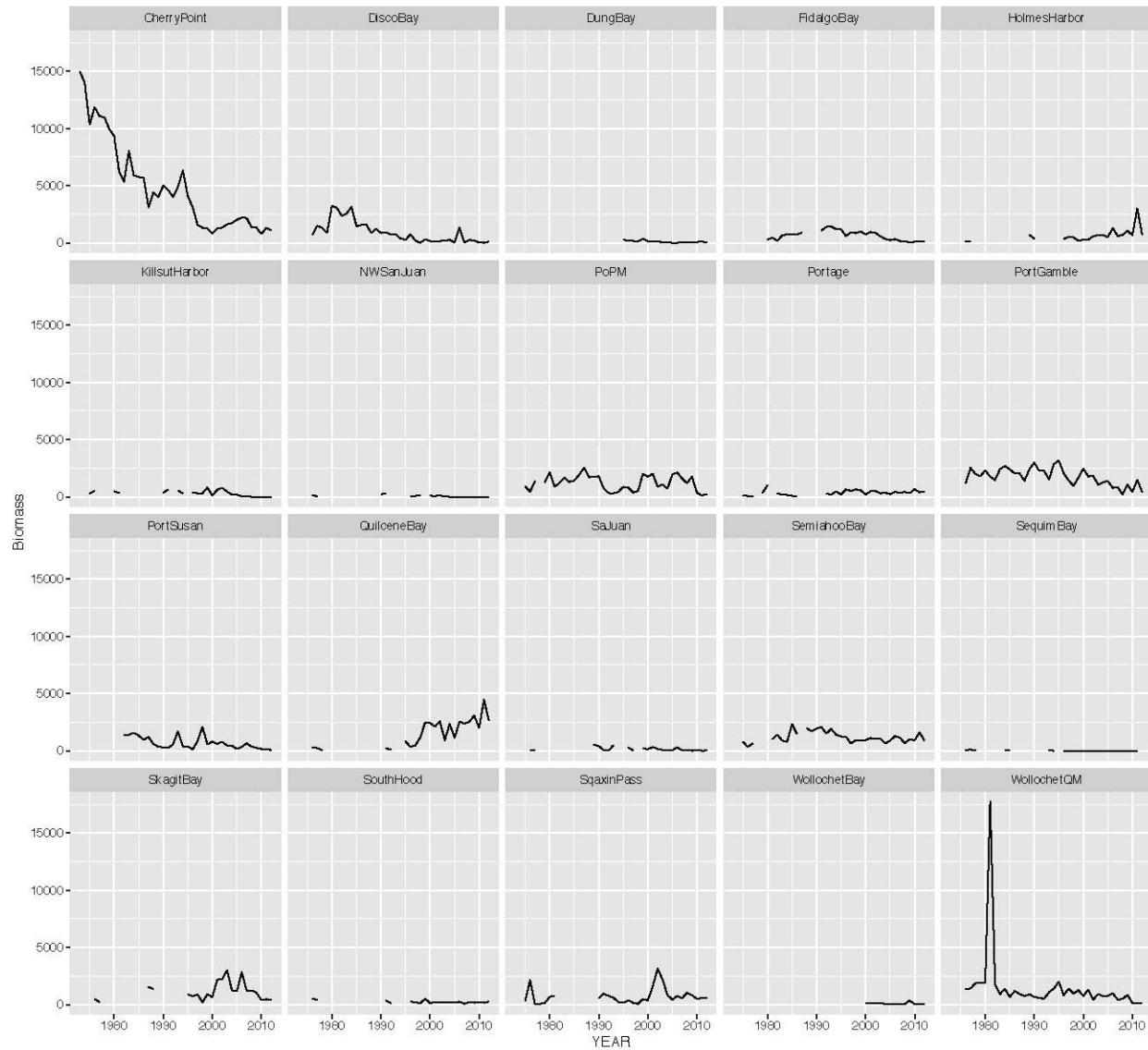
Figure S12: Pacific herring spawning biomass by stock from Siple and Francis 2015.

Figure S13: MARSS model (described in Appendix S3) for Pacific herring spawning biomass by stock.

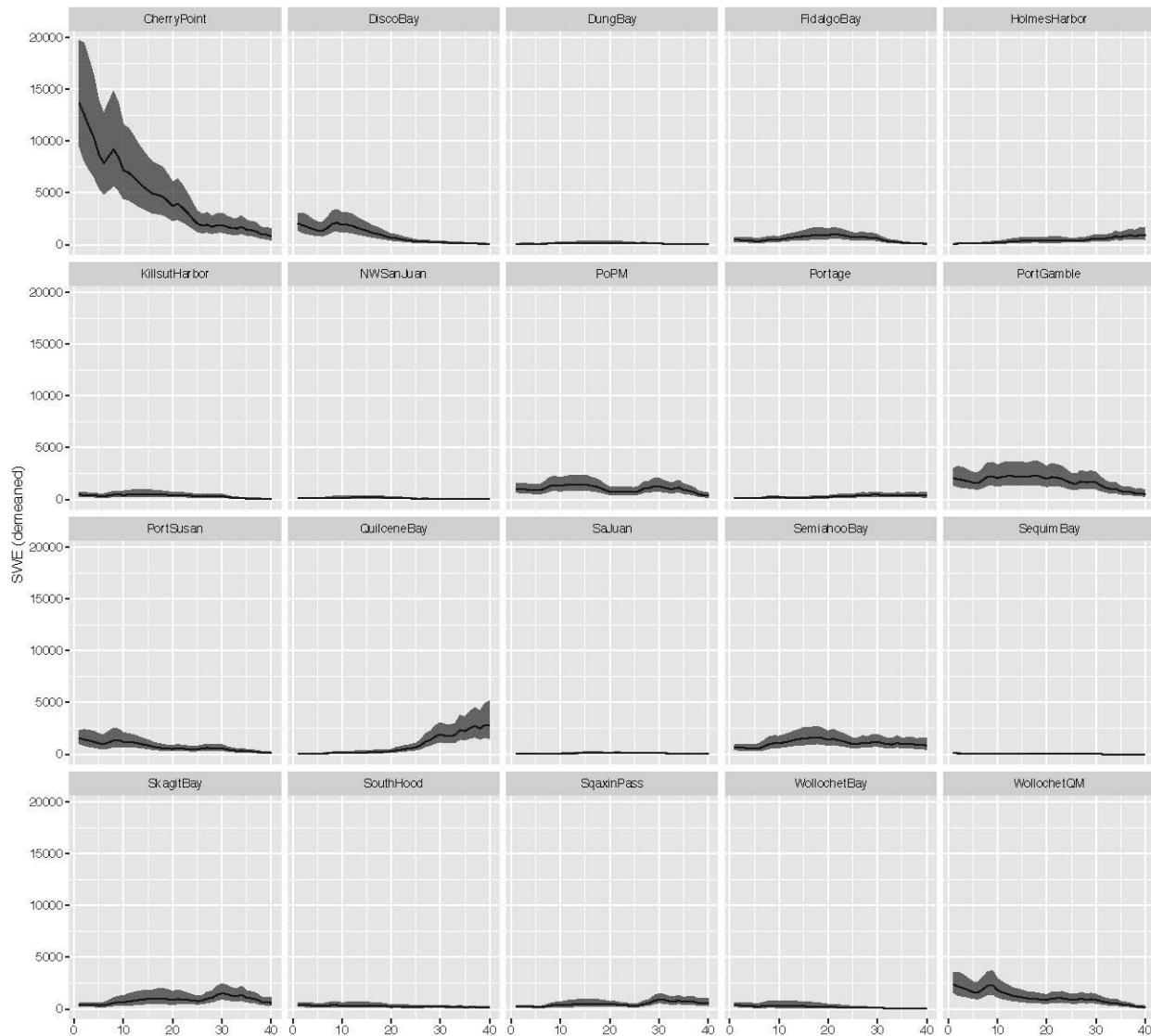


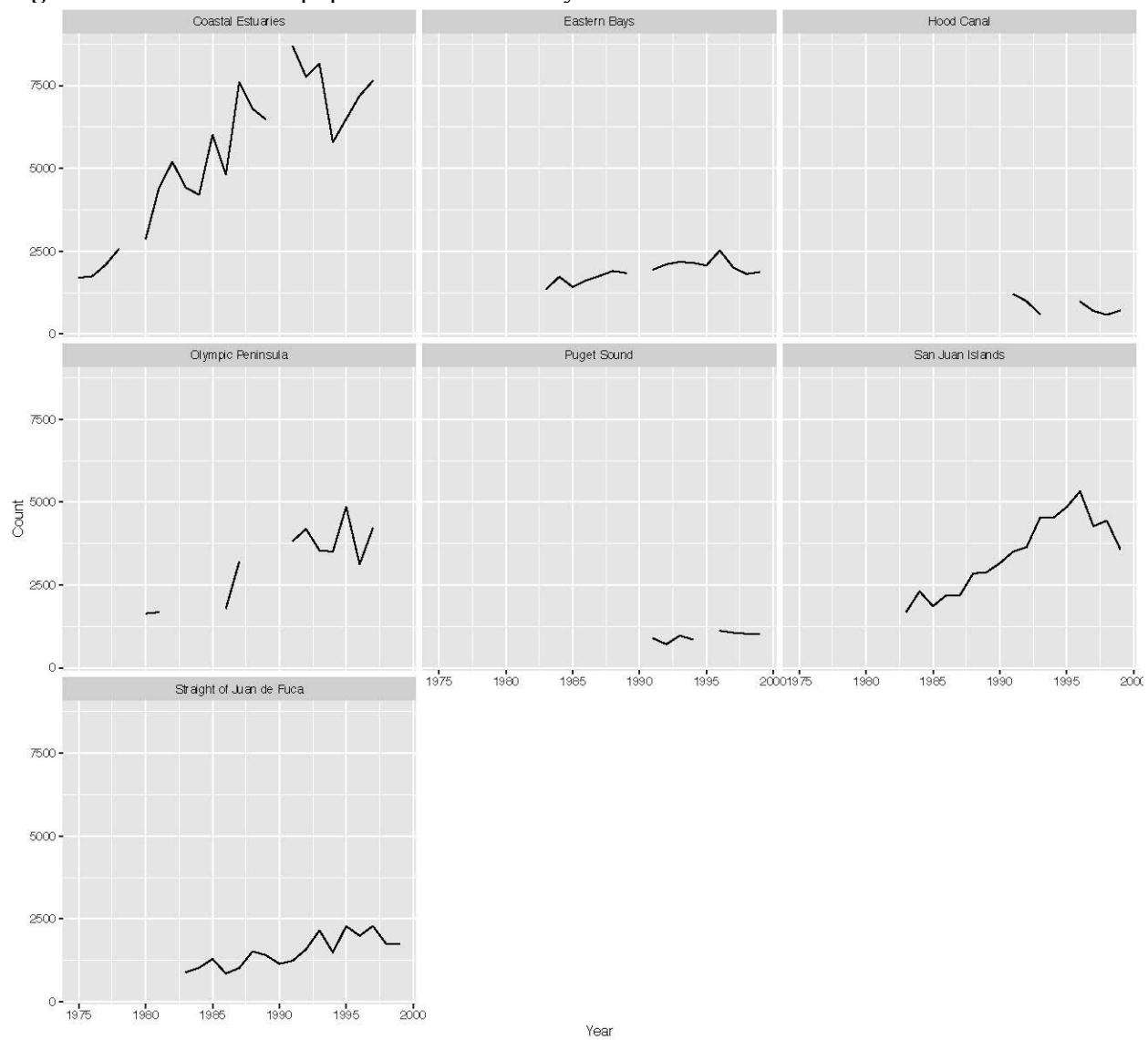
Figure S14: Harbor seal population estimates by stock from Jeffries et al. 2003.

Figure S15: MARSS model (described in Appendix S3) for harbor seal population counts fit by stock.

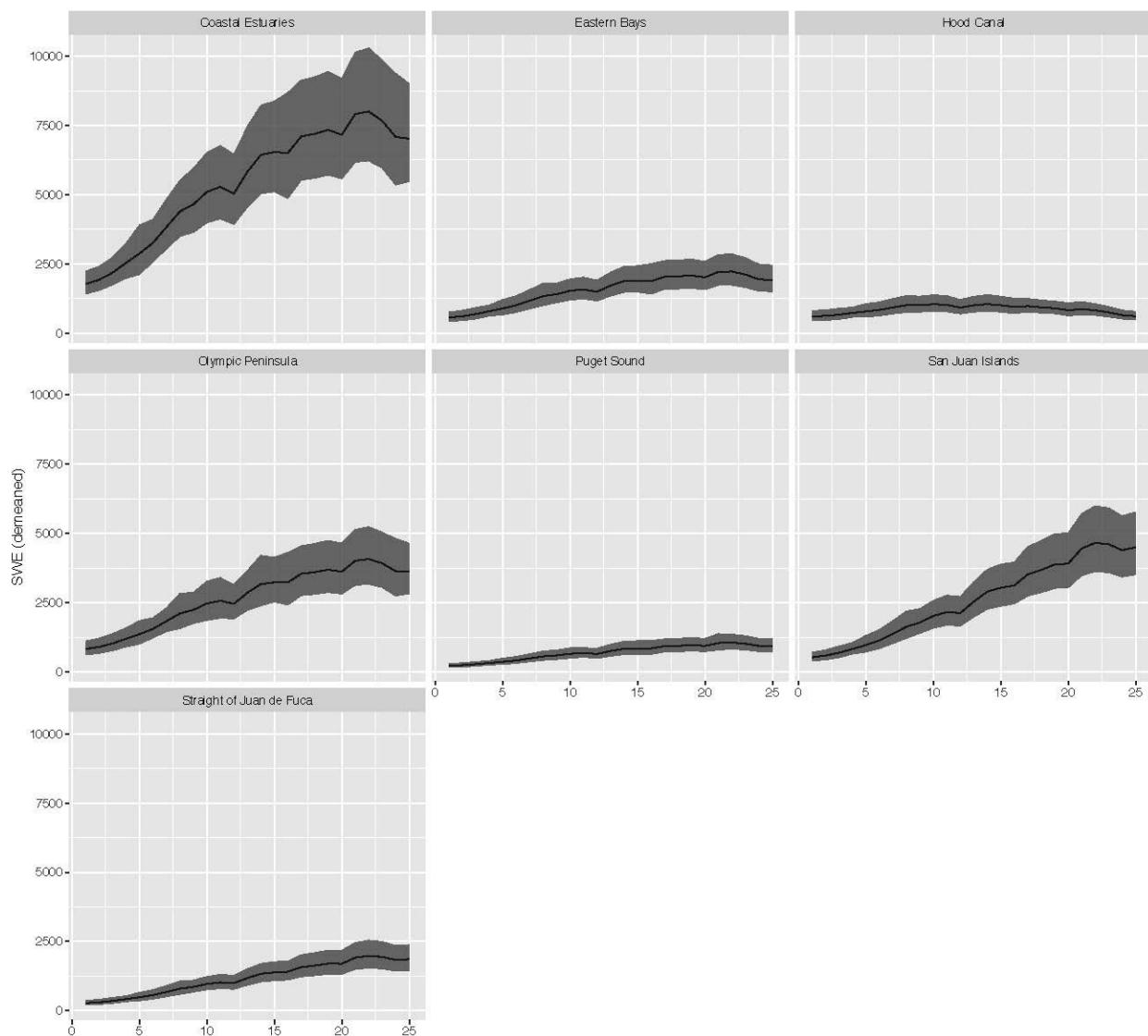


Table S1: Equations for single and multi-trophic enrichment factor parameterizations of trophic position and the associated assumptions for each parameterization using the values described in Table 1 in the main text. i refers to an individual trophic amino acid and o refers to a source amino acid, in this case phenylalanine. In addition to $\beta_{(i-o), N}$ (Figure S3) refers to $\beta_{(i-o)}$ for non-vascular plants, the same equations were used with $\beta_{(i-o), NV}$ (equation 6, Figure S4). Applying $\beta_{(i-o), NV}$ has the additional assumption that both vascular and nonvascular plants contribute to the coastal food web in which harbor seals forage and that the contributions of each can be calculated from bulk $\delta^{13}\text{C}$ data (equations 2 & 3).

Parameterization Assumptions	Equation
1. Assumes that all trophic transfers are best represented by the average TDF in this system	$\text{Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 1$
2. Includes harbor seal specific TDF ($\text{TDF}_{(i-o), h}$) which assumes one trophic transfer is from high quality prey (and urea excretion) and assumes average TDF accurately represents all other trophic transfers	$\text{Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - \text{TEF}_{(i-o), h} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 2$
3. Includes a TDF derived from basal food web consumers (zooplankton / herbivores; $\text{TDF}_{(i-o), p}$) which assumes one trophic transfer is from low quality prey and assumes average TDF accurately represents all other trophic transfers	$\text{Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - \text{TEF}_{(i-o), p} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 2$
4. Includes a TDF derived from basal food web consumers (zooplankton / herbivores; $\text{TDF}_{(i-o), p}$) and a harbor seal specific TDF ($\text{TDF}_{(i-o), h}$). This assumes one trophic transfer is from low quality prey and a second is from high quality prey (and urea excretion). Assumes average TDF accurately represents all other trophic transfers	$\text{Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - \text{TEF}_{(i-o), p} - \text{TEF}_{(i-o), h} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 3$

Table S2: Trophic amino acid specific parameter values for β and trophic enrichment factors (TEF) to test parameterization of trophic position calculations using multiple TEFs and β values. The source amino acid (o) for all parameters was phenylalanine (Supplementary Material Appendix 1, Table S1, Figures S2 & S3). Values are mean \pm SD.

Trophic Amino Acid (i)	$\beta_{(i-o), N}$ Nielsen et al. 2015	$\beta_{(i-o), V}$ Vander Zanden et al. 2013	$\beta_{(i-o), NV}$ This study	$TEF_{(i-o), j}$ Germain et al. 2013	$TEF_{(i-o)}$ Nielsen et al. 2015
Glutamic acid (Glu)	2.9 ± 2.0	-8.7 ± 1.1	-3.9 ± 1.2	3.4 ± 2.4	6.6 ± 1.7
Alanine (Ala)	2.8 ± 2.2	-8.0 ± 1.0	-3.6 ± 1.1	2.5 ± 2.9	6.8 ± 2.2
Aspartic Acid (Asp)	1.8 ± 2.9	-7.3 ± 1.1	-4.2 ± 1.0	3.5 ± 1.8	$5.4 \pm 1.8^*$
Valine (Val)	3.4 ± 2.9	-6.8 ± 1.0	-2.6 ± 0.9	7.5 ± 3.7	4.6 ± 3.4
Proline (Pro)	2.7 ± 2.1	$-7.7 \pm 1.2^*$ Not reported used average of other amino acids	-5.1 ± 1.1	5.5 ± 3.4	5.0 ± 1.8

Table S3: Covariates used to test ocean condition as a bottom-up driver of harbor seal trophic ecology. Total number of models tested = 35.

	Time Series Description	Length	Source
Discharge	Total discharge from the Columbia River at Dalles, WA during summer months of high discharge (May-Oct) from monthly U.S. Geological Survey discharge data.	1879-2018	Data Source: USGS 14105700
Sea Surface Temperature (SST)	Average of monthly NOAA Extended Reconstructed SST for summer (Jul-Sep) in coastal Washington (48°N, 125°W).	1854-2019	Data Source: NOAA ERSST V5 SST data was obtained from NOAA_ERSST_V5 data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at https://www.esrl.noaa.gov/psd/ (Huang et al. 2017).
Upwelling	Mean coastal upwelling index (CUI) coastal Washington (45°N, 125°W) using Bakun upwelling calculation based on Ekman's theory of mass transport due to wind stress, for spring (Apr-Jun) and summer (Jun-Sep).	1946-2019.	Data Source: NOAA ERD SWFSC
North Pacific Gyre Oscillation	2nd dominant mode of sea surface height variability in the northeast Pacific. Correlates with fluctuations in salinity nutrients and chlorophyll-a.	1950-2019	Data Source: Di Lorenzo et al. 2008. NPGO
Multivariate ENSO Index	The extended Multivariate ENSO Index (MEI) uses Principle Component analysis on six variables: sea-level pressure, u and v component of the surface wind vector, sea surface temperature and cloudiness fraction in the tropical Pacific.	1950-2019	Data Source: NOAA/ESRL (https://psl.noaa.gov/enso/mei/ext/table.ext.html) via California Current Integrated Ecosystem Assessment MEI
Pacific Decadal Oscillation	Same as eastern Bering Sea	1900-2018	Data Sources: PDQ ; Zhang et al. 1997; Mantua et al 1997

Table S4: Covariates used to test prey availability as a bottom-up driver of harbor seal trophic ecology. Total number of models tested = 26.

	Time Series Description	Length	Source
Herring Biomass	Adult herring spawning biomass from egg deposition surveys for the estimated from Washington State Department of Fish and wildlife by Siple and Francis 2015.(MARSS output section S5, Figures S11 & S12)	1973-2012	Siple, M.C. and T.B. Francis. 2015. Population diversity in Pacific herring of the Puget Sound, USA.
Hake Biomass	Pacific Hake (whiting) relative spawning biomass in US and Canadian waters.	1973-2012	Berger et al. 2017. Table 8 total spawning biomass.
Chinook Salmon Spawners	Chinook salmon spawner summary data including all populations with a time series with data from at least 1973. Includes: Cedar River, Ceweeman River, Elochoman River, Grays and Chinook Rivers, Green River, Kalama River, Lewis River, Lower Cowlitz River, Lower and Upper Sauk River, Lower and Upper Skagit River, McKenzie River, Mid-Hood Canal, Nisqually River, Puyallup River, Skokomish River, Skykomish River, Snoqualmie River, Suiattle River, Toutle River, Upper Gorge Tributaries, White River and White Salmon River.	1973-2012	Northwest Fisheries Science Center, 2020: SPS Abundance - Salmon spawner abundance data compilation and database management, https://www.webapps.nwfsc.noaa.gov/apex/f?p=261:1::NO::P1_ARCHIVE_NOTE_CHEC_K:1&cs=1A0A1845C9A3C7202FD5C2934C6FD9410#
Chinook Salmon Smolt Production	Hatchery release data from the Regional Mark Information System and Wild Salmon Production data summarized by Chasco et al. 2017. Data was summed across both datasets for total juvenile salmon production.	1973-2012	RMIS: https://www.rmis.org/rmis_login.php?action=Login&system=cwt Summarized: https://github.com/bchasco/COAST_WIDE
Harbor Seal Abundance	Harbor seal population estimates based on coastal estuary, eastern Bays, Hood Canal, Olympic Peninsula, Puget Sound, San Juan Islands, and the Strait of Juan de Fuca counts. (MARSS output section S5, Figures S13 & S14)	1975-2012	Jeffries, S., H. Huber, J. Calambokidis and J. Laake. 2003. Trends and status of harbor seals in Washington state: 1978-1999. The Journal of Wildlife Management 67: 207-218.

Table S5: Full candidate model set ($n = 35$) for ocean condition modelling. The same candidate models were used for the physiological delay, 1-year ecological delay, and 2-year ecological delay models.

Ocean Condition Candidate Models

Covariates
1. Null
2. Location Only
3. PDO, Location
4. NPGO, Location
5. MEI, Location
6. Upwelling (Spring), Location
7. NPGO, PDO, Location
8. PDO, Upwelling (Spring), Location
9. NPGO, Upwelling (Spring), Location
10. MEI, Upwelling (Spring), Location
11. SST (Summer), Location
12. SST (Summer), PDO, Location
13. SST (Summer), NPGO, Location
14. SST (Summer), MEI, Location
15. SST (Summer), Upwelling (Spring), Location
16. SST (Summer), PDO, Upwelling (Spring), Location
17. SST (Summer), NPGO, Upwelling (Spring), Location
18. SST (Summer), MEI, Upwelling (Spring), Location
19. Upwelling (Summer), Location
20. Upwelling (Summer), PDO, Location
21. Upwelling (Summer), NPGO, Location
22. Upwelling (Summer), MEI, Location
23. Upwelling (Summer), NPGO, Upwelling (Spring), Location
24. Columbia Discharge (High), Location

25. Columbia Discharge (High), PDO, Location
 26. Columbia Discharge (High), NPGO, Location
 27. Columbia Discharge (High), MEI, Location
 28. Upwelling (Spring), Location
 29. Columbia Discharge (High), PDO, Upwelling (Spring), Location
 30. Columbia Discharge High, NPGO, Upwelling (Spring), Location
 31. Columbia Discharge High, MEI, Upwelling (Spring), Location
 32. Columbia Discharge (High), SST (Summer), Location
 33. Columbia Discharge (High), Upwelling (Summer), Location
 34. SST (Summer), Upwelling (Summer), Location
 35. SST (Summer), Upwelling (Summer), Columbia Discharge (High), Location
-

Table S6: Full candidate model set ($n = 26$) for prey availability modelling. The same candidate models were used for the physiological delay, 1-year ecological delay, and 2-year ecological delay models.

Food Web Candidate Models	
<i>Covariates</i>	
1.	Null
2.	Location Only
3.	Herring Spawning Biomass, Location
4.	Chinook Escapements, Location
5.	Chinook Smolt Production, Location
6.	Hake Spawning Biomass, Location
7.	Herring Spawning Biomass, Chinook Escapements, Location
8.	Herring Spawning Biomass, Hake Spawning Biomass, Location
9.	Herring Spawning Biomass, Chinook Smolt Production, Location
10.	Chinook Escapements, Hake Spawning Biomass, Location
11.	Chinook Escapements, Chinook Smolt Production, Location
12.	Chinook Smolt Production, Hake Spawning Biomass, Location
13.	Chinook Escapement, Chinook Smolt Production, Hake Spawning Biomass, Location
14.	Herring Spawning Biomass, Chinook Smolt Production, Hake Spawning Biomass, Location
15.	Chinook Escapements, Chinook Smolt Production, Herring Spawning Biomass, Location
16.	Herring Spawning Biomass, Hake Spawning Biomass, Chinook Escapements, Location
17.	Harbor Seal Abundance, Location
18.	Harbor Seal Abundance, Herring Spawning Biomass, Location
19.	Harbor Seal Abundance, Chinook Escapements, Location
20.	Harbor Seal Abundance, Chinook Smolt Production, Location
21.	Harbor seal Abundance, Hake Spawning biomass, Location
22.	Harbor Seal Abundance, Herring biomass, Chinook Escapements, Location
23.	Harbor Seal Abundance, Herring Spawning Biomass, Hake Spawning Biomass, Location
24.	Harbor Seal Abundance, Herring Spawning Biomass, Chinook Smolt Production, Location

25. Harbor Seal Abundance, Chinook Escapements, Hake Spawning Biomass, Location
 26. Harbor Seal Abundance, Chinook Smolt Production, Hake Spawning Biomass, Location
-
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For Review Only

Table S7: Top ten ocean condition models with the most support (lowest AIC_C) with a physiological delay applied.

Physiological Delay Top 10 Models (ocean condition)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
23. Upwelling (Summer), NPGO, Upwelling (Spring), Location	742.75	0
35. SST (Summer), Upwelling (Summer), Columbia Discharge (High), Location	743.39	0.63
33. Columbia Discharge (High), Upwelling (Summer), Location	744.12	1.36
19. Upwelling (Summer), Location	744.3	1.55
34. SST (Summer), Upwelling (Summer), Location	744.7	1.95
21. Upwelling (Summer), NPGO, Location	745.25	2.5
22. Upwelling (Summer), MEI, Location	745.55	2.8
20. Upwelling (Summer), PDO, Location	746.11	3.36
26. Columbia Discharge (High), NPGO, Location	754.16	11.41
30. Columbia Discharge High, NPGO, Upwelling (Spring), Location	754.71	11.96

Table S8: Top ten ocean condition models with the most support (lowest AIC_C) with a 1-year ecological delay applied.

1-Year Ecological Delay Top 10 Models (ocean condition)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
15. SST (Summer), Upwelling (Spring), Location	734.84	0
16. SST (Summer), PDO, Upwelling (Spring), Location	736.55	1.7
18. SST (Summer), MEI, Upwelling (Spring), Location	736.65	1.81
17. SST (Summer), NPGO, Upwelling (Spring), Location	736.8	1.95
14. SST (Summer), MEI, Location	738.91	4.07
11. SST (Summer), Location	740.21	5.37
32. Columbia Discharge (High), SST (Summer), Location	741.3	6.46
12. SST (Summer), PDO, Location	741.34	6.49
34. SST (Summer), Upwelling (Summer), Location	741.99	7.15
13. SST (Summer), NPGO, Location	742.04	7.2

Table S9: Top ten ocean condition models with the most support (lowest AIC_C) with a 2-year ecological delay applied.

2-Year Ecological Delay Top 10 Models (ocean condition)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
24. Columbia Discharge (High), Location	742.09	0
33. Columbia Discharge (High), Upwelling (Summer), Location	742.83	0.74
26. Columbia Discharge (High), NPGO, Location	743.06	0.97
25. Columbia Discharge (High), PDO, Location	743.54	1.45
28. Upwelling (Spring), Location	743.86	1.77
27. Columbia Discharge (High), MEI, Location	744.04	1.95
32. Columbia Discharge (High), SST (Summer), Location	744.07	1.98
35. SST (Summer), Upwelling (Summer), Columbia Discharge (High), Location	744.48	2.38
29. Columbia Discharge (High), PDO, Upwelling (Spring), Location	744.56	2.47
30. Columbia Discharge High, NPGO, Upwelling (Spring), Location	745.06	2.97

Table S10: Top ten prey availability models with the most support (lowest AIC_C) with a physiological delay applied.

Physiological Delay Top 10 Models (Prey Availability)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
14. Herring Spawning Biomass, Chinook Smolt Production, Hake Spawning Biomass, Location	547.29	0
12. Chinook Smolt Production, Hake Spawning Biomass, Location	547.58	0.29
26. Harbor Seal Abundance, Chinook Smolt Production, Hake Spawning Biomass, Location	549.48	2.2
13. Chinook Escapement, Chinook Smolt Production, Hake Spawning Biomass, Location	549.5	2.21
23. Harbor Seal Abundance, Herring Spawning Biomass, Hake Spawning Biomass, Location	549.54	2.25
6. Hake Spawning Biomass, Location	549.55	2.27
21. Harbor seal Abundance, Hake Spawning Biomass, Location	551.18	3.89
10. Chinook Escapements, Hake Spawning Biomass, Location	551.46	4.18
5. Chinook Smolts Production, Location	552.72	5.43
16. Herring Spawning Biomass, Hake Spawning Biomass, Chinook Escapements, Location	552.97	5.69

Table S11: Top ten prey availability models with the most support (lowest AIC_C) with a 1-year ecological applied.

1-Year Ecological Top 10 Models (Prey Availability)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
13. Chinook Escapement, Chinook Smolt Production, Hake Spawning Biomass, Location	554.76	0
12. Chinook Smolt Production, Hake Spawning Biomass, Location	555.28	0.53
11. Chinook Escapements, Chinook Smolt Production, Location	555.56	0.8
14. Herring Spawning Biomass, Chinook Smolt Production, Hake Spawning Biomass, Location	555.91	1.15
26. Harbor Seal Abundance, Chinook Smolt Production, Hake Spawning Biomass, Location	556.78	2.03
5. Chinook Smolts Production, Location	557.22	2.47
15. Chinook Escapements, Chinook Smolt Production, Herring Spawning Biomass, Location	557.5	2.74
20. Harbor Seal Abundance, Chinook Smolt Production, Location	559.09	4.33
9. Herring Spawning Biomass, Chinook Smolt Production, Location	559.22	4.46
24. Harbor Seal Abundance, Herring Spawning Biomass, Chinook Smolt Production, Location	560.99	6.23

Table S12: Top ten prey availability models with the most support (lowest AIC_C) with a 2-year ecological delay applied.**2-Year Ecological Top 10 Models (Prey Availability)**

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
11. Chinook Escapements, Chinook Smolt Production, Location	480.69	0
10. Chinook Escapements, Hake Spawning Biomass, Location	481.41	0.72
7. Herring Spawning Biomass, Chinook Escapements, Location	484.2	3.51
4. Chinook Escapements, Location	484.9	4.21
12. Chinook Smolt Production, Hake Spawning Biomass, Location	485.17	4.48
5. Chinook Smolts Production, Location	486.5	5.81
6. Hake Spawning Biomass, Location	486.56	5.87
19. Harbor Seal Abundance, Chinook Escapements, Location	486.74	6.05
9. Herring Spawning Biomass, Chinook Smolt Production, Location	487.91	7.22
1. Null	488.12	7.43

Table S13: Mean standard precision for amino acids calculated as the average standard deviation of standard triplicate injections.

Amino Acid	Mean Precision
Phenylalanine	0.34
Glutamic Acid	0.56
Alanine	0.46
Proline	0.48
Valine	0.38
Aspartic Acid	0.83
Norleucine	0.40

For Review Only

Table S14: Pearson correlation coefficients for harbor seal trophic position calculated from five trophic amino acids.

Trophic Amino Acid	Glutamic acid (Glu)	Alanine (Ala)	Aspartic Acid (Asp)	Proline (Pro)	Valine (Val)
Glutamic acid (Glu)	-				
Alanine (Ala)	0.79	-			
Aspartic Acid (Asp)	0.25	0.29	-		
Proline (Pro)	0.46	0.61	0.17	-	
Valine (Val)	0.58	0.61	0.18	0.39	-

For Review Only

Table S15: Covariates included in the best models using standard linear models and only glutamic acid to calculate trophic position. Supported models is the number of models with delta AIC < 2.

Model	Covariates	Supported Models	Comparison to hierarchical models
<i>Ocean Condition Models</i>			
Physiological Delay	Summer upwelling, Columbia River discharge	14	Summer upwelling was included in best model and 6 others
1-year ecological delay	Sea surface temperature, spring upwelling	3	Sea surface temperature was included in all supported models
2-year ecological delay	Summer upwelling, MEI	6	Columbia River discharge was included in one supported glutamic acid only model
<i>Food Web Model</i>			
Physiological Delay	Location	2	Best hierarchical model (herring spawning biomass) was included in one supported glutamic acid only models
1-year ecological delay	Chinook smolts	3	Hake spawning biomass was not included in the supported models
2-year ecological delay	Location	6	Chinook smolt production was included in 2 supported models

Table S16: Data summary showing mean trophic position calculated from glutamic acid (trophic) and phenylalanine (source), number of samples (n), and standard deviation (sd) for each year. Standard deviation of trophic position was calculated using the standard deviations for TEFs and β (Appendix S1:Table S2) and the analytical error for glutamic acid and phenylalanine (Appendix S1:Table S13) following the methods of Blum et al. 2013.

Year	mean	SD	n
1928	4.3	0.2	3
1937	4.0	0.3	1
1942	4.4	0.1	9
1959	4.9	0.4	1
1969	4.5	0.1	9
1970	4.6	0.2	4
1971	4.5	0.3	2
1972	5.0	0.2	6
1975	4.1	0.3	1
1976	4.0	0.2	3
1977	4.7	0.1	14
1978	4.8	0.2	4
1979	4.2	0.1	5
1980	4.6	0.3	2
1981	4.7	0.2	4
1982	4.5	0.1	7
1983	4.2	0.2	3
1986	4.5	0.4	1
1987	4.6	0.1	8
1988	4.8	0.4	1

1989	4.5	0.3	2
1991	4.8	0.2	4
1992	4.7	0.2	5
1994	4.5	0.4	1
1996	4.3	0.3	1
1998	4.8	0.3	3
1999	4.1	0.3	1
2004	4.4	0.4	1
2006	4.0	0.2	2
2007	4.6	0.2	4
2008	4.7	0.3	2
2011	4.1	0.3	1
2012	4.5	0.4	1
2013	4.5	0.2	6
2014	4.0	0.3	1

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1 **Title:** Delayed trophic response of a marine predator to ocean condition and prey availability
2 during the past century

3 **Running Title:** Delayed predator trophic response

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

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

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

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

10

11 **Open Research Statement:** (3) Harbor seal stable isotope data are provided as private-for-peer
12 review on a repository [available here](#). Upon publication data will become public with a
13 permanent doi hosted through Dryad. (2) Some data are already published and publicly and the
14 sources are described in the supplementary material.

15

16 **Abstract**

17 Understanding the response of predators to ecological change at multiple temporal scales
18 can elucidate critical predator-prey dynamics that would otherwise go unrecognized. We
19 performed compound-specific nitrogen stable isotope analysis (CSIA) of amino acids on 153
20 harbor seal museum skull specimens to determine how trophic position of this marine predator
21 has responded to ecosystem change over the past century. The relationships between harbor seal
22 trophic position, ocean condition, and prey abundance, were analyzed using hierarchical
23 modelling of a multi-amino acid framework and applying 1-, 2-, and 3- year temporal lags. We
24 identified delayed responses of harbor seal trophic position to both physical ocean conditions
25 (upwelling, sea surface temperature, freshwater discharge) and prey availability (Pacific hake,
26 Pacific herring and Chinook salmon). However, the magnitude and direction of the trophic
27 position response to ecological changes depended on the temporal delay. For example, harbor
28 seal trophic position was negatively associated with summer upwelling, but had a 1- year
29 delayed response to summer sea surface temperature, indicating some predator responses to to
30 climateecosystem change extremes are not immediately observable. These results highlight the
31 importance of considering dynamic responses of predators to their environment to their
32 environment as multiple ecological factors are often changing simultaneously and predator
33 response oecurs at multiple temporal sealescan take years to propagate up the food.

34 **Keywords**

35 *Stable isotope, trophic position, harbor seal, amino acid, Washington, Salish Sea, Chinook*
36 *salmon, Phoca vitulina, Pacific herring, Columbia River, sea surface temperature*

37 **Introduction**

38 The regulation of food web structure by resources (bottom-up control) and the presence
39 of top predators (top-down control) is fundamental for understanding food web responses to
40 environmental, ecological, and anthropogenic change (Carpenter et al. 1985, Hunter and Price
41 1992, Estes et al. 1998). Ecological communities are continuously experiencing both biotic and
42 abiotic disturbances (Paine et al. 1998) and the ability of food webs to dynamically respond to
43 these changes is crucial for ecosystem stability (Ghedini et al. 2015). In marine food webs,
44 physical ocean conditions can impact primary production and ultimately constrain energy
45 availability and thus biomass at higher trophic levels (Ware and Thomson 2005, Chassot et al.
46 2010, Moore et al. 2018). Large-scale changes in nutrient availability (Rykaczewski and Dunne
47 2010), primary productivity (Chassot et al. 2010), and top predator abundance over the past
48 century (Magera et al. 2013) means many food webs are experiencing shifts in multiple
49 mechanisms of regulation in tandem. However, impacts of ecological change do not immediately
50 propagate through the complete food web (Duguid et al. 2019, Smith et al. 2017) Similarly, the
51 removal of top predators from an ecosystem as a result of human activities such as fishing can
52 decrease predation pressure and alter abundance in both adjacent and non-adjacent trophic levels
53 (Heithaus et al. 2008, Steneck 2012). However, large-scale changes in nutrient availability
54 (Rykaczewski and Dunne 2010), primary productivity (Chassot et al. 2010), and top predator
55 abundance over the past century (Magera et al. 2013) means many food webs are experiencing
56 shifts in multiple mechanisms of regulation in tandem, making it challenging to identify
57 dominant drivers structuring ecosystems food webs over the long term.

58 Marine predators respond to multiple types of bottom-up drivers (i.e., ocean condition,
59 prey availability) and the different temporal scales over which they respond is crucial for

60 understanding community stability. Delayed predator responses to environmental perturbations
61 are prevalent in marine system, as impacts do not immediately propagate through the complete
62 food web (Duguid et al. 2019, Smith et al. 2017). Given communities can shift from bottom-up
63 to top-down control, particularly in response to changing climate conditions (Kratina et al. 2012),
64 delayed predator responses to climate conditions has implications for abundance and mortality
65 rates of prey.

66 Historical marine predator data that span multiple environmental, ecological, and
67 anthropogenic contexts are useful for identifying time scales over which predators respond to
68 ecosystem drivers. Compound-specific stable isotope analysis (CSIA) of amino acid nitrogen can
69 serve as a tracer of historical predator response to ecological and environmental change by
70 deriving retrospective trophic position estimates from museum specimens (McMahon et al. 2019,
71 Feddern et al. 2021). Source amino acids (i.e., phenylalanine, lysine, methionine) exhibit
72 minimal trophic discrimination (the difference in $^{15}\text{N}/^{14}\text{N}$ between trophic and source amino
73 acids in consumers from a trophic transfer) and thus are a proxy for the nitrogen stable isotope
74 signature of primary producers at the base of the food web. In contrast, trophic amino acids (i.e.,
75 alanine, glutamic acid, valine, proline) demonstrate trophic enrichment (McMahon and
76 McCarthy 2016) that varies for individual amino acids. Combined, this approach allows for
77 reconstruction of historic trophic position estimates under changing environmental conditions
78 when characterizing the isotopic baseline of past ecosystems may not be possible (McMahon et
79 al. 2019). Thus, CSIA is well suited to identify long-term drivers of food web dynamics when
80 analyzed with historic indices of ocean condition and prey availability.

81 Reconstructing time series of predator trophic position requires careful consideration of
82 physiological and ecological parameters that contribute to stable isotope values. First, taxa

83 exhibit different trophic enrichment factors based on excretion pathways, diet type (omnivory,
84 herbivory, carnivory), and growth (Nielsen et al. 2015). Second, the nitrogen production pathway
85 of vascular (i.e., seagrasses) versus nonvascular (i.e., marine diatoms) primary producers impart
86 distinct stable isotope fractionation factors (referred to as β) as inorganic sources of nitrogen are
87 converted to tissues (Ramirez et al. 2021). Assumptions about the relative contributions of
88 vascular versus nonvascular plants can therefore impact trophic position estimates (Choi et al.
89 2017). Finally, there is a delay between the time a prey source is consumed and when that prey
90 source has been ~~fully~~ assimilated by (and thus measurable in) ~~the consumer~~ tissues
91 (Martinez del Rio and Carleton 2012), ~~referred to as the ‘turnover time’.~~ Turnover times Rate of
92 assimilation must be considered when comparing trophic position data to ocean condition and
93 prey availability covariates, as the consumer response to an ecological change will not be
94 immediately observable in consumer tissues.

95 Nearshore coastal ecosystems provide a model system to assess long-term changes of
96 food web drivers using archival museum specimens of a marine predator by applying CSIA.
97 Food webs of coastal Washington and the Salish Sea have experienced dramatic restructuring
98 over the past century due to declines and subsequent recoveries of marine predators (Jeffries et
99 al. 2003Jefferson et al. 2021, Ohlberger et al. 2019). Decades of state-financed population control
100 programs resulted in harbor seals (*Phoca vitulina*) reaching a historic low in the 1970's, with an
101 estimated abundance of approximately 1,000 individuals (Jeffries et al. 2003Jefferson et al.
102 2021). Following the cessation of bounties in 1960 and the passage of the Marine Mammal
103 Protection Act in 1972, ~~top predator abundance increased dramatically. Benefitting from a~~
104 ~~relatively short life history, generalist diet, and legislation restricting mortality,~~ harbor seal
105 populations increased 10-fold between 1970 and 2003 (Jeffries et al. 2003Jefferson et al. 2021)

106 due to legislation restricting mortality. The increase in abundance of this top predator has been
107 implicated in the declines in economically and ecologically important prey species in the region
108 (Chasco et al. 2017, Nelson et al. 2019), specifically, Chinook salmon (*Oncorhynchus*
109 *tshawytscha*). (*Oncorhynchus tshawytscha*). Chinook salmon are listed as endangered in the
110 region (WDFW 2017) and are an important prey species for the endangered southern resident
111 orca (Marshall et al. 2015). Simultaneously, the region has also experienced changes in nutrients
112 (Mohamedali et al. 2011), climate regimes (Corwith and Wheeler 2002, Mantua and Hare 2002)
113 and abundances of other important prey species such as Pacific herring (*Clupea pallasii*, Siple
114 and Francis 2016).

115 Harbor seals are a useful predator to trace ecosystem drivers in Washington. Harbor seals
116 are generalist, opportunistic, predators known to forage on species with recent abundance
117 changes, specifically Pacific salmon (*Oncorhynchus spp.*) and Pacific herring (*Clupea pallasii*).
118 In addition, Pacific hake (*Merluccius productus*) make up a large portion of their diet along with
119 other forage fish and gadid species (Lance et al. 2012). Harbor seals have high site fidelity and
120 home ranges up to 100 km (Hardee 2008). Coastal Washington and Washington inland waters
121 (Salish Sea) are comprised of genetically distinct harbor seal stocks (Jefferson et al. 2021).

122 Here we examined a century of harbor seal trophic position data in coastal Washington
123 and the Salish Sea. The objective of this work is to identify the time scales at which physical
124 ocean conditions and prey availability exert bottom-up control on marine food webs as indicated
125 by predator trophic ecologyposition. We assumed a correlation between trophic position and prey
126 species abundance is the result of increased or decreased consumption of that species. Similarly,
127 we assume a correlation between trophic position and ocean condition indicates an
128 environmentally induced change in food web structure the alters harbor seal prey availability.

129 ~~Additionally, In conducting this work, we~~ established a multi-amino acid framework for
130 measuring trophic position that improves ~~precision and~~ ecological accuracy by applying a
131 species-specific trophic discrimination factor (McMahon et al. 2019, [Nielsen et al. 2015](#)). We
132 also included a system specific β rather than a universal value, and applied temporal lags to
133 account for both physiological and ecological delays in consumer response.

134 **Methods**

135 *Sample collection and analysis*

136 Samples were obtained using methods described in Feddern et al. (2021). Briefly, harbor
137 seal bone was obtained from four museum institutions (the Burke Museum, the Slater Museum,
138 the Royal British Columbia Museum, and the Smithsonian Institute) and the National Marine
139 Mammal Laboratory (NOAA) (Appendix S2: Table S1). [A total of 153 specimens were sampled](#)
140 [with field collection dates ranging 1928-2014 \(Figure 1\)](#). Specimens were treated by maceration
141 in warm water and stored in acid free boxes. [Only adult specimens were](#)
142 [sampled](#) and [prioritized long-term temporal coverage](#). Specimens were divided into two main
143 regions [based on genetic stock delineations and expected foraging ranges](#): coastal Washington
144 and the Salish Sea (which included 18 specimens from British Columbia). [Specimens that](#)
145 [provided long term temporal coverage and included](#) [Specimens with](#) sex, length, [and](#) age, [and](#)
146 [month of collection](#) -data were [also](#) prioritized but this information was not available for all
147 sampled specimens. [Museum specimens were primarily salvaged from beaches. While cause of](#)
148 [death was usually unknown, most adult strandings in the region are the result of trauma \(i.e.,](#)
149 [fishing entanglements, boat strikes\) or infectious disease \(Ashley et al. 2020\).](#) [A total of 153](#)
150 [specimens were sampled with field collection dates ranging 1928-2014 \(Figure 1\)](#).

151 *Trophic position determination*

152 Bone collagen was decalcified, acid hydrolyzed, derivatized, and analyzed for nitrogen
153 CSIA ($\delta^{15}\text{N}$) of 12 individual amino acids. Collagen samples were measured in triplicate with a
154 laboratory standard containing a 12 amino acid mixture of known stable isotope value and a
155 linear drift correction was applied. Full analytical details are described in Appendix S1: Section
156 S1. Previous controlled feeding studies have determined the trophic enrichment factor (TEF) for
157 harbor seals is substantially lower than the conventional literature value of 7.6‰ (Germain et al.
158 2013) and thus applying a harbor seal-specific TEF is more accurate (McMahon [et al.](#) and
159 [McCarthy](#) 2016⁵). Therefore, trophic position was calculated using a harbor seal-specific [TEF](#),
160 described by McMahon et al. (2015) as-a "multi-TEF" approach, using the following equation:

161 1. *Trophic Position* = $\left(\frac{\delta^{15}\text{N}_{(i-o)} - \overline{\text{TEF}}_{(i-o), j} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 2,$

162 where $\delta^{15}\text{N}_i$ is the measured stable isotope value of a trophic amino acid i in a sample and $\delta^{15}\text{N}_o$
163 is the stable isotope value of a source amino acid o in a sample. $\delta^{15}\text{N}_{(i-o)}$ represents the total
164 trophic enrichment that has occurred throughout the food web measurable from predator tissues.
165 $\text{TEF}_{(i-o),j}$ is the trophic enrichment factor between trophic amino acid i and source amino acid o of
166 a specific consumer j (in this study, harbor seals) which occurs when consumer j assimilates
167 prey. $\beta_{(i-o), N}$ is the difference in enrichment between a specific trophic amino acid i and source
168 amino acid o for non-vascular primary producers N that occurs when primary producers
169 assimilate inorganic nitrogen (Nielsen et al. 2015; Appendix S1: Table S2). $\overline{\text{TEF}}_{(i-o)}$ represents
170 the mean trophic enrichment that occurs at other trophic levels in the food web, and is calculated
171 from the mean difference between trophic amino acid i and source amino acid o across all
172 consumers described in Nielsen et al. (2015).

173 β differs substantially between vascular and nonvascular primary producers (Ramirez et
174 al. 2021; Appendix S1: Table S2). In food webs that assimilate organic matter from both vascular

175 and nonvascular plants, including many nearshore food webs, β will be intermediate. In addition
176 to testing a value that represents nonvascular primary producers exclusively ($\beta_{(i-o), N}$), we also
177 applied a two-source mixing model using harbor seal carbon stable isotope data similar to Choi
178 et al. (2017). This generates a β that is weighted ($\beta_{(i-o), NV}$) based on the contributions of both
179 vascular and nonvascular plants specific to the Washington nearshore ecosystem by first
180 calculating the percent contribution of vascular plants to the food web:

181
$$2. \%V = \frac{\delta^{13}C_H - \delta^{13}C_N}{\delta^{13}C_V - \delta^{13}C_N} / 100,$$

182 where $\delta^{13}C_H$ is the mean observed $\delta^{13}C$ value for Washington harbor seals; $\delta^{13}C_V$ is the carbon
183 stable isotope end member for vascular plants, v (-9.5 ‰, derived from seagrasses *Zostera spp.*);
184 and $\delta^{13}C_N$ is the carbon stable isotope end member for nonvascular plants, n (-19.5 ‰, derived
185 from phytoplankton). Carbon end members were specific to the Washington nearshore
186 ecosystems (Howe and Simenstad 2015). $\%V$ is the percent contribution of vascular plants to the
187 food web in which harbor seals forage. This assumes the trophic enrichment of ^{13}C is generally
188 negligible (0–1‰, Deniro and Epstein 1978). $\beta_{(i-o), NV}$ was then derived by:

189
$$3. \beta_{(i-o), NV} = (\beta_{(i-o), V} * \%V) + (\beta_{(i-o), N} * (1 - \%V)),$$

190 where $\beta_{(i-o), N}$ is the enrichment between an individual trophic amino acid i and source amino acid
191 o for aquatic phytoplankton and $\beta_{(i-o), V}$ represents the trophic enrichment of seagrass which are
192 vascular plants (Appendix S1: Table S2).

193 *Quantifying bottom-up drivers of foraging-trophic position*

194 To identify the most important explanatory variables of ocean condition and prey
195 availability on predator trophic position, we fit two sets of candidate models using a multi-amino
196 acid (glutamic acid, aspartic acid, alanine, proline, valine) hierarchical model. We selected 12
197 putative explanatory variables based on the length of the time series and divided them *a priori*

198 into our two categories of interest, ocean condition and prey availability, representing our
199 expected primary forcing mechanisms (Appendix S1: Tables S3 & S4). We fit the candidate
200 models to trophic position and covariate data, and the candidate model set included a null and
201 location-only model (Appendix S1: Tables S54 & S65). Location (Salish Sea or coastal
202 Washington) was included as a factor in all candidate models except the null model. Due to the
203 correlation between the multivariate El Niño Southern Oscillation index and the Pacific Decadal
204 Oscillation only one of these covariates were included in a single model. All timeseries were
205 standardized around a mean of 0 and standard deviation of 1. To avoid collinearity, no more than
206 four covariates (including location) were included in an individual model.

207 Nielsen et al. (2015) determined that the use of multiple amino acids improves estimates
208 of trophic position. Therefore, we used multiple trophic amino acids i (alanine, glutamic acid,
209 valine and proline) and one source amino acid o (phenylalanine) to calculate trophic position.
210 We selected amino acids based on: their prevalence in previous studies to derive parameters for
211 equation 2; tissue turnover time relative to the source amino acid, phenylalanine; and their
212 concentrations in bone collagen. The hierarchical linear model took the following structure:

$$213 \quad 4. \quad y_t = \alpha_k + \beta X_{t-d} + \epsilon,$$

214 where y represents harbor seal trophic position from year t and k represents four different trophic
215 amino acids (factors) used to calculate trophic position included as a random effects. X is a
216 matrix of continuous bottom-up drivers in year t . β is a vector of predicted effects (coefficients)
217 of bottom-up drivers included in the model (Appendix S1: Tables S32 & S43) on harbor seal
218 trophic position, and α is the random effect representing predicted trophic position when all
219 included bottom-up drivers are at an average value (represented by 0) in the coastal region of
220 Washington for each trophic amino acid k . The variable d is the temporal lag between a change

221 in bottom-up drivers and when that change is reflected in harbor seal bone collagen. This lag can
222 be due to both physiological (tissue turnoverisotope incorporation rate) or ecological effects (rate
223 of propagation through the food web). Time (year, Appendix S1: Section S4, Fig. S6), sex, size
224 (Appendix S1: Section S3, Fig. S4 & S5), and seasonalitymonth of collection (month, Appendix
225 S1: Fig. S1), were also considered as predictors of trophic position but no significant associations
226 were identified and thus these parameters were not included in the hierarchical modeling
227 (Appendix S1: Section S3). The best performing models for both of these approaches were
228 selected using Akaike's Information Criterion (Akaike 1973) with a correction for small sample
229 size (AIC_c). Inclusion of predictors in the model with the most support is indicative of ecological
230 parameters that alter harbor seal foraging ecology or food web dynamics. Additionally,
231 magnitude and sign of the coefficients for included predictors can be interpreted as the degree of
232 trophic position change induced by consuming different species, life stages of species, or groups
233 of species, caused by a given predictor.

234 A change in dietary stable isotope composition of bone collagen is assumed to be
235 reflected diet over the past 1–2 years of the individual's life in bone collagen after approximately
236 1 year (Hobson and Clark 1992, Newsome et al. 2006, Riofrío-Lazo and Auriolles-Gamboa
237 2013). This means the stable isotope composition of bone collagen is time averaged over
238 approximately the last year of the harbor seal's life. Therefore, the last month of a harbor seal's
239 life should have minimal influence on the stable isotope composition of bone collagen and as a
240 result we assume cause of death does not impact trophic position (Appendix S1: Text S7). A 1-
241 year lag (d) was applied to all harbor seal trophic position estimates to account for the
242 physiological delay from tissue turnoverstable isotope incorporation ratetime of bone collagen,
243 where the collagen in a harbor seal collected in year t reflects what the individual ate in the

244 previous year, $t-1$. Delayed harbor seal foraging response to ecosystem dynamics was also tested
245 by applying additional 2-year and 3-year lags to trophic position data; these models represent a
246 1-year and 2-year ecological delay in addition to the 1-year physiological delay ~~for tissue~~
247 ~~turnover time~~. For example, the association between harbor seal trophic position and
248 environmental conditions 2 years before the collection year would indicate that there was a 1-
249 year delay between when the environmental condition changed and when the resultant changes
250 propagated through the food web, after accounting ~~for the 1-year tissue turnover time for the~~
251 ~~isotopes to be incorporated into bone collagen~~. To ~~check the assumption of no confirm there was~~
252 ~~no~~ collinearity in predictors in the models with most support ($\Delta AIC_c < 2$), we consulted matrix
253 scatterplots ~~using the car package (Fox and Weisberg 2019) in R (R Development Core Team,~~
254 ~~2020)~~ and calculated variance inflation factors. ~~All analyses were conducted in R (R~~
255 ~~Development Core Team, 2020).~~

256 Results

257 Drivers of predator trophic position

258 Among the physical variables tested, summer upwelling, sea surface temperature and
259 Columbia River discharge during high flow months all impacted harbor seal trophic position but
260 on different temporal scales. There was model selection uncertainty at all three temporal lags
261 (Appendix S1: Table S7-S9) but covariates and their coefficient estimates were consistent across
262 the most supported models ($\Delta AIC_c < 2$) (Fig. 2). There were five physiological delay models
263 (Fig. 2c) with substantial support ($\Delta AIC_c < 2$) all of which included location (Salish Sea versus
264 coastal Washington) as a factor with a coefficient of -0.29 (95% CI [-0.40, -0.19]) and a negative
265 coefficient for summer upwelling (-0.04[-0.07, -0.02]). There were four models with substantial
266 support for the 1-year ecological delay (Fig. 2b) all of which included a negative coefficient for

267 summer sea surface temperature (-0.2 [-0.28, -0.11]) and a positive coefficient for spring
268 upwelling (0.03 [0.0, 0.05]). Columbia River discharge during high flow months was included in
269 the five 2-year ecological delay models with the most support (Fig 2a) and had the highest
270 impact on harbor seal trophic position with a coefficient of 0.4 [0.22, 0.57]. All other coefficients
271 did not differ substantially from 0 (Figure 2). Summer upwelling exhibited an immediate impact
272 on harbor seal trophic position that resulted in overall lower trophic position during the same
273 year (after accounting for tissue turnover; Fig. 2c). Summer sea surface temperature showed a
274 delayed impact, where harbor seals foraged lower in the food web the year following summers
275 with higher-than-average sea surface temperatures (-0.2 [-0.28, -0.11], Fig. 2). The coefficients
276 for upwelling (Fig. 2a-c) in all models were small compared to sea surface temperature (Fig. 2b)
277 and Columbia River discharge (Fig. 2a). Location had an ecologically significant coefficient of ~
278 -0.3 [-0.40, -0.19]) which was similar across all supported models at all three lags, demonstrating
279 harbor seals in the Salish Sea feed lower in the food web than their coastal Washington
280 counterparts.

281 Location, Chinook salmon abundance, and hake and herring spawning biomass were the
282 biological variables strongly associated with harbor seal trophic position. Similar to the ocean
283 condition analysis, there was model selection uncertainty but covariates and their coefficients
284 were similar across supported models (Appendix S1: Tables S10-S12, Figure 3). Chinook smolt
285 production (0.08 [0.02, 0.16]), and hake (0.13 [0.05, 0.21]) and herring spawning biomass (-0.06
286 [-0.14, 0.02]) were correlated with harbor seal trophic position in the two physiological delay
287 models with substantial support ($\Delta AIC_c < 2$) but the effect of herring spawning biomass on
288 harbor seal trophic position was not significantly different from 0 (Fig. 2f). Hake spawning
289 biomass and Chinook salmon escapement were included in three out of four 1-year ecological

290 delay models with substantial support (Fig. 2f) and both were included in the best model.
291 Chinook salmon smolt production (combined index of hatchery releases and wild production of
292 Chinook salmon) was included in all four models with substantial support at the same lag (Fig.
293 2f). Both Chinook salmon smolt production (0.12 [0.06, 0.20]) and hake spawning biomass (0.06
294 [-0.0, 0.14]) in the 1-year ecological delay model were positively correlated with harbor seal
295 trophic position (Fig. 2f). Thus, harbor seals fed higher in the food web one year after hake
296 spawning biomass and Chinook salmon smolt production was high (Fig. 3). In contrast, Chinook
297 escapement counts were negatively correlated at the same time lag (-0.07 [-0.14,0.0]). Covariates
298 and the magnitude and direction of their coefficients were similar in the 2-year ecological delay
299 model (Fig. 2d) compared to the 1-year ecological delay model (Fig. 2e) but only three models
300 had substantial support (Fig. 2d).

301 *Parameterization of the trophic position equation*

302 Inclusion of multiple trophic enrichment factors (Appendix S1: Section S2), multiple
303 trophic amino acids, and a system-specific β in the trophic position equation improved trophic
304 position estimates (Appendix S1: Figures S2 & S3) compared to the more commonly applied
305 single trophic enrichment factor, nonvascular β parameter, and using only the canonical trophic
306 amino acid, glutamic acid (Appendix S1: Section S6). Harbor seals are known to consume both
307 adult and juvenile hake, Pacific herring, and Pacific salmon. Based on known foraging patterns
308 thus a trophic position of 3.5 – 5 would be considered ecologically realistic for harbor seals
309 previous research (Germain et al. 2012), based on known foraging strategies and previous
310 research (Germain et al. 2012). Seventy-six % of observations were considered ecologically
311 realistic when applying a system-specific $\beta_{(i-o),NV}$, harbor seal-specific trophic enrichment factor,
312 and including the amino acids glutamic acid, valine, alanine, aspartic acid, and proline

313 (Appendix S1: Figures S3.2). This parameterization offered a substantial improvement over other
314 parameterizations of the trophic position equation, which ranged from 15% to 80% of
315 observations being ecologically realistic, and was more parsimonious than similarly performing
316 equations (Appendix S1: Figures S2.4). However, aspartic acid was more variable than other
317 trophic amino acids in all parameterizations and thus was omitted from the hierarchical
318 modelling analysis (Appendix S1: Section S6).

319 Discussion

320 Harbor seals ~~occupy differently in~~ in trophic positions depending on ecological
321 conditions and exhibit delayed trophic responses to ecological perturbations. We found that both
322 ocean conditions and prey availability impact predator trophic position, however, the magnitude
323 and time scale at which predators exhibited trophic position responses to these bottom-up drivers
324 varied. In fact, some of the most influential drivers of predator trophic position (i.e., freshwater
325 discharge) had a multi-year delay in predator trophic position. Some effects of ecosystem change
326 on nearshore marine predators will not be immediately observable based on our results and
327 others (Smith et al. 2017). Furthermore, changes in ocean conditions can alter top-down pressure
328 on the ecological community in subsequent years, as generalist top predators shift their trophic
329 ecology in response to their environment. ~~- Our data did not include observations of recent~~
330 ~~extreme marine heatwave events but our results show delayed, linear, predator responses to~~
331 ~~environmental shifts. Anticipating delayed ecological responses to environmental conditions is~~
332 ~~important given environmental perturbations are becoming more common and severe in the~~
333 ~~northeast Pacific Ocean (Suryan et al. 2021) and ecological impacts will not always be~~
334 ~~immediately observable. Our results suggest that following years with extreme ocean conditions,~~

335 ~~ecological responses will continue to manifest for multiple years into the future as impacts~~
336 ~~propagate through the food web~~

337 *Delayed trophic position response to environmental conditions*

338 Multiple studies have shown that ocean conditions such as sea surface temperature,
339 upwelling, and freshwater discharge impact abundance and recruitment of nearshore fishes in
340 coastal Washington (Reum et al. 2011, Greene et al. 2015, Duguid et al. 2019). Our results show
341 trophic position of top predators (harbor seals) can also have delayed responses also respond to
342 bottom-up forcing of ocean conditions with up to a 2-year ecological delay. Abiotic factors in the
343 region alter resources, primary productivity, and prey availability that propagates through the
344 entire coastal Washington food web (Ware and Thomson 2005, Feddern et al. 2021). Reum et al.
345 (2011) found age-0 Pacific herring abundance in Puget Sound is positively correlated with
346 annual upwelling in the Strait of Georgia. This increase in abundance of low trophic level,
347 juvenile, fish could explain the correlation between harbor seal trophic position and upwelling
348 (Figure 2C). In addition, reproductive success of Salish Sea predators (Smith et al. 2017) and fish
349 species (Duguid et al. 2019) have been correlated to sea surface temperature and, like harbor seal
350 trophic position (Figure 2B), the responses to sea surface temperature are delayed by a year. For
351 some species of seabirds in the region, breeding success also responds to ocean conditions but
352 exhibits a temporally lagged response (Duguid et al. 2019). Our results show trophic position of
353 top predators (harbor seals) can also have delayed responses to bottom-up forcing of ocean
354 conditions with up to a 2-year ecological delay. For example, the Columbia River introduces
355 terrestrial derived nutrients associated with increased primary production and fish production.
356 Harbor seals consume a greater proportion of higher trophic level prey sources in years following
357 above average Columbia River discharge. Freshwater discharge introduces terrestrial derived

358 nutrients to nearshore environments and in the case of large river plumes can influence
359 upwelling. In Washington, freshwater derived nutrients have been associated with increases in
360 primary production and fish abundance at multiple trophic levels (Ware and Thomson 2005;
361 Kudela et al. 2008). Based on our results and others, abiotic factors associated with freshwater
362 discharge alters resources that eventually propagate through the food web and can impact
363 predator trophic position. Based on our results and others (Ware and Thomson 2005, Feddern et
364 al. 2021) abiotic factors associated with freshwater discharge alters resources, primary
365 productivity, and prey availability that propagates through the entire coastal Washington food
366 web. The impact of this bottom-up force is observable in top predator trophic position but this
367 response is delayed and not observable for two years.

368 *Delayed trophic position response to prey abundance*

369 Harbor seal trophic position responds to the abundance of multiple prey species and the
370 magnitude and direction of the response depends on both the individual species and temporal
371 delay. Pacific hake and Pacific herring have frequently been documented as common prey
372 sources in Washington harbor seal diet (Thomas et al. 2011, Lance et al. 2012). For some species
373 of hake, trophic level can differ by as much as 0.6 among individuals of different size classes
374 (Iitembu et al. 2012). In years when Pacific hake spawning biomass is high, and the years
375 following high spawning biomass, harbor seal trophic position increases, indicating harbor seals
376 are opportunistically feeding on large, adult-stage hake (Fig. 3d). This agrees with previous
377 harbor seal scat studies in the region, which have shown that Pacific hake are a major component
378 of harbor seal diet but the relative abundance varies between years. In contrast to Pacific hake,
379 harbor seal trophic position exhibited a negative relationship with herring spawning biomass.
380 The relative abundance of adult to juvenile herring in harbor seal diet also varies between years

381 (Lance et al. 2012) and harbor seals are known to preferentially consume juveniles during [the](#)
382 herring spawning season and adult herring during the non-spawning season (Thomas et al. 2011).
383 Our results agree with these findings and indicate a trophic [position](#) shift in response to herring
384 spawning biomass (Fig. 2c), which is likely a result of increased juvenile consumption during the
385 spawning season. Alternatively, this result may be due to covariation with a third variable. For
386 example, upwelling was also correlated to harbor seal trophic position in the physiological delay
387 model and is known to impact herring abundance (Reum et al. 2011).

388 Harbor seals opportunistically consume more low-trophic level [smolts-juvenile salmon](#)
389 when they are abundant which occurs in the two years after high spawner abundance (Fig. 3).
390 Escapement counts represent the number of adult salmon that return to freshwater to spawn after
391 they have been both fished and predated on and serve as a strong predictor of out migrating
392 smolts during the next two years. After hatching, fry and parr reside in freshwater for 12-18
393 months before migrating to estuaries. The 1- and 2- year delayed negative response of harbor
394 seal trophic position to Chinook salmon escapements counts agrees with previous studies
395 documenting harbor seal consumption of out-migrating smolts (Fig. 3d, Thomas et al. 2017,
396 Lance et al. 2012). In contrast, a combined index of hatchery Chinook smolt production and wild
397 Chinook smolt production offers the best predictor of adult salmon availability to harbor seals
398 (Fig. 3). The positive relationship between harbor seal trophic position and smolt production
399 indicates harbor seals are consuming a greater proportion of higher trophic level fish in the years
400 following above average smolt production. Chinook salmon spend 1-7 years [in](#) the ocean before
401 returning to freshwater to spawn, and escapement counts only represents the age class of fish that
402 are returning to spawn in a given year. In contrast, smolt production in the current year and
403 during the previous two years provides an index of adult salmon abundance [in the ocean](#) that are

404 available to and predated upon by harbor seals (Fig. 3d). Notably, the salmon abundance
405 estimates in this study were specific to Washington Chinook salmon. It is possible that harbor
406 seal trophic position estimates have stronger associations with metrics of total abundance of all
407 species of Pacific salmon if harbor seals [are not selective of the salmon they species consumed](#) [do not selectively forage on a specific species](#). However, data available for other species in the
408 region did not provide enough temporal overlap with the trophic position data and thus were
409 omitted. Regardless, this analysis indicates both adult and juvenile Chinook salmon contribute to
410 harbor seal trophic ecology and predation on both age classes may be an important component
411 for at sea survival of Washington Chinook salmon.

413 Management of predators that consume threatened, economically important, prey species
414 such as harbor seals requires extensive tradeoffs (Marshall et al 2015). Harbor seals demonstrate
415 large variations in trophic [ecology position](#) in response to location, prey availability, and ocean
416 condition thus, they exert dynamic top-down effects on the community in which they forage. The
417 balance of top-down versus bottom-up effects on food webs in response to resource perturbations
418 is determined by a top predator's ability to exploit subsidies (McCary et al. 2021). [Thus our](#)
419 results also show the response of trophic position (and assumed predation) change is often
420 delayed on the order of 1-2 years in response to ecological conditions. Currently, model
421 estimates of total biomass of Chinook salmon consumed by harbor seals is assumed to be static
422 through time (Chasco et al. 2015). Based on our results and others (Wilson et al. 2014, Lance et
423 al. 2012) this is likely inaccurate as seasonality, spatial location, and individual behavior impact
424 harbor seal predation. This variability in foraging ecology should be carefully considered when
425 assessing tradeoffs of predator management decisions to ensure realized expectations for
426 stakeholders. Spatially distinct management strategies that are reevaluated in the context of

427 changing ecological conditions will likely be important for managing harbor seal prey given their
428 dynamic foraging strategies and trophic responses.

429 *Advances in the application of amino acid based trophic position calculations*

430 CSIA is a powerful tool for reconstructing historical ecological data that requires
431 consideration for system specific dynamics for accurate trophic position estimates. Despite its
432 benefits compared to traditional bulk stable isotope analysis, CSIA is sensitive to the
433 parameterization of [the](#) trophic position equation (McMahon et al. 2019, Germain et al. 2013; [SI](#)
434 [Appendix S1](#): Figures S2 and S3). Application of a multi-TEF approach has led to consistent
435 underestimates of trophic position compared to known feeding ecology (McMahon et al 2019,
436 McMahon [et al. and McCarthy](#) 2016⁶⁵, Germain et al. 2015) despite its more realistic
437 representation of metabolic pathways compared to a single-TEF approach (Appendix S1: Fig. S2
438 & S3). Thus, the utility and reliability of CSIA for trophic position studies for retrospective
439 analyses requires careful consideration of the trophic enrichment factors, tissue turnover, and β
440 applied. Harbor seals are expected to exhibit a trophic position ranging from approximately 3.5
441 to 5 and only 12%-66% of data fell within this range when applying $\beta_{(i-o),N}$ (Appendix S1: Fig.
442 S2). Seagrasses are abundant in coastal Washington and the Salish Sea and there is evidence of
443 food web coupling in these coastal environments (Howe and Simenstad 2015).

444 [Therefore](#)[Therefore](#), vascular primary producers are expected to contribute to these food webs
445 requiring a system specific β value. Variation in vascular plant abundance over time could result
446 in temporal changes to the relative contribution of these primary producers to the food web
447 which would require the application of a time-varying β . We did not find evidence of temporal
448 trends in $\delta^{13}\text{C}$ data in harbor seals (Feddern et al. 2021) which would be expected if seagrass
449 contribution to the food web was time-varying and therefore a temporally static β was

450 appropriate for this study. By applying a system specific β based on expected proportions of
451 primary producer ecophysiology types entering the food web, we significantly improved the
452 realism of our trophic position estimates. We therefore recommend using a multi-trophic
453 enrichment factor approach with taxa specific trophic enrichment factors and system-specific β
454 when there is evidence of vascular plant contributions to the food web.

455 **Conclusions**

456 More research is needed to investigate [the degree to which how](#) top predator trophic
457 position change can serve as an indicator of top-down control on the community, which
458 undoubtedly depends on food web structure of a given system (i.e., degree of omnivory,
459 connectance). Regardless, delayed predator dynamics are not limited to marine or nearshore
460 environments, although the temporal scales for delayed trophic responses for other predators and
461 systems warrants investigation. Anticipating [delayed responses](#) may be equally important for
462 identifying long-term ecological consequences in response to future climate perturbations [_5](#)
463 especially as extreme climate events become frequent and more severe.

464 The regulation of food web structure by resources is foundational for understanding
465 ecosystem response to perturbations. Based on our findings, nearshore marine predators exhibit a
466 trophic position response to ecological change on multiple temporal scales, as different
467 ecological perturbations propagate through the food web at different rates. As such, changes to
468 predator trophic ecology can have consequences throughout the food web that are not
469 immediately realized [especially following environmental perturbations. Impacts of the Another](#)
470 [example of delayed ecological responses to climate extremes is the](#) 2014-2016 marine heatwave
471 in the Gulf of Alaska (the longest lasting event of the past decade) [the impacts of which](#) are still
472 being observed and some ecological responses have persisted for up to 5 years (Suryan et al.

473 2021). Delayed responses of marine predators should be considered when anticipating ecological
474 responses following extreme environmental and ecological events-change as top-down pressure
475 on the community in subsequent years is likely to change as predators shift their trophic ecology
476 in response to their environment.

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637 **Figure Captions**

638 **Figure 1:** Spatial distribution of harbor seal specimens (a) collected in the Salish Sea (yellow)

639 and coastal Washington (blue) with the year of specimen collection and total number of

640 specimens (n) for each year from 1928-2014 in the Salish Sea (b) and coastal Washington (c).

641 Darker colors on the map (a) indicate multiple specimens from one location.)

642 **Figure 2:** Coefficient estimates (dots) for the best ocean condition (a-c) and prey availability (d-

643 f) hierarchical models with 95% confidence intervals (whiskers). Y-axis labels describe each

644 covariate for supported models ($\Delta\text{AIC}_c < 2$) and x-axis is the coefficient estimate for each

645 covariate (magnitude of trophic level change in response to the covariate). Colors correspond to

646 the temporal lags applied to the 2-year ecological delay models (pink, a and f), 1-year ecological

647 delay models (blue, b and e) and physiological delay models (green, c and d).

648 **Figure 3:** Conceptual diagram interpreting the mechanism of trophic position response (d) to

649 estimated model coefficients (Fig. 2d-f) included in the best food web models ($\Delta\text{AIC}_c < 2$) for

650 the 2-year ecological delay models (a, pink arrows), 1-year ecological delay models (b, blue

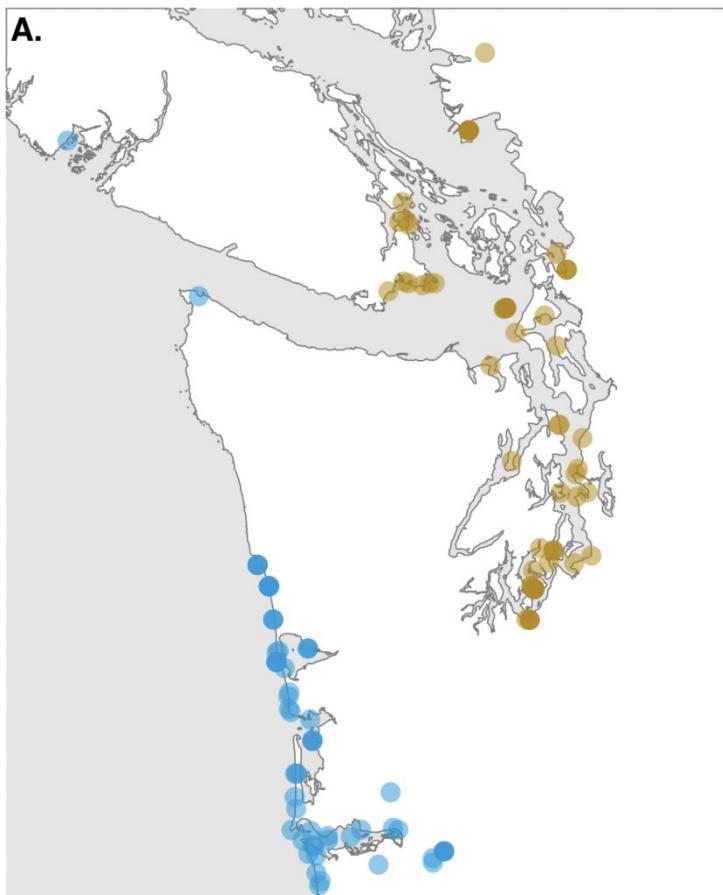
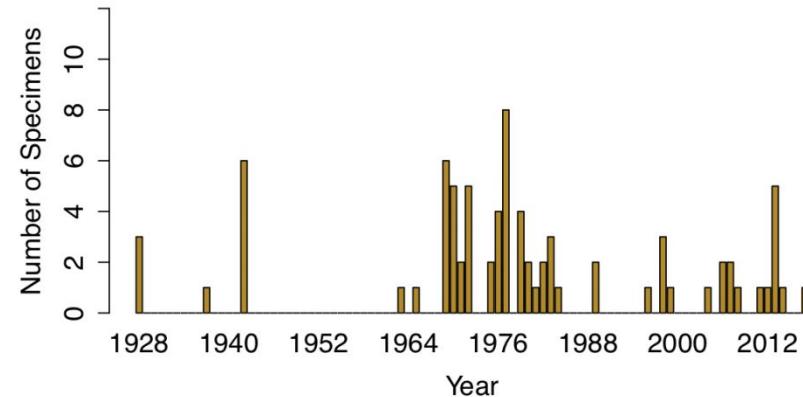
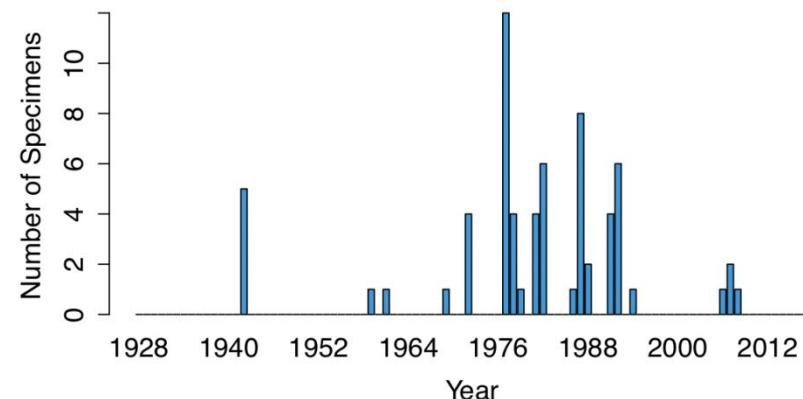
651 arrows) and the physiological delay models (c, green arrows). Solid arrows indicate indirect

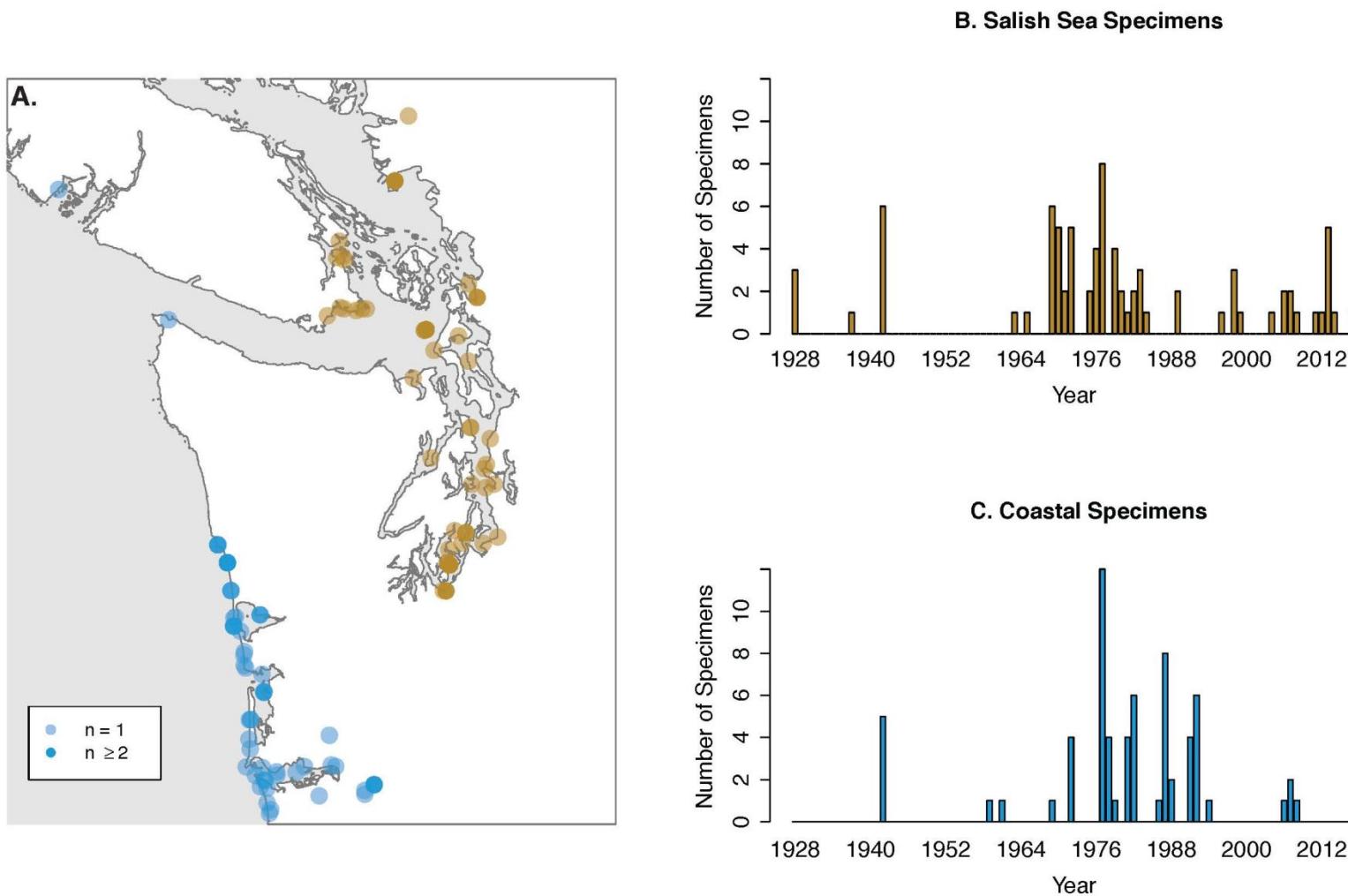
652 effects of covariates on harbor seal trophic position, signs indicate the direction of trophic

653 position response based on coefficient estimates, and dashed arrows conceptually represent the

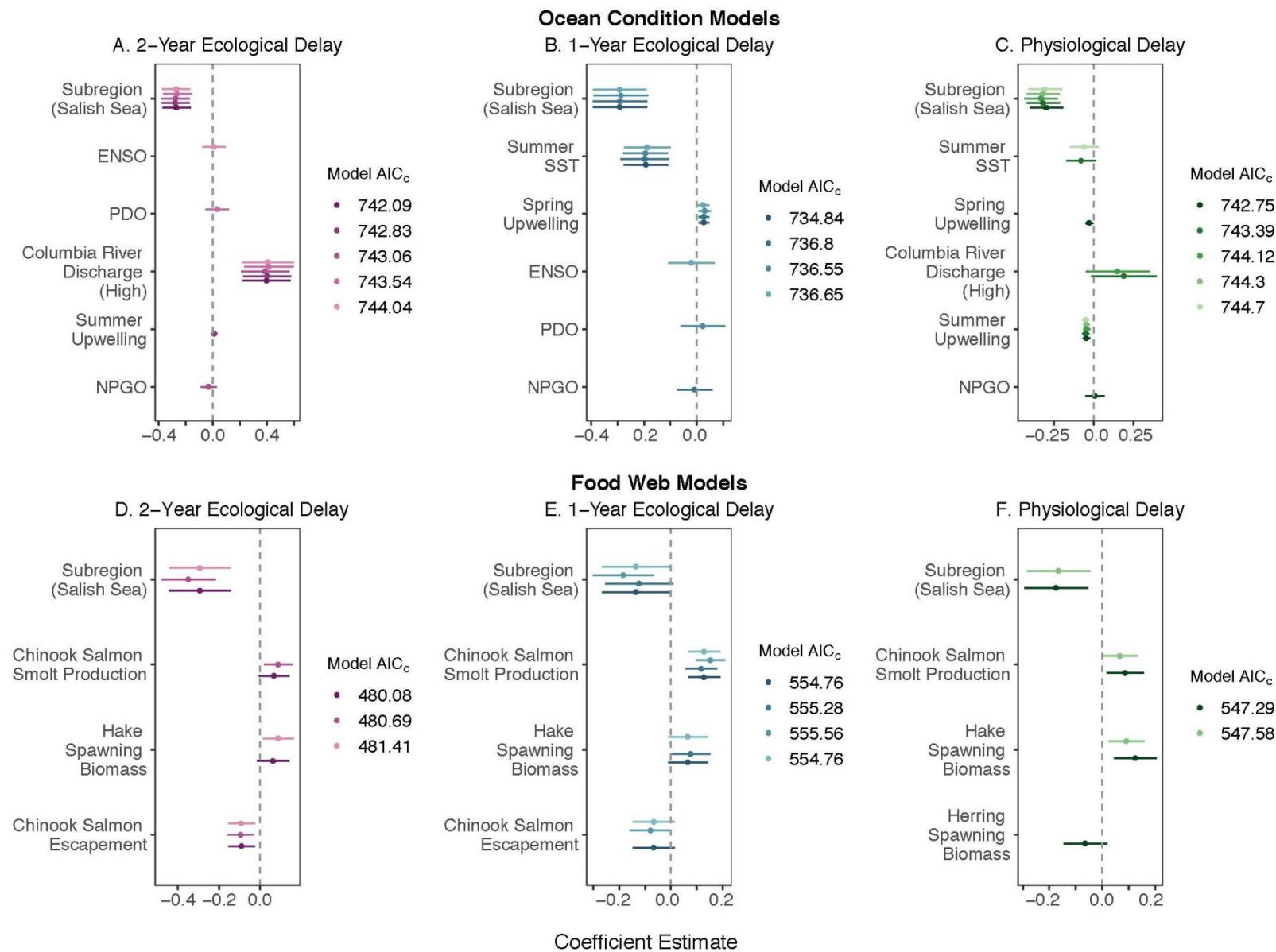
654 mechanism directly impacting harbor seal trophic position.

655 Fig. 1

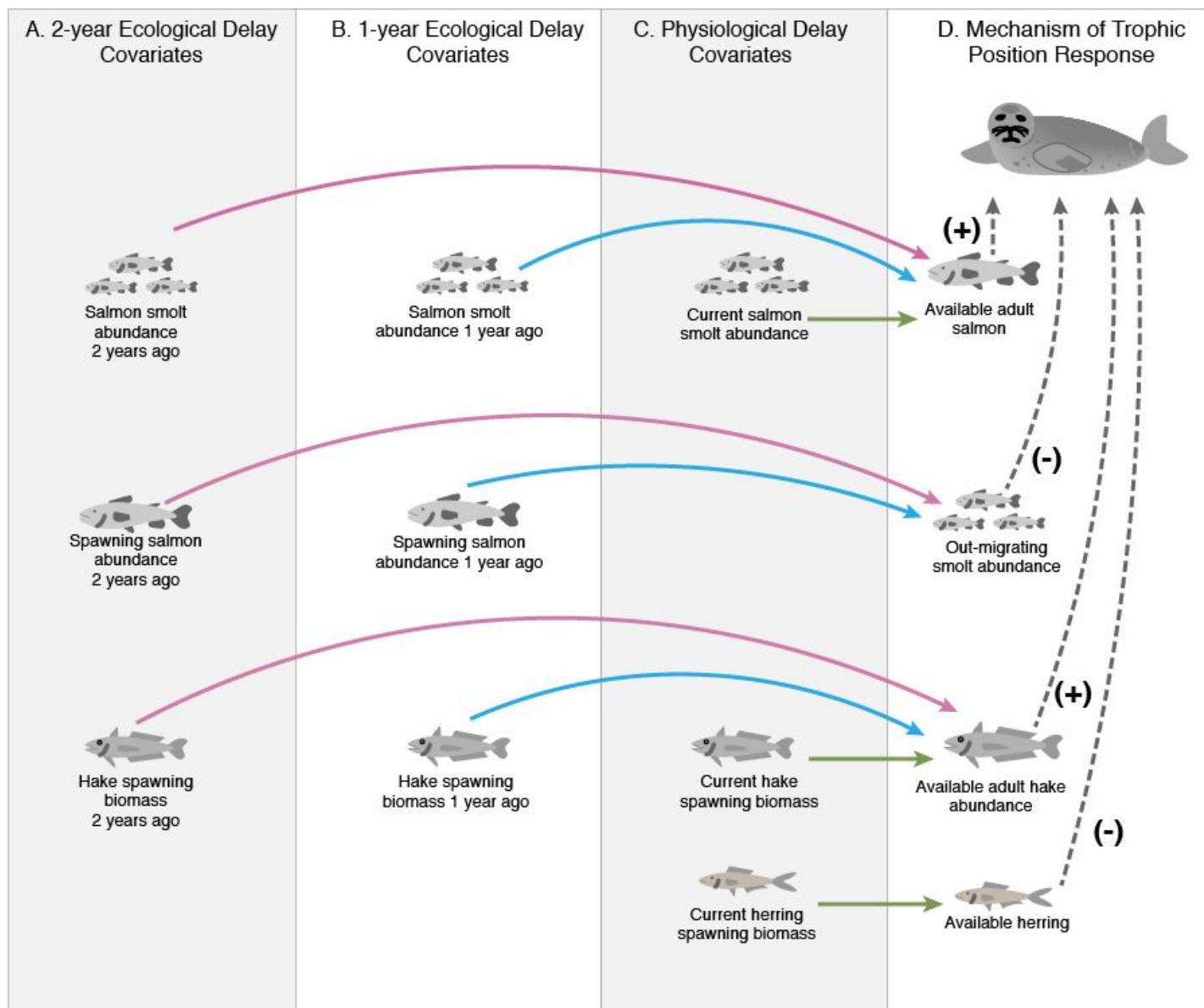
**B. Salish Sea Specimens****C. Coastal Specimens**



658 Fig. 2



659 Fig. 3



Supporting Information. Feddern, M.L., G.W. Holtgireve, and E.J. Ward. 2021. Delayed trophic response of a marine predator to ocean condition and prey availability during the past century. *Ecology*.

Section S1. Methods for compound specific stable isotope analysis

Collagen samples have been analyzed for both CSIA and bulk $\delta^{15}\text{N}$ which require 10 mg of purified collagen (100 mg of bone). Preliminary analyses were conducted to determine the highest rate of collagen return from bone sampled from different parts of the skull to minimize destruction. Samples were primarily taken from the internal occipital shelf to maintain external integrity. Bone was decalcified using 0.2 M HCl for 24-72 hours depending on bone thickness, followed by centrifugation and nanopure water rinse. Removal of humic acids was conducted using 0.125 M NaOH for 20 hours. Samples were washed to a neutral pH, then solubilized in 0.01N HCl. Once solubilized samples were blown down under N_2 to prevent isotopic fractionation, and freeze dried. Freeze dried collagen was analyzed for bulk isotopic composition of nitrogen by the UW IsoLab (isolab.ess.washington.edu) using a coupled elemental analyzer-isotope ratio mass spectrometer following the standard protocols of the laboratory. C:N ratios were calculated from this data, which is a measure of the quality for carbon and nitrogen analyses of bone collagen for isotopic analysis. No observations were outside of the acceptable range of 2.7-3.6; indicating there was no substantial loss of glycine or addition of nitrogen due to microbial processing from mortality, decay, curation, and analysis.

$\delta^{15}\text{N}$ of eleven amino acids (alanine, glycine, proline, aspartic acid, leucine, isoleucine, valine, threonine, serine, glutamic acid, phenylalanine) were measured in the UW Facility for Compound-Specific Isotope Analysis of Environmental Samples. Samples were prepared following the procedures developed by Chikaraishi et al. (2007) and protocols by Rachel Jeffrey's lab at University of Liverpool UK which are modifications of that published by Metges et al. (1996) and Popp et al. (2007). Briefly, proteins were hydrolyzed in 6N HCl and purified

using a cation exchange column. 20 µL or norleucine was added as an internal standard. Amino acids were esterified using isopropanol acetyl chloride, and derivatized via acylation with 4:1 toluene: pivaloyl chloride. Samples were brought up in ethyl acetate and analyzed using a coupled gas chromatography-combustion-isotope ratio mass spectrometer system (GC-C-irMA; Thermo Scientific Trace GC + GC IsoLink coupled to a Delta V irMS) in continuous flow mode monitoring masses (m/z) 28 and 29. A 30 m x 0.32 mm x 0.50 µm Agilent Technologies DB-35 capillary column with 35% Phenyl and 65% polysiloxane stationary phase and moderate polarity (Chikaraishi et al. 2010) with an inlet temperature of 260 C, column flow of 2 ml/min and oven ramp of 9 °C min⁻¹. For each run a 12 amino acid external standard with known isotopic composition was injected four times to condition the column followed by sample injections. Samples were injected in triplicate, with the 12 amino acid standard mixture injected every two samples (or six injections). A two-hour column oxidation was performed after 6 samples (25 injections) followed by a 30-minute backflush. δ¹⁵N was measured as:

$$S1. \delta^{15}\text{N} (\text{\% vs. air}) = \left(\frac{(^{15}\text{N}/^{14}\text{N})_{\text{Sample}}}{(^{15}\text{N}/^{14}\text{N})_{\text{Air}}} - 1 \right) * 1000$$

For each machine run, a linear model was fit for each individual amino acid using the following equation:

$$S2. \text{Std}_{aa} = m_{aa}t + b_{aa}$$

Where *m* represents the slope of the precision drift, *t* represents the injection number since last column oxidation, and *Std* represents the δ¹⁵N of an individual amino acid, *aa*, for a standard observation. The data was then corrected using the following equations:

$$S3. D_{aa,t} = \text{Std}_{aa,t} - \text{True}$$

Where $D_{aa,t}$ is the difference between an observed standard $\delta^{15}\text{N}$ ($Std_{aa,t}$) for a given amino acid (aa) at a given injection number (t) and the true $\delta^{15}\text{N}$ for that standard. Then:

$$\text{S4. } \text{Sample}_{\text{corrected, aa, t}} = \text{Sample}_{\text{obs,aa,t}} - D_{aa,t}$$

Where the drift value, $D_{aa,t}$, is subtracted from the sample value for a given amino acid and a given injection to correct the observed sample values for precision drift since last column oxidation. Mean sample corrected values for the triplicate injections were used for all analyses and trophic position calculations. Norleucine had lower precision in standards compared to phenylalanine, therefore no correction using the internal standard was applied. Mean precision for a given aa standard was calculated using the standard deviation of the external standard injections for a given run after drift correction and taking a mean of each run's standard deviation (Table S135). Conditioning injections (first four standard injections) were omitted from this calculation.

Section S2. Accounting for variability in trophic enrichment factors

Trophic enrichment factors are variable based on animal diet (omnivory, carnivory, herbivory), pathways of nitrogen excretion, and trophic level (Nielsen et al. 2015, McMahon et al. 2015) with ~~ominivory omnivory~~, carnivory and higher trophic levels demonstrating the lowest trophic enrichment for most amino acids. Trophic enrichment has ultimately been attributed to diet quality (similarity in tissues between consumer and prey) and mode of nitrogen excretions, although the relative impacts of each is difficult to discern, especially considering most controlled feeding studies include low-trophic level ammonia excretion but not high trophic level species (i.e., adult hake or salmon). In coastal Washington, most trophic transfers are between high diet quality, piscivorous fish (ammonia excretion) with a high-quality transfer between fish and harbor seal (urea excretion). Studies using multiple trophic enrichment factors based on the food web structure and consumption type produce more accurate trophic position estimations especially for higher level consumers (McMahon et al 2015, McMahon et al. 2016, McMahon et al. 2019).

We applied multiple trophic position calculation frameworks for harbor seals to determine the best approach (Tables S1 & S2) by identifying the percentage of data that fell within an ecologically realistic trophic position range for harbor seals. We also applied these approaches to herring, a known harbor seal prey species, with data from Germain et al. 2013. Based on known foraging patterns, we anticipate harbor seals have an average trophic position of 3.5 to 5 and herring will have an average trophic position of 2.5-2.9. Equation 2 produced the most accurate herring trophic position estimates for most amino acids, however valine produced an impossibly low estimate of trophic position. In contrast, equation 3 produced the most accurate results for most amino acids compared to harbor seals, but these estimates were still unrealistically low for some amino acids (proline, valine), which is common for CSIA (Table S1,

McMahon et al. 2016). Additionally, this is not the most ecologically accurate parameterization, as it assumes all trophic transfers are of high prey quality, where there must be at least one herbivorous-low quality trophic transfer in the food web from phytoplankton to zooplankton (parameterization of equation 4, Table S1). It also assumes prey quality (carnivorous) and trophic level of the consumer is more important than nitrogen excretion pathway (urea versus ammonia) for some amino acids but not others. Seemingly, these assumptions impact trophic position estimates from individual trophic amino acids differently which will likely be an important consideration for future studies applying a multi-amino acid framework. It is possible that these reflect biases in conventional trophic position estimates (i.e., stomach content analysis) as proposed by McMahon (2015) or there may be biases in controlled feeding studies. For example, growth rate of individuals in controlled feeding studies may not accurately reflect those in natural ecosystems which may lead to overestimates in trophic enrichment if they are higher in natural systems compared to controlled feeding experiments. This may be plausible in the Washington food web as consumption of juvenile fish is common at multiple trophic levels, and juveniles presumably have higher growth rates than adults.

Section S3. Identifying size and sex-based trends in harbor seal trophic position

Only a subset of the samples included month of collection, sex, and length metadata and therefore separate month, length, and sex specific analyses were fit to the data to test whether they should be considered as predictors for the ocean condition and prey availability data. Standard linear models (equation S5) with: 1) sex as a factor, 2) length as a continuous covariate and 3) month as a continuous covariate were fit to both Salish Sea and coastal WA for each individual trophic amino acid. These models were used to test whether trophic position varies with length and sex, whether these trends are consistent between amino acids, and whether one year was an appropriate approximation for tissue turnover of bone collagen. The standard linear models took the following structure:

$$S5. \mathbf{y}_i = \alpha + \boldsymbol{\beta} \mathbf{X} + \epsilon$$

where y represents harbor seal trophic position calculated from phenylalanine and a trophic amino acid i , \mathbf{X} is a matrix of bottom-up drivers for a given model, $\boldsymbol{\beta}$ is a vector of covariates (sex, length, month, location), and α is the intercept. There were no significant differences in trophic position between male and female harbor seals in either the Salish Sea (Figure S~~65~~A) or coastal Washington (Figure S~~65~~B); this relationship was consistent across amino acids. Similarly, trophic position did not change based on harbor seal length (Figure S~~54~~). Interestingly, the exception to this finding was trophic position calculated by proline, which showed a significant decline with size. Mean harbor seal trophic position calculated from proline for harbor seals ranging from 150 - 180 cm in standard was 0.6 lower than harbors seals that were less than 120 cm of standard length (Figure S~~54~~). Trophic position calculated from alanine, aspartic acid and valine also showed negative trends with size, although the trend was not statistically significant, while trophic position calculated from glutamic acid was positive but

also not statistically significant. There was also no observed ‘seasonality’ in harbor seal trophic position (Figure S²⁴) indicating 1-year physiological delay was a reasonable approximation for tissue turnover time of skull bone collagen.

Harbor seals in Washington do not have distinct trophic ecology based on adult size (Figure S⁵⁴) or sex (Figure S⁶⁵). Bjorkland et al. (2015) did not observe sex or size (weight) based differences in bulk $\delta^{15}\text{N}$ values in harbor seals in the San Juan Islands in the Salish Sea between 2007 and 2008. Our results agree with this finding and with similar studies of other Pacific pinniped species (Drago et al. 2009, Dehn et al. 2007). While both male and female harbor seals have a similar trophic position, it is possible sex and size-based differences in foraging strategies within a similar trophic position exist (Bjorkland et al. 2015, Wilson et al. 2014). Additionally, this study focused on adult harbor seals and changes in trophic position between juveniles, sub adults and adults are possible as indicated by pinniped studies (Zhao et al. 2004). Regardless, our results show long-term consistencies in the trophic niche exploited by both male and female harbor seals regardless of adult size in Washington.

Section S4. Identifying temporal trends in harbor seal trophic position

To understand any changes through time to harbor seal foraging ecology over the past 100 years that were not explained by the tested environmental and food web covariates (Tables S3 & S4), generalized additive models (GAMs) were fit the residuals for the best ocean condition-prey model with a smooth term by year and a k term of 5. These analyses (Figures S⁶⁷ & S⁹⁸) were compared to the raw time series of harbor seal trophic position data (Figure S⁷⁶) to identify trends through time that are unexplained by the covariates included in this analysis.

Trends in harbor seal trophic position through time were different between the Salish Sea and coastal Washington (Figure S⁷⁶). The time series of the glutamic acid trophic position in coastal Washington had a significant positive trend through time (Figure S^{76b}) that increased from 1948-1968 and remained relatively constant following 1975. Trophic position calculated from alanine and proline showed similar trends, although the alanine trophic position trend was not statistically significant (Figure S^{76a}). In contrast, harbor seal trophic position in the Salish Sea calculated from glutamic acid, alanine, aspartic acid, and proline has been relatively stable over the past century, but the trophic position calculated from valine showed a significant decline since 1968.

There were no trends through time for the model residuals for any amino acid after accounting for environmental (Figure S⁸⁷) and food web (Figure S⁹⁸) conditions at all three time lags. This indicates that prey availability and ocean conditions account for most temporal variation observed in the trophic position time series (Figure S⁷⁶). However, valine was a notable exception, which demonstrated a decreasing trend through time in model residuals for all of the models with the most support.

Section S5. Methods for Multivariate Autoregressive State-Space (MARSS) Model

A MARSS model was fit to herring stock spawning biomass and harbor seal stock population

size in order to get total population and total biomass estimates for these species for each year.

Harbor seal datasets and herring biomass were collected by stock ($n = 7$ and $n = 20$, respectively)

but did not have observations for every for every year (Figures S124 & S143). Two MARSS

models were fit to the data, one for each species, to estimate population and biomass for each

year for each for each stock (Figures S132 & S154). For both datasets process error (Q) assumed

equal variance and covariance across stocks, and observation error (R) was assumed to be equal

across stocks. U and x_0 were both set to unequal, thus assuming they vary across stocks. Model

states (Figures S132 & S154) were summed across years for total biomass (herring) and

population size (harbor seals) estimates and used as covariates for prey availability models.

Harbor seal data has not been collected since 2000 and we assumed the population has remained

constant from 2000-2010.

Section S6. Using multi-trophic amino acid analysis compared to only glutamic acid

Mean harbor seal trophic position estimates were similar across trophic amino acids however some were more variable than others. The standard deviation of trophic position was higher for proline (4.6 ± 0.7 , mean \pm 1SD), and valine (3.7 ± 0.8) and included more ecologically unrealistic values compared to glutamic acid (4.5 ± 0.4) and alanine (3.9 ± 0.4). Trophic position calculated from aspartic acid (4.1 ± 1.0) had the highest standard deviation and also demonstrated a trend through time compared to other amino acid trophic position calculations (Figure S76).

Application of a multi-amino acid trophic position calculation 1) offered a more realistic parameterization of the trophic position equation, 2) improved model certainty and 3) produced similar covariate coefficients compared to a glutamic acid only parameterization (Table S6). Examination of the distribution of trophic position calculations for each individual trophic amino acid shows variability in accuracy and variance for single trophic amino acid calculations (Figures S32 & S43). For example, aspartic acid had a much wider variance compared to other amino acids (Figures S32 & S43) and also produced different trends through time (Figure S76).

It is likely differences in tissue turnover time between individual amino acids and phenylalanine contribute to the variance of the trophic position estimates derived from individual trophic amino acids. Downs et al. (2014) found phenylalanine takes 780 hours to reach 50% turnover in shrimp. This is comparable to glutamic acid, alanine, and valine which take 940, 642, and 942 hours respectively which are substantially lower than aspartic acid which requires 1530 hours. The discrepancy between tissue turnover times between aspartic acid and phenylalanine is likely the cause of the broad distribution for aspartic acid derived trophic position compared to other trophic amino acids, as aspartic acid is incorporating the nitrogen isotope signature over a

substantially larger time period relative to phenylalanine and thus may incorporate more prey switching and/or changes in the isotopic signature of primary producers.

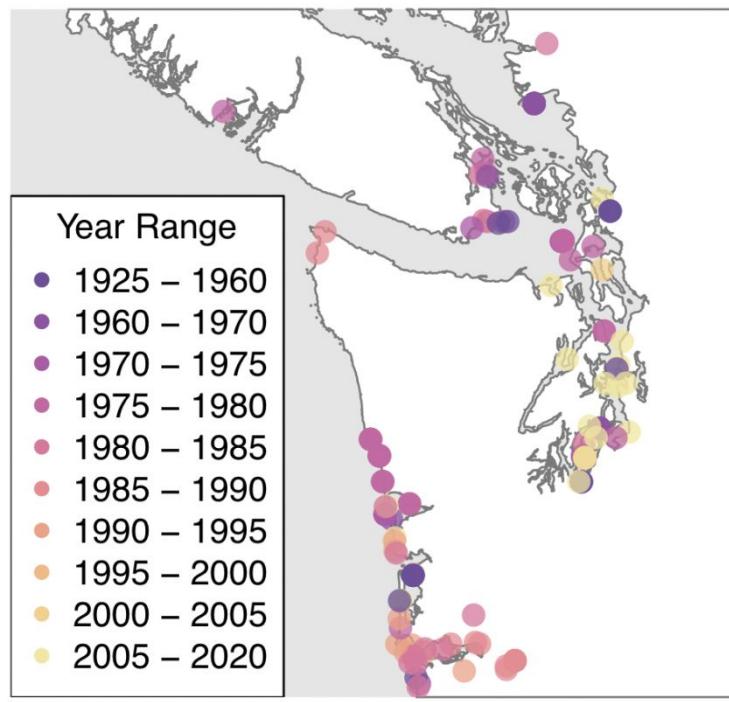
Addition of alanine to the glutamic acid only model resulted in the largest difference in model certainty. A glutamic acid – alanine model supported the same best models for both the environmental and prey models at all time lags. The combined tissue turnover of glutamic acid and alanine of shrimp (791 hours) is very similar to that of phenylalanine (780 hours) ensuring both the trophic and source amino acids were incorporated over a similar time scale (albeit the trophic amino acids were a wider time scale). Benefits of a multi-amino acid trophic position equation may not require four amino acids as previously suggested (Nielsen et al. 2015) but rather carefully selected trophic amino acids to ensure the trophic amino acids are incorporated over a similar time scale as the source amino acids. If tissue turnover times are unable to be approximated, utilizing four trophic amino acids or two source amino acids as suggested by Nielsen et al. (2015) would likely provide the same benefit as fewer, carefully selected amino acids based on tissue turnover times.

Section S7 Tissue turnover time assumption validation

Tissue turnover time of bone collagen in large mammals is not well studied due to the challenges of repeatedly measuring bone in a controlled feeding study. Hobson et al. (1992) found the half-life of carbon in bone collagen of Japanese quails (*Coturnix japonica*) is 170 days. A comparative study of the $\delta^{15}\text{N}$ values in elephant seal bone and tooth dentin found the $\delta^{15}\text{N}$ value in skull (maxilla and mandible) bone collagen was significantly correlated with the previous two years of tooth dentin (Riofrío-Lazo and Aurioles-Gamboa 2013). Another comparative study of northern fur seal (*Callorhinus ursinus*) and California sea lion (*Zalophus californianus*) young-of-year estimated that complete bone collagen turnover takes approximately 8 months (Newsome et al. 2006). Complete bone collagen turnover should be slower in adults than growing young-of-year. Altogether, this indicates that the $\delta^{15}\text{N}$ values in skull bone collagen is time averaged over the past 1 – 2 years of the seals life.

To further test the assumption that stable isotope composition of bone collagen of adult harbor seals reflect the last year of the animals life, month was tested as a smoothed predictor with up to 12 knots for trophic position estimates using a generalized additive model (GAM). Support for a significant smoothing term or trend in the data would identify and seasonality in the data, which would be expected if tissue turnover time is consistently less than a year. There was no support for a smoothing effect by month in generalized additive models of $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{13}\text{C}$ values which would have indicated any seasonal variability in isotope composition and thus a turnover time of less than a year ($p < 0.05$; Appendix S1:Figure S2).

Figure S1: Temporal distribution of sampled harbor seal museum specimens in coastal Washington and the Salish Sea. Colors denotes time period specimens were collected.



View Only

Figure S24: Analysis of seasonality of harbor seal trophic position for five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) calculated using the source amino acid phenylalanine and equation 2 (Table S2; Figure S43.2) with a weighted beta. Color corresponds to trophic amino acid, line shows the fit of a generalized additive model with a smoothed term by month (1 = January, 12 = December) and a k of 12. Smoothed terms were not significant.

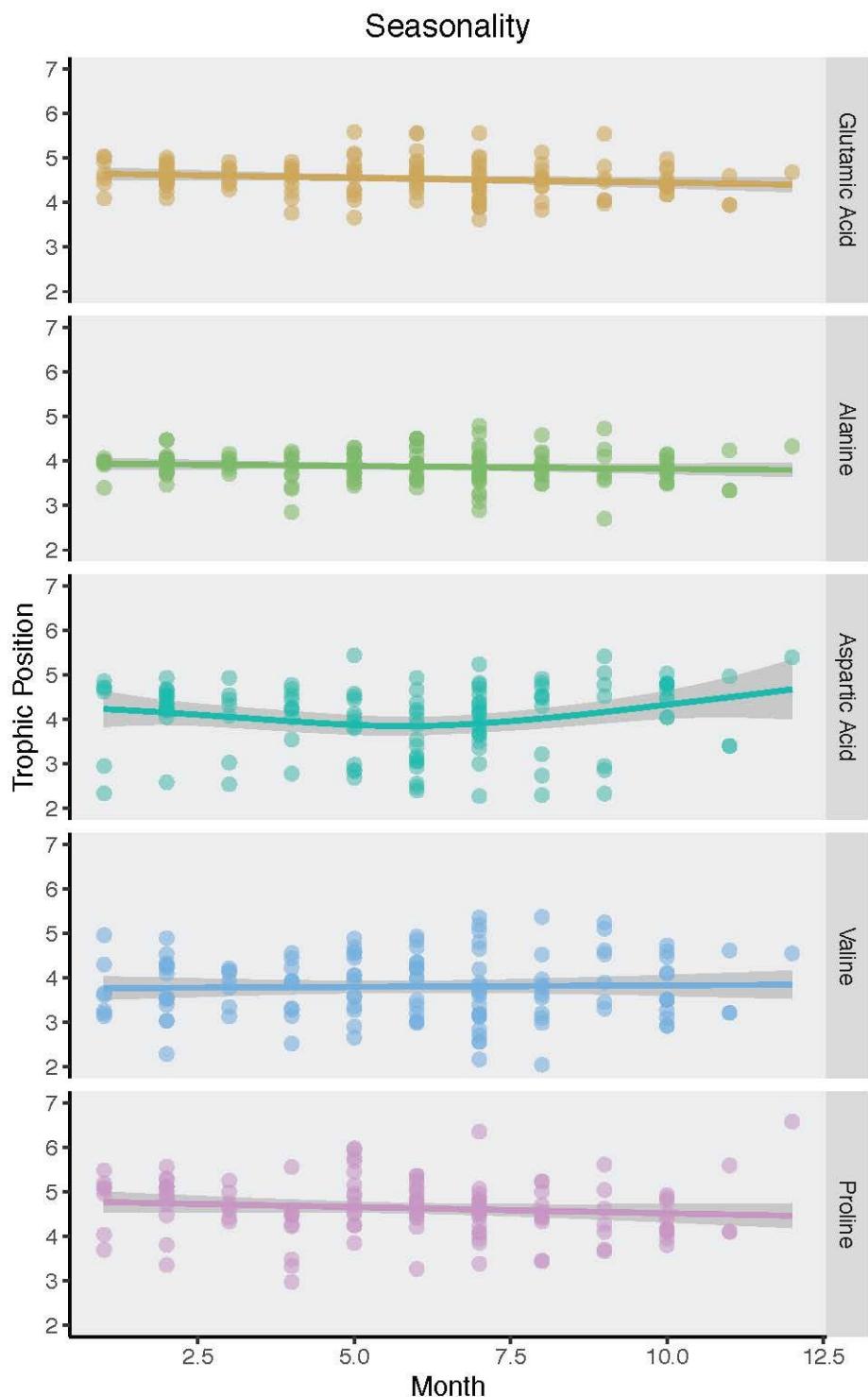


Figure S32: Distributions (density of probability, y-axis) of calculated trophic position (x-axis) for harbor seals in this study. Equations (1-4) refer to Table S1 and parameter values described in Table 1 of the main text. Colors correspond to trophic amino acids (Tr) and the grey box represents ecologically realistic trophic positions for harbor seals if they were to predate 1 trophic position above herring (trophic position of 2.5, minimum expected value) and one trophic position below killer whales (trophic position of 6, maximum). The value within the grey box corresponds to the percentage of observed trophic position values that fell within the ecologically realistic range.

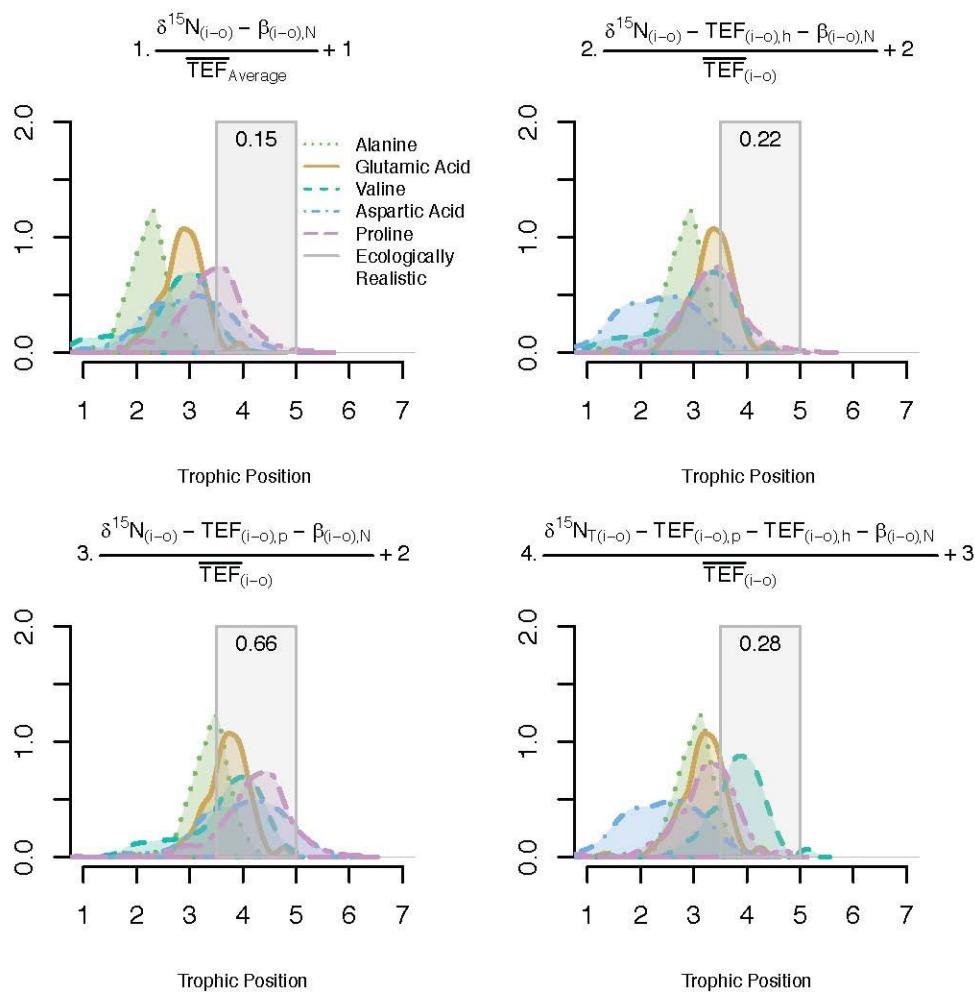


Figure S43: Distributions (density of probability, y-axis) of calculated trophic position (x-axis) for harbor seals in this study applying equations (1-4) in Table S1 with $\beta_{(i-o),NV}$ instead of $\beta_{(i-o),N}$ as described in Table 1 of the main text.

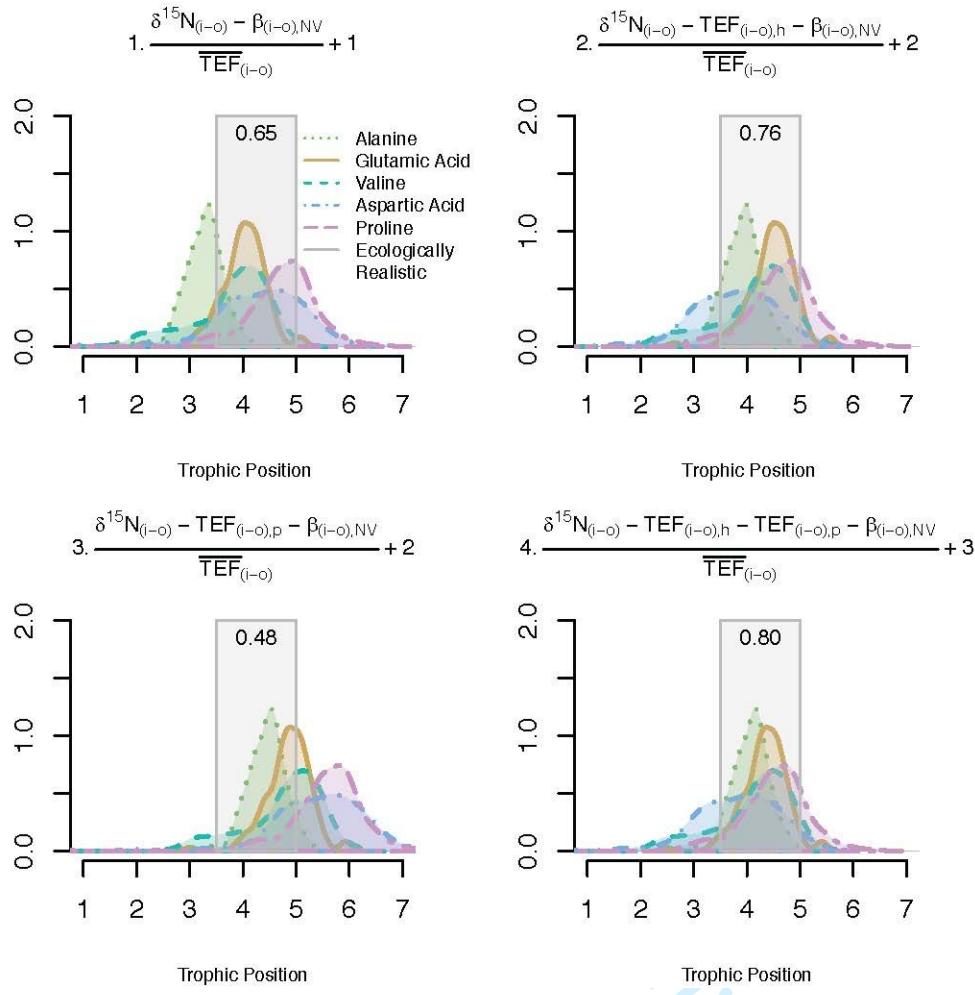


Figure S54: Relationship between harbor seal size (standard length, cm) and trophic position calculated using five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline). The line shows the fit of a generalized additive model with a smoothed term by year and a k of 6 and * denotes a significant smoothed term.

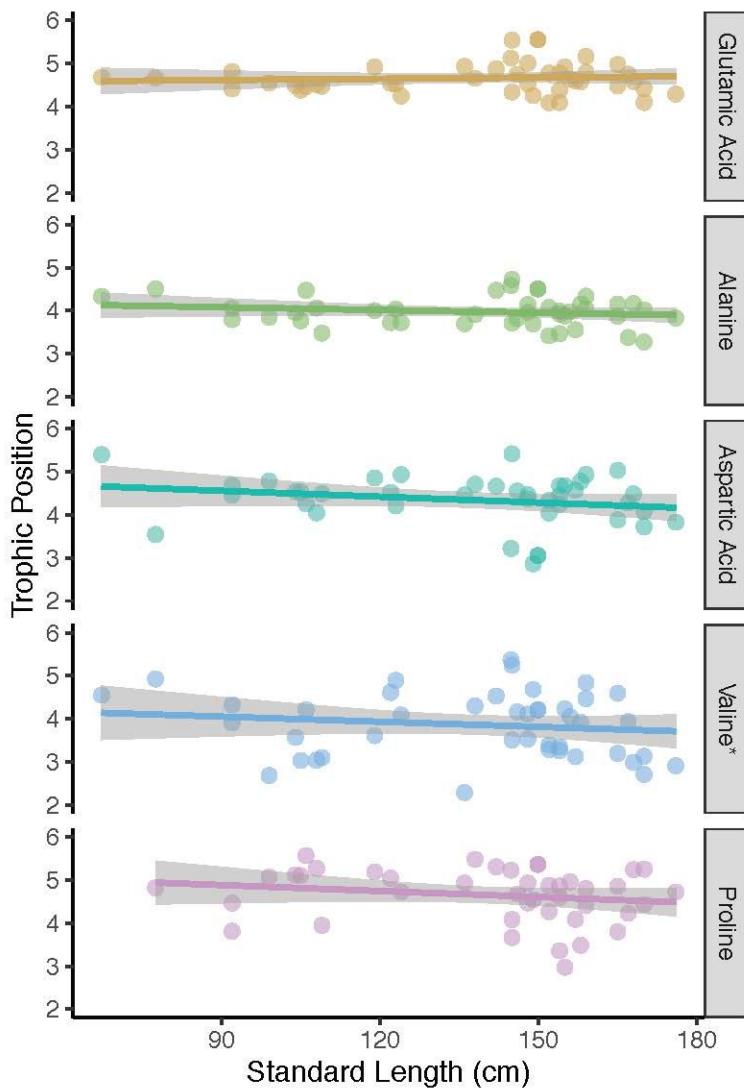


Figure S65: Sex specific trophic position for male (M) and female (F) harbor seals pooled over the past century and calculated using five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) for a) Salish Sea and b) coastal Washington specimens.

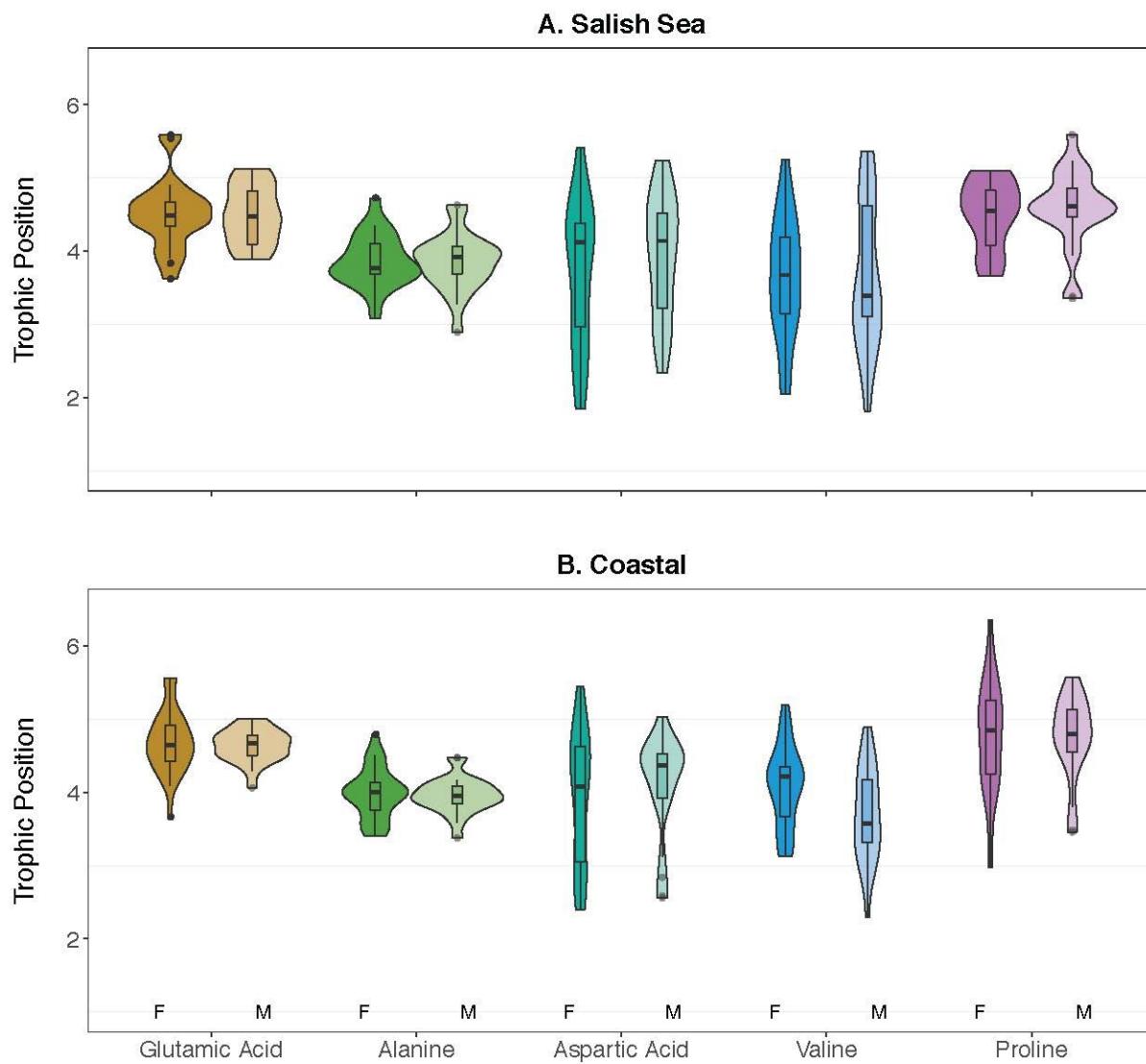


Figure S76: Time series of harbor seal trophic position in a) coastal Washington and b) the Salish Sea for five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) calculated using the source amino acid phenylalanine. Color corresponds to trophic amino acid, while 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.

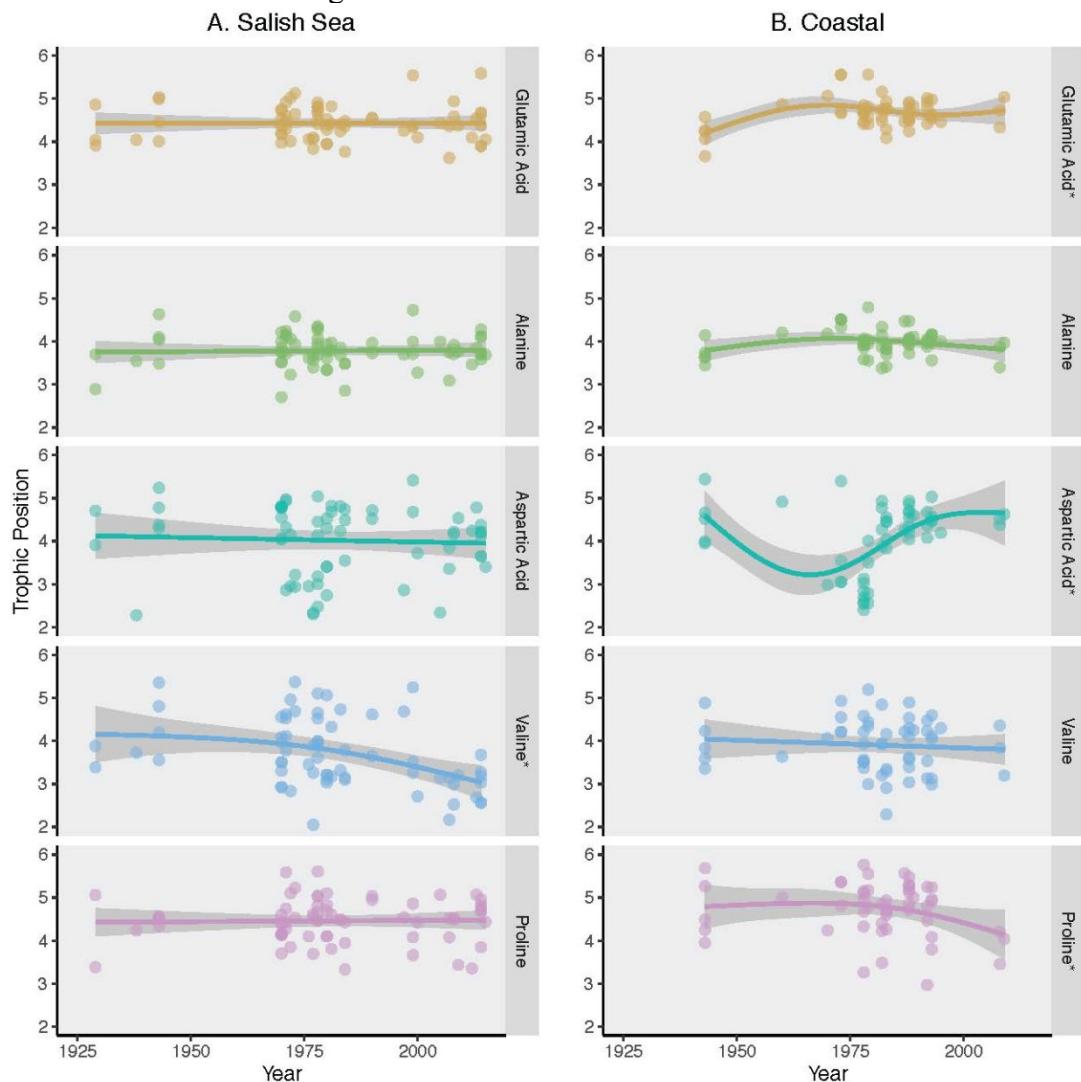


Figure S87: Time series of residuals by year for the three ocean condition models (physiological delay, 1-year ecological delay, 2-year ecological delay) with the most support for the four different trophic amino acids used in the models (glutamic acid, alanine, valine, and proline) with trophic position calculated using the source amino acid phenylalanine. Color corresponds to trophic amino acid, line shows the fit of a generalized additive model with a smoothed term by year and a k of 6. * denotes a significant smoothed term.

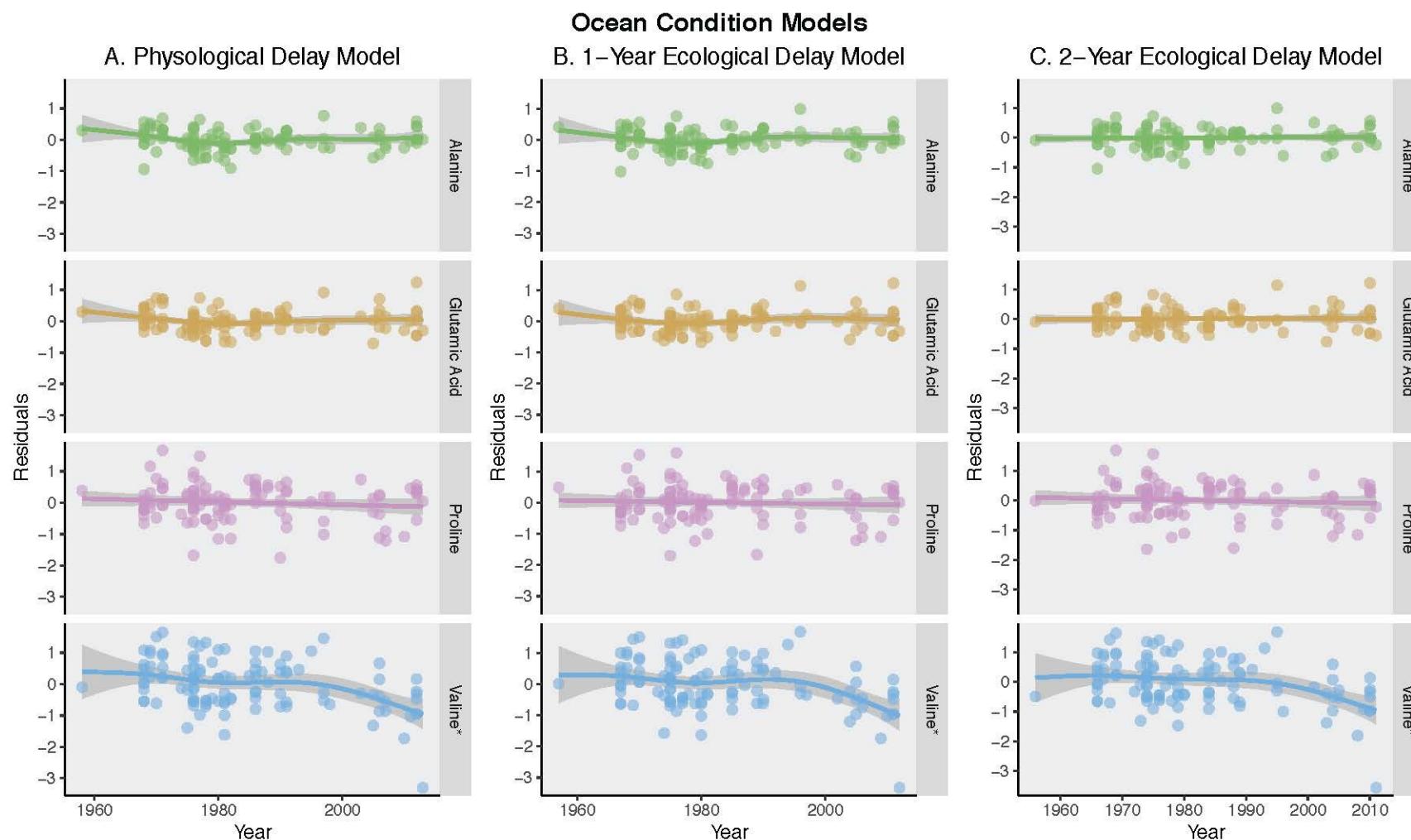


Figure S98: Time series of residuals by year for the three food web models (physiological delay, 1-year ecological delay, 2-year ecological delay) with the most support for the four different trophic amino acids used in the models (glutamic acid, alanine, valine, and proline) with trophic position calculated using the source amino acid phenylalanine. Color corresponds to trophic amino acid, line shows the fit of a generalized additive model with a smoothed term by year and a k of 6. * denotes a significant smoothed term.

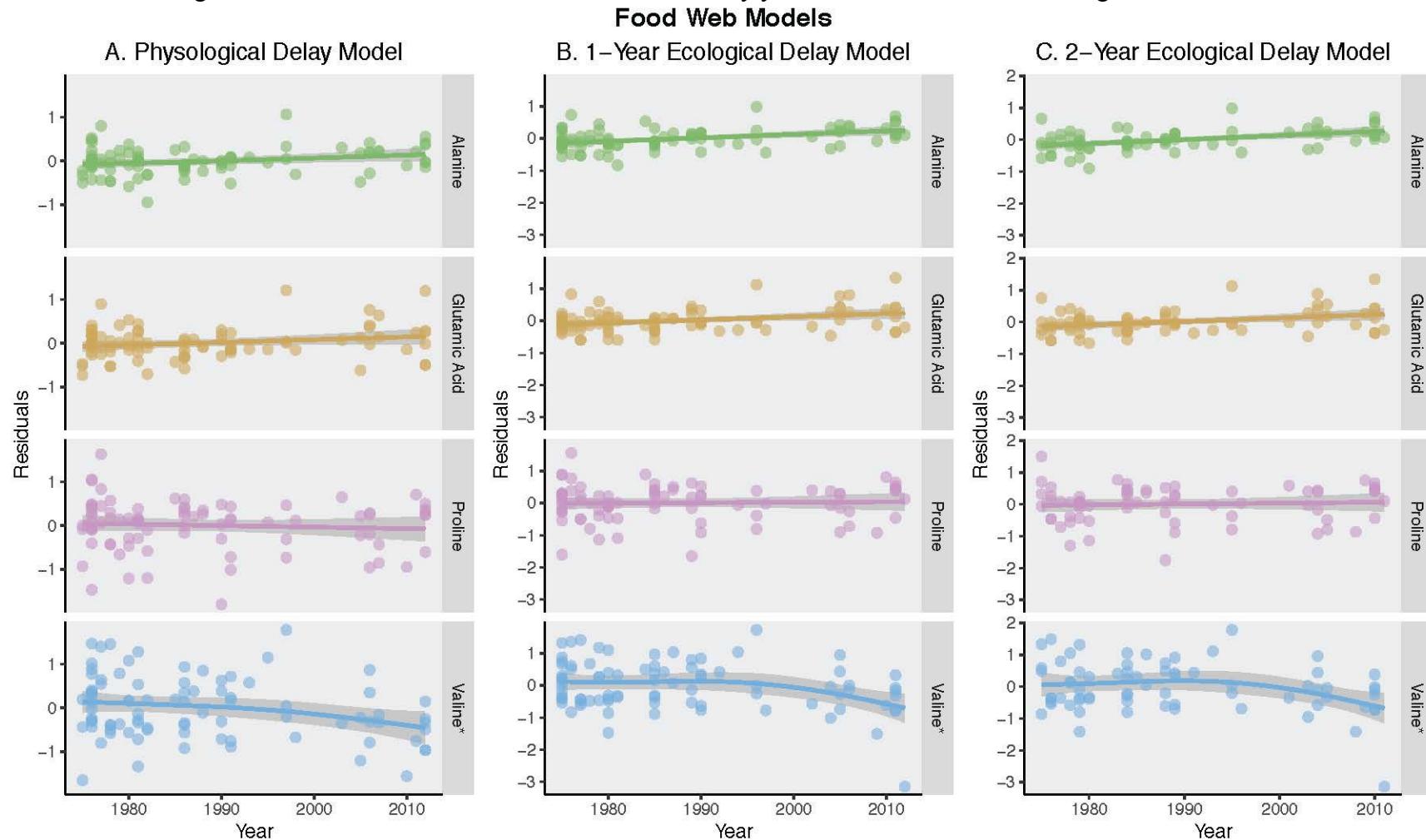


Figure S109: Residual plots for the physiological delay, 1-year ecological delay, and 2-year ecological delay ocean condition models with the most support.

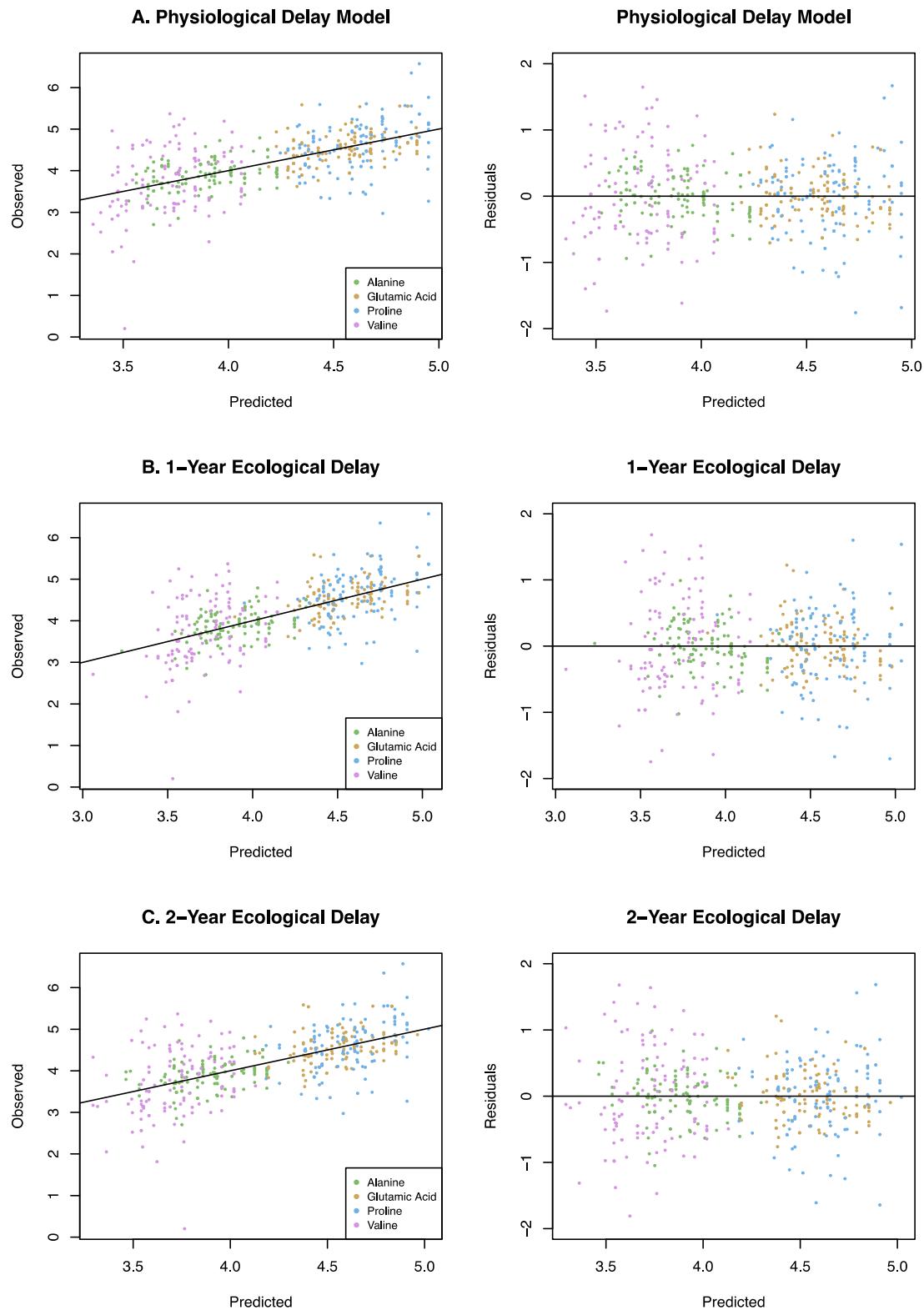
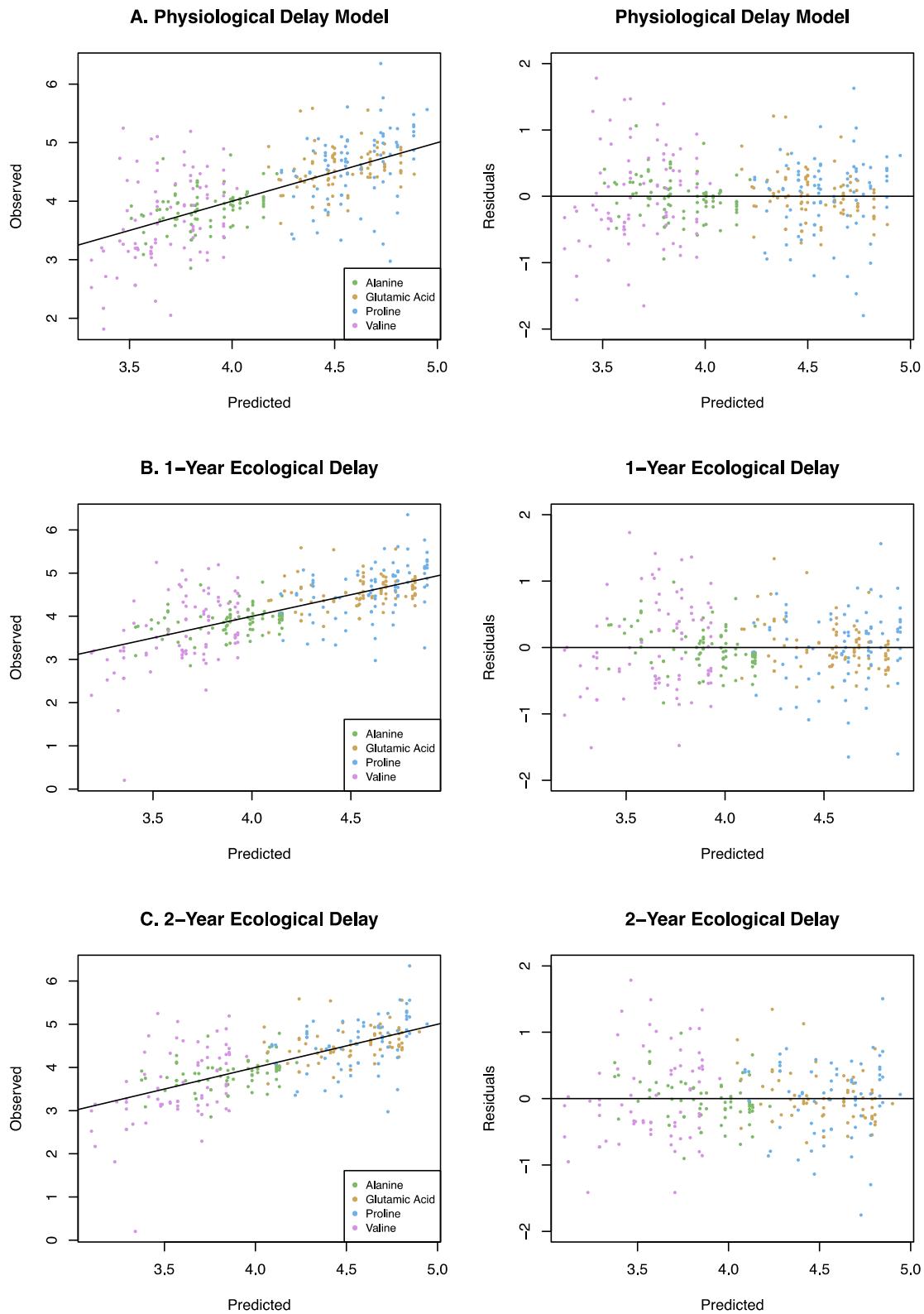


Figure S110: Residual plots for the physiological delay, 1-year ecological delay, and 2-year ecological delay food web models with the most support.



| **Figure S124:** Pacific herring spawning biomass by stock from Siple and Francis 2015.

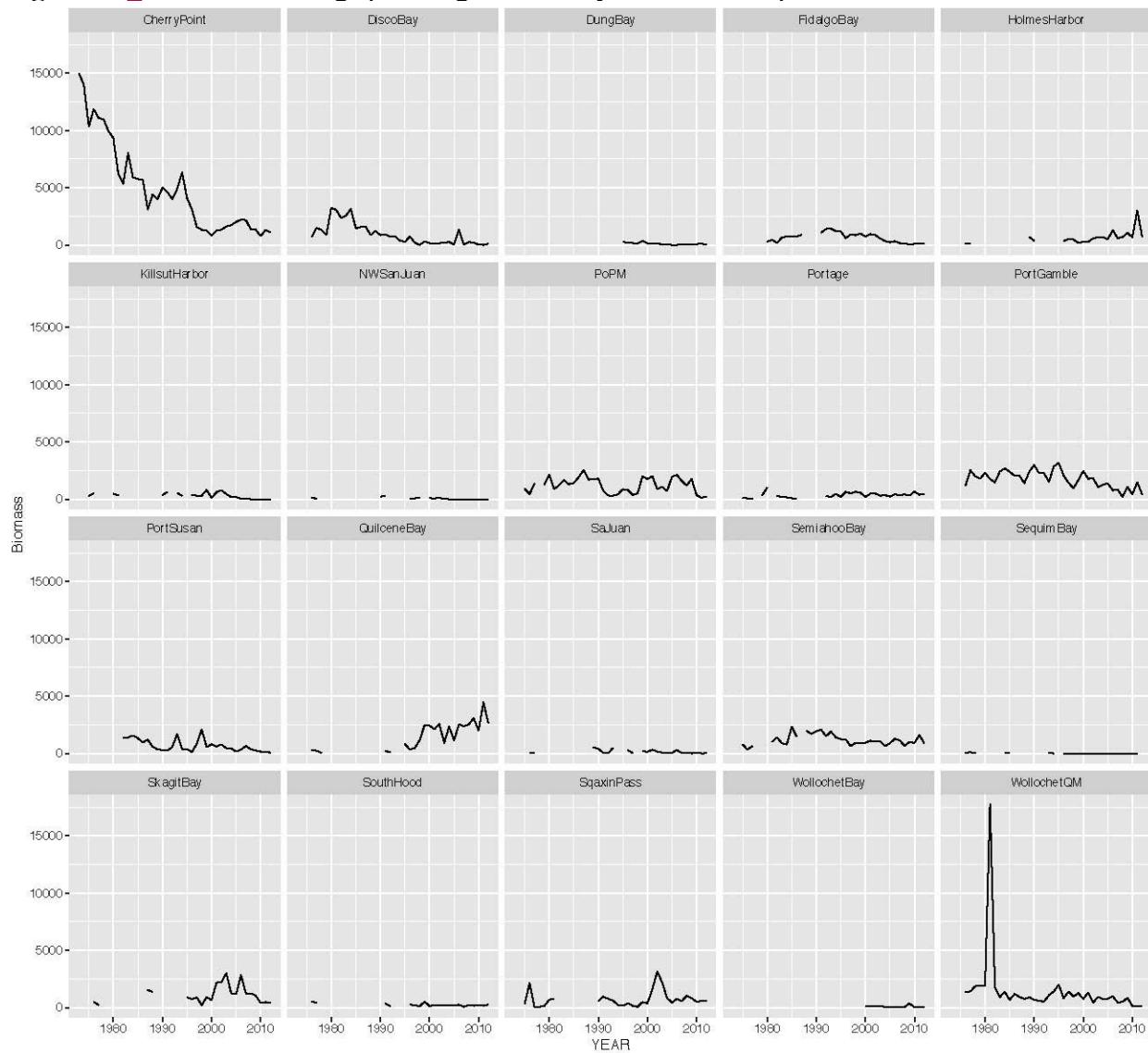


Figure S132: MARSS model (described in Appendix S3) for Pacific herring spawning biomass by stock.

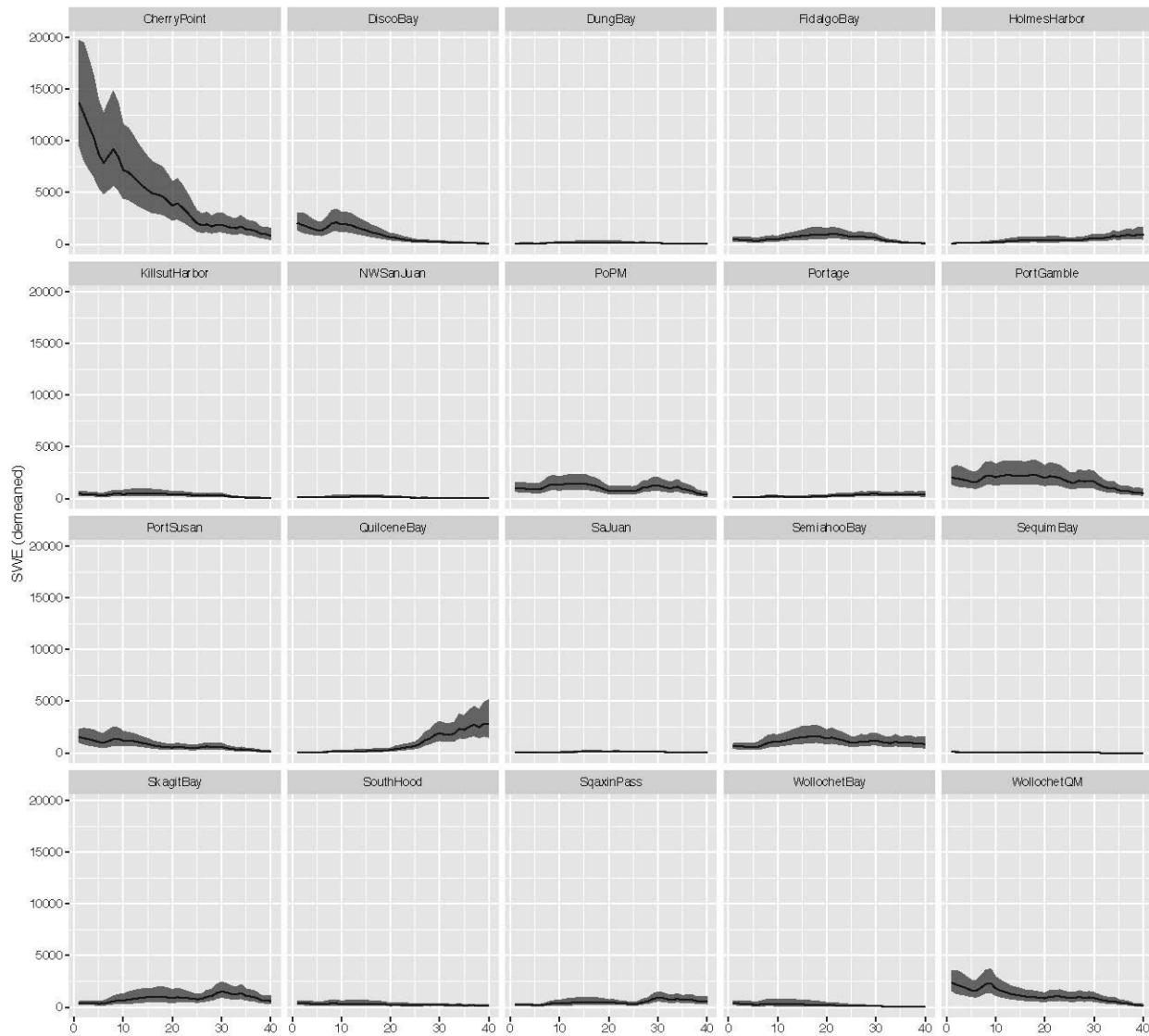


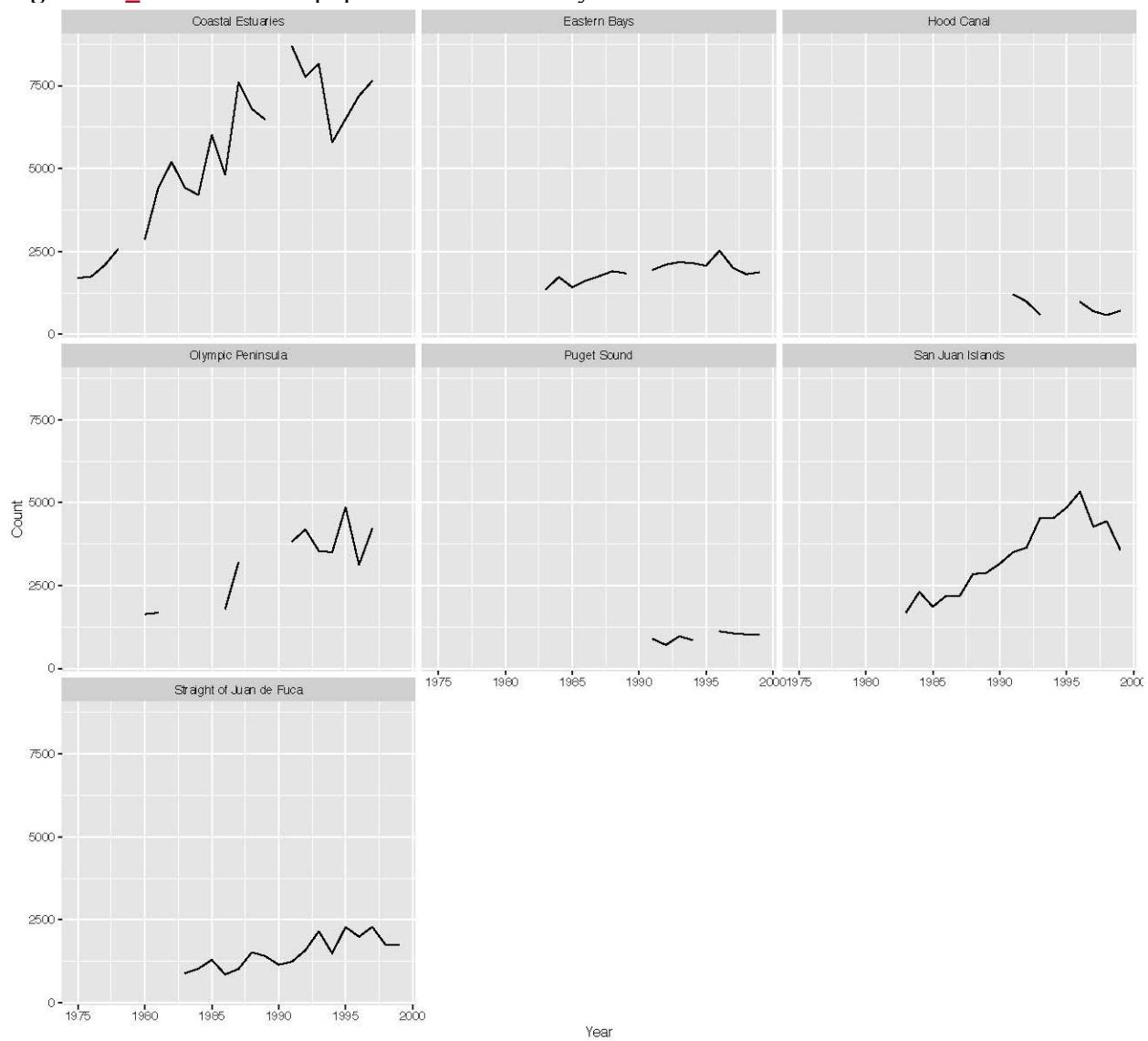
Figure S143: Harbor seal population estimates by stock from Jeffries et al. 2003.

Figure S154: MARSS model (described in Appendix S3) for harbor seal population counts fit by stock.

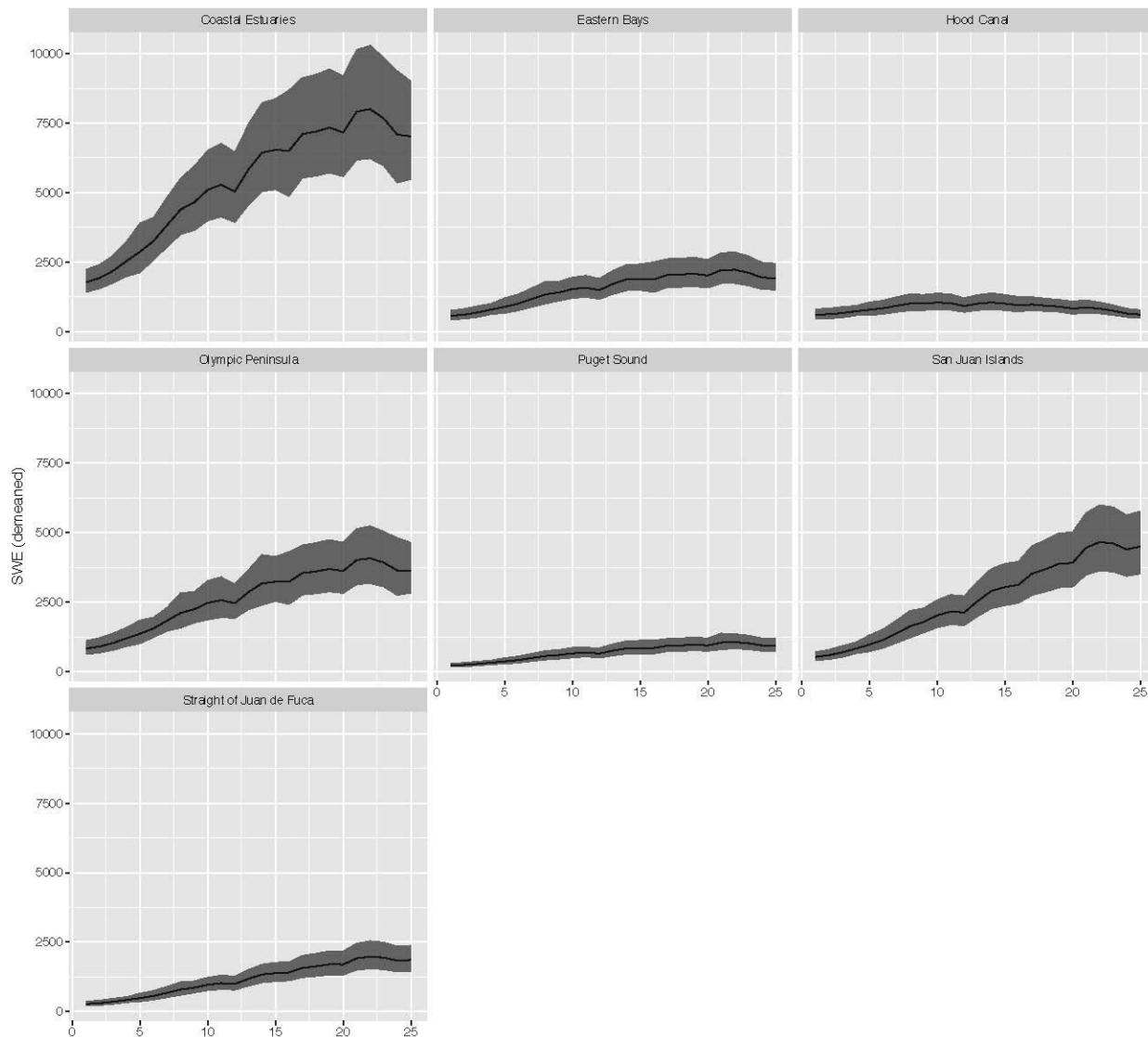


Table S1: Equations for single and multi-trophic enrichment factor parameterizations of trophic position and the associated assumptions for each parameterization using the values described in Table 1 in the main text. i refers to an individual trophic amino acid and o refers to a source amino acid, in this case phenylalanine. In addition to $\beta_{(i-o), N}$ (Figure S34) refers to $\beta_{(i-o)}$ for non-vascular plants, the same equations were used with $\beta_{(i-o), NV}$ (equation 6, Figure S42). Applying $\beta_{(i-o), NV}$ has the additional assumption that both vascular and nonvascular plants contribute to the coastal food web in which harbor seals forage and that the contributions of each can be calculated from bulk $\delta^{13}\text{C}$ data (equations 2 & 3).

Parameterization Assumptions	Equation
1. Assumes that all trophic transfers are best represented by the average TDF in this system	$\text{Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 1$
2. Includes harbor seal specific TDF ($\text{TDF}_{(i-o), h}$) which assumes one trophic transfer is from high quality prey (and urea excretion) and assumes average TDF accurately represents all other trophic transfers	$\text{Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - \text{TEF}_{(i-o), h} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 2$
3. Includes a TDF derived from basal food web consumers (zooplankton / herbivores; $\text{TDF}_{(i-o), p}$) which assumes one trophic transfer is from low quality prey and assumes average TDF accurately represents all other trophic transfers	$\text{Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - \text{TEF}_{(i-o), p} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 2$
4. Includes a TDF derived from basal food web consumers (zooplankton / herbivores; $\text{TDF}_{(i-o), p}$) and a harbor seal specific TDF ($\text{TDF}_{(i-o), h}$). This assumes one trophic transfer is from low quality prey and a second is from high quality prey (and urea excretion). Assumes average TDF accurately represents all other trophic transfers	$\text{Trophic Position} = \left(\frac{\delta^{15}\text{N}_{(i-o)} - \text{TEF}_{(i-o), p} - \text{TEF}_{(i-o), h} - \beta_{(i-o), N}}{\overline{\text{TEF}}_{(i-o)}} \right) + 3$

Table S2: Trophic amino acid specific parameter values for β and trophic enrichment factors (TEF) to test parameterization of trophic position calculations using multiple TDGs-TEFs and β values. The source amino acid (o) for all parameters was phenylalanine (Supplementary Material Appendix 1, Table S1, Figures S2 & S3). Values are mean \pm SD.

Trophic Amino Acid (i)	$\beta_{(i-o), N}$ Nielsen et al. 2015	$\beta_{(i-o), V}$ Vander Zanden et al. 2013	$\beta_{(i-o), NV}$ This study	$TEF_{(i-o), j}$ Germain et al. 2013	$TEF_{(i-o)}$ Nielsen et al. 2015
Glutamic acid (Glu)	2.9 <u>\pm 2.0</u>	-8.7 <u>\pm 1.1</u>	-3.9 <u>\pm 1.2</u>	3.4 <u>\pm 2.4</u>	6.6 <u>\pm 1.7</u>
Alanine (Ala)	2.8 <u>\pm 2.2</u>	-8.0 <u>\pm 1.0</u>	-3.6 <u>\pm 1.1</u>	2.5 <u>\pm 2.9</u>	6.8 <u>\pm 2.2</u>
Aspartic Acid (Asp)	1.8 <u>\pm 2.9</u>	-7.3 <u>\pm 1.1</u>	-4.2 <u>\pm 1.0</u>	3.5 <u>\pm 1.8</u>	5.4 <u>\pm 1.8*</u>
Valine (Val)	3.4 <u>\pm 2.9</u>	-6.8 <u>\pm 1.0</u>	-2.6 <u>\pm 0.9</u>	7.5 <u>\pm 3.7</u>	4.6 <u>\pm 3.4</u>
Proline (Pro)	2.7 <u>\pm 2.1</u>	-7.7 <u>\pm 1.2*</u>	-5.1 <u>\pm 1.1</u>	5.5 <u>\pm 3.4</u>	5.0 <u>\pm 1.8</u>
Not reported used average of other amino acids					

Table S3: Covariates used to test ocean condition as a bottom-up driver of harbor seal trophic ecology. Total number of models tested = 35.

	Time Series Description	Length	Source
Discharge	Total discharge from the Columbia River at Dalles, WA during summer months of high discharge (May-Oct) from monthly U.S. Geological Survey discharge data.	1879-2018	Data Source: USGS 14105700
Sea Surface Temperature (SST)	Average of monthly NOAA Extended Reconstructed SST for summer (Jul-Sep) in coastal Washington (48°N, 125°W).	1854-2019	Data Source: NOAA ERSST V5 SST data was obtained from NOAA_ERSST_V5 data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at https://www.esrl.noaa.gov/psd/ (Huang et al. 2017).
Upwelling	Mean coastal upwelling index (CUI) coastal Washington (45°N, 125°W) using Bakun upwelling calculation based on Ekman's theory of mass transport due to wind stress, for spring (Apr-Jun) and summer (Jun-Sep).	1946-2019.	Data Source: NOAA ERD SWFSC
North Pacific Gyre Oscillation	2nd dominant mode of sea surface height variability in the northeast Pacific. Correlates with fluctuations in salinity nutrients and chlorophyll-a.	1950-2019	Data Source: Di Lorenzo et al. 2008. NPGO
Multivariate ENSO Index	The extended Multivariate ENSO Index (MEI) uses Principle Component analysis on six variables: sea-level pressure, u and v component of the surface wind vector, sea surface temperature and cloudiness fraction in the tropical Pacific.	1950-2019	Data Source: NOAA/ESRL (https://psl.noaa.gov/enso/mei/ext/table.ext.html) via California Current Integrated Ecosystem Assessment MEI
Pacific Decadal Oscillation	Same as eastern Bering Sea	1900-2018	Data Sources: PDQ ; Zhang et al. 1997; Mantua et al 1997

Table S4: Covariates used to test prey availability as a bottom-up driver of harbor seal trophic ecology. Total number of models tested = 26.

	Time Series Description	Length	Source
Herring Biomass	Adult herring spawning biomass from egg deposition surveys for the estimated from Washington State Department of Fish and wildlife by Siple and Francis 2015.(MARSS output section S5, Figures S11 & S12)	1973-2012	Siple, M.C. and T.B. Francis. 2015. Population diversity in Pacific herring of the Puget Sound, USA.
Hake Biomass	Pacific Hake (whiting) relative spawning biomass in US and Canadian waters.	1973-2012	Berger et al. 2017. Table 8 total spawning biomass.
Chinook Salmon Spawners	Chinook salmon spawner summary data including all populations with a time series with data from at least 1973. Includes: Cedar River, Ceweeman River, Elochoman River, Grays and Chinook Rivers, Green River, Kalama River, Lewis River, Lower Cowlitz River, Lower and Upper Sauk River, Lower and Upper Skagit River, McKenzie River, Mid-Hood Canal, Nisqually River, Puyallup River, Skokomish River, Skykomish River, Snoqualmie River, Suiattle River, Toutle River, Upper Gorge Tributaries, White River and White Salmon River.	1973-2012	Northwest Fisheries Science Center, 2020: SPS Abundance - Salmon spawner abundance data compilation and database management, https://www.webapps.nwfsc.noaa.gov/apex/f?p=261:1::NO::P1_ARCHIVE_NOTE_CHEC_K:1&cs=1A0A1845C9A3C7202FD5C2934C6FD9410#
Chinook Salmon Smolt Production	Hatchery release data from the Regional Mark Information System and Wild Salmon Production data summarized by Chasco et al. 2017. Data was summed across both datasets for total juvenile salmon production.	1973-2012	RMIS: https://www.rmis.org/rmis_login.php?action=Login&system=cwt Summarized: https://github.com/bchasco/COAST_WIDE
Harbor Seal Abundance	Harbor seal population estimates based on coastal estuary, eastern Bays, Hood Canal, Olympic Peninsula, Puget Sound, San Juan Islands, and the Strait of Juan de Fuca counts. (MARSS output section S5, Figures S13 & S14)	1975-2012	Jeffries, S., H. Huber, J. Calambokidis and J. Laake. 2003. Trends and status of harbor seals in Washington state: 1978-1999. The Journal of Wildlife Management 67: 207-218.

Table S5: Full candidate model set ($n = 35$) for ocean condition modelling. The same candidate models were used for the physiological delay, 1-year ecological delay, and 2-year ecological delay models.

Ocean Condition Candidate Models

Covariates
1. Null
2. Location Only
3. PDO, Location
4. NPGO, Location
5. MEI, Location
6. Upwelling (Spring), Location
7. NPGO, PDO, Location
8. PDO, Upwelling (Spring), Location
9. NPGO, Upwelling (Spring), Location
10. MEI, Upwelling (Spring), Location
11. SST (Summer), Location
12. SST (Summer), PDO, Location
13. SST (Summer), NPGO, Location
14. SST (Summer), MEI, Location
15. SST (Summer), Upwelling (Spring), Location
16. SST (Summer), PDO, Upwelling (Spring), Location
17. SST (Summer), NPGO, Upwelling (Spring), Location
18. SST (Summer), MEI, Upwelling (Spring), Location
19. Upwelling (Summer), Location
20. Upwelling (Summer), PDO, Location
21. Upwelling (Summer), NPGO, Location
22. Upwelling (Summer), MEI, Location
23. Upwelling (Summer), NPGO, Upwelling (Spring), Location
24. Columbia Discharge (High), Location

25. Columbia Discharge (High), PDO, Location
 26. Columbia Discharge (High), NPGO, Location
 27. Columbia Discharge (High), MEI, Location
 28. Upwelling (Spring), Location
 29. Columbia Discharge (High), PDO, Upwelling (Spring), Location
 30. Columbia Discharge High, NPGO, Upwelling (Spring), Location
 31. Columbia Discharge High, MEI, Upwelling (Spring), Location
 32. Columbia Discharge (High), SST (Summer), Location
 33. Columbia Discharge (High), Upwelling (Summer), Location
 34. SST (Summer), Upwelling (Summer), Location
 35. SST (Summer), Upwelling (Summer), Columbia Discharge (High), Location
-

Table S6: Full candidate model set ($n = 26$) for prey availability modelling. The same candidate models were used for the physiological delay, 1-year ecological delay, and 2-year ecological delay models.

Food Web Candidate Models	
<i>Covariates</i>	
1.	Null
2.	Location Only
3.	Herring Spawning Biomass, Location
4.	Chinook Escapements, Location
5.	Chinook Smolt Production, Location
6.	Hake Spawning Biomass, Location
7.	Herring Spawning Biomass, Chinook Escapements, Location
8.	Herring Spawning Biomass, Hake Spawning Biomass, Location
9.	Herring Spawning Biomass, Chinook Smolt Production, Location
10.	Chinook Escapements, Hake Spawning Biomass, Location
11.	Chinook Escapements, Chinook Smolt Production, Location
12.	Chinook Smolt Production, Hake Spawning Biomass, Location
13.	Chinook Escapement, Chinook Smolt Production, Hake Spawning Biomass, Location
14.	Herring Spawning Biomass, Chinook Smolt Production, Hake Spawning Biomass, Location
15.	Chinook Escapements, Chinook Smolt Production, Herring Spawning Biomass, Location
16.	Herring Spawning Biomass, Hake Spawning Biomass, Chinook Escapements, Location
17.	Harbor Seal Abundance, Location
18.	Harbor Seal Abundance, Herring Spawning Biomass, Location
19.	Harbor Seal Abundance, Chinook Escapements, Location
20.	Harbor Seal Abundance, Chinook Smolt Production, Location
21.	Harbor seal Abundance, Hake Spawning biomass, Location
22.	Harbor Seal Abundance, Herring biomass, Chinook Escapements, Location
23.	Harbor Seal Abundance, Herring Spawning Biomass, Hake Spawning Biomass, Location
24.	Harbor Seal Abundance, Herring Spawning Biomass, Chinook Smolt Production, Location

25. Harbor Seal Abundance, Chinook Escapements, Hake Spawning Biomass, Location
 26. Harbor Seal Abundance, Chinook Smolt Production, Hake Spawning Biomass, Location
-
-

For Review Only

Table S7: Top ten ocean condition models with the most support (lowest AIC_C) with a physiological delay applied.

Physiological Delay Top 10 Models (ocean condition)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
23. Upwelling (Summer), NPGO, Upwelling (Spring), Location	742.75	0
35. SST (Summer), Upwelling (Summer), Columbia Discharge (High), Location	743.39	0.63
33. Columbia Discharge (High), Upwelling (Summer), Location	744.12	1.36
19. Upwelling (Summer), Location	744.3	1.55
34. SST (Summer), Upwelling (Summer), Location	744.7	1.95
21. Upwelling (Summer), NPGO, Location	745.25	2.5
22. Upwelling (Summer), MEI, Location	745.55	2.8
20. Upwelling (Summer), PDO, Location	746.11	3.36
26. Columbia Discharge (High), NPGO, Location	754.16	11.41
30. Columbia Discharge High, NPGO, Upwelling (Spring), Location	754.71	11.96

Table S8: Top ten ocean condition models with the most support (lowest AIC_C) with a 1-year ecological delay applied.

1-Year Ecological Delay Top 10 Models (ocean condition)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
15. SST (Summer), Upwelling (Spring), Location	734.84	0
16. SST (Summer), PDO, Upwelling (Spring), Location	736.55	1.7
18. SST (Summer), MEI, Upwelling (Spring), Location	736.65	1.81
17. SST (Summer), NPGO, Upwelling (Spring), Location	736.8	1.95
14. SST (Summer), MEI, Location	738.91	4.07
11. SST (Summer), Location	740.21	5.37
32. Columbia Discharge (High), SST (Summer), Location	741.3	6.46
12. SST (Summer), PDO, Location	741.34	6.49
34. SST (Summer), Upwelling (Summer), Location	741.99	7.15
13. SST (Summer), NPGO, Location	742.04	7.2

Table S9: Top ten ocean condition models with the most support (lowest AIC_C) with a 2-year ecological delay applied.

2-Year Ecological Delay Top 10 Models (ocean condition)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
24. Columbia Discharge (High), Location	742.09	0
33. Columbia Discharge (High), Upwelling (Summer), Location	742.83	0.74
26. Columbia Discharge (High), NPGO, Location	743.06	0.97
25. Columbia Discharge (High), PDO, Location	743.54	1.45
28. Upwelling (Spring), Location	743.86	1.77
27. Columbia Discharge (High), MEI, Location	744.04	1.95
32. Columbia Discharge (High), SST (Summer), Location	744.07	1.98
35. SST (Summer), Upwelling (Summer), Columbia Discharge (High), Location	744.48	2.38
29. Columbia Discharge (High), PDO, Upwelling (Spring), Location	744.56	2.47
30. Columbia Discharge High, NPGO, Upwelling (Spring), Location	745.06	2.97

Table S10: Top ten prey availability models with the most support (lowest AIC_C) with a physiological delay applied.

Physiological Delay Top 10 Models (Prey Availability)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
14. Herring Spawning Biomass, Chinook Smolt Production, Hake Spawning Biomass, Location	547.29	0
12. Chinook Smolt Production, Hake Spawning Biomass, Location	547.58	0.29
26. Harbor Seal Abundance, Chinook Smolt Production, Hake Spawning Biomass, Location	549.48	2.2
13. Chinook Escapement, Chinook Smolt Production, Hake Spawning Biomass, Location	549.5	2.21
23. Harbor Seal Abundance, Herring Spawning Biomass, Hake Spawning Biomass, Location	549.54	2.25
6. Hake Spawning Biomass, Location	549.55	2.27
21. Harbor seal Abundance, Hake Spawning biomass, Location	551.18	3.89
10. Chinook Escapements, Hake Spawning Biomass, Location	551.46	4.18
5. Chinook Smolts Production, Location	552.72	5.43
16. Herring Spawning Biomass, Hake Spawning Biomass, Chinook Escapements, Location	552.97	5.69

Table S11: Top ten prey availability models with the most support (lowest AIC_C) with a 1-year ecological applied.

1-Year Ecological Top 10 Models (Prey Availability)

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
13. Chinook Escapement, Chinook Smolt Production, Hake Spawning Biomass, Location	554.76	0
12. Chinook Smolt Production, Hake Spawning Biomass, Location	555.28	0.53
11. Chinook Escapements, Chinook Smolt Production, Location	555.56	0.8
14. Herring Spawning Biomass, Chinook Smolt Production, Hake Spawning Biomass, Location	555.91	1.15
26. Harbor Seal Abundance, Chinook Smolt Production, Hake Spawning Biomass, Location	556.78	2.03
5. Chinook Smolts Production, Location	557.22	2.47
15. Chinook Escapements, Chinook Smolt Production, Herring Spawning Biomass, Location	557.5	2.74
20. Harbor Seal Abundance, Chinook Smolt Production, Location	559.09	4.33
9. Herring Spawning Biomass, Chinook Smolt Production, Location	559.22	4.46
24. Harbor Seal Abundance, Herring Spawning Biomass, Chinook Smolt Production, Location	560.99	6.23

Table S12: Top ten prey availability models with the most support (lowest AIC_C) with a 2-year ecological delay applied.**2-Year Ecological Top 10 Models (Prey Availability)**

<i>Covariates</i>	<i>AICc</i>	<i>delta AICc</i>
11. Chinook Escapements, Chinook Smolt Production, Location	480.69	0
10. Chinook Escapements, Hake Spawning Biomass, Location	481.41	0.72
7. Herring Spawning Biomass, Chinook Escapements, Location	484.2	3.51
4. Chinook Escapements, Location	484.9	4.21
12. Chinook Smolt Production, Hake Spawning Biomass, Location	485.17	4.48
5. Chinook Smolts Production, Location	486.5	5.81
6. Hake Spawning Biomass, Location	486.56	5.87
19. Harbor Seal Abundance, Chinook Escapements, Location	486.74	6.05
9. Herring Spawning Biomass, Chinook Smolt Production, Location	487.91	7.22
1. Null	488.12	7.43

Amino Acid	Mean Precision
Phenylalanine	0.34
Glutamic Acid	0.56
Alanine	0.46
Proline	0.48
Valine	0.38
Aspartic Acid	0.83
Norleucine	0.40

Table S13: Mean standard precision for amino acids calculated as the average standard deviation of standard triplicate injections.

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Table S14: Pearson correlation coefficients for harbor seal trophic position calculated from five trophic amino acids.

Trophic Amino Acid	Glutamic acid (Glu)	Alanine (Ala)	Aspartic Acid (Asp)	Proline (Pro)	Valine (Val)
Glutamic acid (Glu)	-				
Alanine (Ala)	0.79	-			
Aspartic Acid (Asp)	0.25	0.29	-		
Proline (Pro)	0.46	0.61	0.17	-	
Valine (Val)	0.58	0.61	0.18	0.39	-

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Table S15: Covariates included in the best models using standard linear models and only glutamic acid to calculate trophic position. Supported models is the number of models with delta AIC < 2.

Model	Covariates	Supported Models	Comparison to hierarchical models
<i>Ocean Condition Models</i>			
Physiological Delay	Summer upwelling, Columbia River discharge	14	Summer upwelling was included in best model and 6 others
1-year ecological delay	Sea surface temperature, spring upwelling	3	Sea surface temperature was included in all supported models
2-year ecological delay	Summer upwelling, MEI	6	Columbia River discharge was included in one supported glutamic acid only model
<i>Food Web Model</i>			
Physiological Delay	Location	2	Best hierarchical model (herring spawning biomass) was included in one supported glutamic acid only models
1-year ecological delay	Chinook smolts	3	Hake spawning biomass was not included in the supported models
2-year ecological delay	Location	6	Chinook smolt production was included in 2 supported models

Table S16: Data summary showing mean trophic position calculated from glutamic acid (trophic) and phenylalanine (source), number of samples (n), and standard deviation (sd) for each year. Standard deviation of trophic position was calculated using the standard deviations for TEFs and β (Appendix S1:Table S2) and the analytical error for glutamic acid and phenylalanine (Appendix S1:Table S13) following the methods of Blum et al. 2013.

<u>Year</u>	<u>mean</u>	<u>SD</u>	<u>n</u>
<u>1928</u>	<u>4.3</u>	<u>0.2</u>	<u>3</u>
<u>1937</u>	<u>4.0</u>	<u>0.3</u>	<u>1</u>
<u>1942</u>	<u>4.4</u>	<u>0.1</u>	<u>9</u>
<u>1959</u>	<u>4.9</u>	<u>0.4</u>	<u>1</u>
<u>1969</u>	<u>4.5</u>	<u>0.1</u>	<u>9</u>
<u>1970</u>	<u>4.6</u>	<u>0.2</u>	<u>4</u>
<u>1971</u>	<u>4.5</u>	<u>0.3</u>	<u>2</u>
<u>1972</u>	<u>5.0</u>	<u>0.2</u>	<u>6</u>
<u>1975</u>	<u>4.1</u>	<u>0.3</u>	<u>1</u>
<u>1976</u>	<u>4.0</u>	<u>0.2</u>	<u>3</u>
<u>1977</u>	<u>4.7</u>	<u>0.1</u>	<u>14</u>
<u>1978</u>	<u>4.8</u>	<u>0.2</u>	<u>4</u>
<u>1979</u>	<u>4.2</u>	<u>0.1</u>	<u>5</u>
<u>1980</u>	<u>4.6</u>	<u>0.3</u>	<u>2</u>
<u>1981</u>	<u>4.7</u>	<u>0.2</u>	<u>4</u>
<u>1982</u>	<u>4.5</u>	<u>0.1</u>	<u>7</u>
<u>1983</u>	<u>4.2</u>	<u>0.2</u>	<u>3</u>
<u>1986</u>	<u>4.5</u>	<u>0.4</u>	<u>1</u>
<u>1987</u>	<u>4.6</u>	<u>0.1</u>	<u>8</u>
<u>1988</u>	<u>4.8</u>	<u>0.4</u>	<u>1</u>

	<u>1989</u>	<u>4.5</u>	<u>0.3</u>	<u>2</u>
	<u>1991</u>	<u>4.8</u>	<u>0.2</u>	<u>4</u>
	<u>1992</u>	<u>4.7</u>	<u>0.2</u>	<u>5</u>
	<u>1994</u>	<u>4.5</u>	<u>0.4</u>	<u>1</u>
	<u>1996</u>	<u>4.3</u>	<u>0.3</u>	<u>1</u>
	<u>1998</u>	<u>4.8</u>	<u>0.3</u>	<u>3</u>
	<u>1999</u>	<u>4.1</u>	<u>0.3</u>	<u>1</u>
	<u>2004</u>	<u>4.4</u>	<u>0.4</u>	<u>1</u>
	<u>2006</u>	<u>4.0</u>	<u>0.2</u>	<u>2</u>
	<u>2007</u>	<u>4.6</u>	<u>0.2</u>	<u>4</u>
	<u>2008</u>	<u>4.7</u>	<u>0.3</u>	<u>2</u>
	<u>2011</u>	<u>4.1</u>	<u>0.3</u>	<u>1</u>
	<u>2012</u>	<u>4.5</u>	<u>0.4</u>	<u>1</u>
	<u>2013</u>	<u>4.5</u>	<u>0.2</u>	<u>6</u>
	<u>2014</u>	<u>4.0</u>	<u>0.3</u>	<u>1</u>

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