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1 **Title:** Recent divergent changes in Alaskan pinniped trophic position detected using compound-
2 specific stable isotope analysis

3 **Running Title:** Recent trophic position changes in pinnipeds

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10

1 **Abstract**

2 Over the past century Alaskan pinnipeds have experienced dramatic changes in
3 abundance, but these changes have been highly variable across species and region. In recent
4 decades, changes in atmospheric forcing and sea surface temperature have been particularly
5 pronounced in the Gulf of Alaska and eastern Bering Sea, impacting the food webs in which
6 Alaskan pinnipeds forage. We used compound-specific stable isotope analysis of nitrogen in
7 amino acids to estimate historic and modern trophic position of harbor seals and Steller sea lions
8 in the Gulf of Alaska and Bristol Bay. We applied a Bayesian hierarchical framework to
9 determine whether shared trends through time exist across pinnipeds (classified by species and
10 region) on decadal scales. Model results identified both shared trends through time and
11 classification-specific decadal changes in pinniped trophic position. The largest change in trophic
12 position occurred in the 2000s and 2010s and was observed in both Steller sea lions and harbor
13 seals in the Gulf of Alaska, but not harbor seals in Bristol Bay or Iliamna Lake. Divergent
14 trophic position patterns in the 2000s were identified in the western stock of Steller sea lions,
15 which increased in trophic position, and sympatric harbor seals in the northern Gulf of Alaska,
16 which decreased in trophic position. Our results indicate that these species have begun exploiting
17 distinct trophic niches or experiencing unique food web conditions in recent decades in the Gulf
18 of Alaska, likely in response to recent climate-induced ecological change in the region.

19

1 **Keywords**

2 Steller sea lion, harbor seal, compound-specific stable isotope analysis, trophic position, Alaska,
3 *Phoca vitulina, Eumetopias jubatus*

1 **1. Introduction**

2 Over the past century, pinniped populations in the northeast Pacific Ocean have
3 experienced changes in adult and pup abundances (Muto et al. 2020). Understanding specific
4 drivers of these population trends is important for management, as multiple stocks have been
5 listed as threatened or endangered over the past two decades (Muto et al. 2020). The observed
6 population dynamics have also corresponded with shifts in both the physical and ecological
7 marine environment, which frequently occur simultaneously. As a result, disentangling drivers of
8 population trends is complex, as multiple factors (environmental conditions, prey availability,
9 anthropogenic disturbances) can change in tandem and potentially act synergistically on pinniped
10 populations.

11 Data on long-term trends in trophic position across regions, species, and populations is
12 one potential way to assess how food web changes have impacted pinnipeds in Alaska. This
13 approach can identify how broad shifts in foraging ecology correspond to changes in abundance
14 and population dynamics. More specifically, examining trophic position during periods of
15 declining versus increasing predator abundance can provide insight into whether foraging
16 behavior and prey availability are important drivers of population dynamics. In this study, we
17 aim to identify whether common temporal trends in trophic ecology exist across harbor seals
18 (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*) and their locations by deriving 70-
19 years of trophic position data from compound-specific stable isotope analysis (CSIA) of museum
20 specimens.

21 Following climatic changes in the 1970s that altered ocean currents and sea surface
22 temperature (Hare and Mantua 2000), most Gulf of Alaska and Bering Sea pinniped populations
23 experienced declines that persisted through the 1990s (Muto et al. 2020). However, these
24 responses differed across populations and species. For example, the western stock of Steller sea

lions (located west of 144°W) decreased from approximately 240,000 animals in the late 1970s to 50,000 in 2000 (Burkanov & Loughlin 2005). Similarly, harbor seal populations in Prince William Sound and Glacier Bay declined by approximately 60% between the 1980s and 2000 (Frost et al. 1999, Womble et al. 2010). In contrast, the eastern stock of Steller sea lions (located east of 144°W) increased by 3-4% per year over the same time period (Figure 2, Muto et al. 2020, Pitcher et al. 2007). More recently, atmospheric circulation anomalies in the northeast Pacific Ocean have resulted in unprecedently warm sea surface temperatures during the past decade (Walsh et al. 2018) and this environmental shift has altered fish abundances (Bond 2015, Litzow et al. 2020). For example, the unprecedented marine heatwave that occurred in 2014 - 2016 triggered dramatic ecosystem change, including a 71% decline in Pacific cod in the Gulf of Alaska (Barbeaux et al. 2020). Declines in phytoplankton biomass, forage fish abundance, and changes in community structure as a whole were also observed (Suryan et al. 2021). During this recent period of environmental change, many pinniped populations have experienced increases or stabilization of population abundance (Muto et al. 2020, Figure 2), although declines in some Gulf of Alaska Steller sea lion populations were observed following the marine heat wave (Suryan et al. 2021).

These variable changes in Alaskan pinniped populations over the past 50 years cannot be attributed to a single cause, as multiple environmental, anthropogenic, and ecological factors have changed simultaneously. For example, the rapid decline of the western stock of Steller sea lions between the 1970s and 1990s has been attributed to myriad factors, including change to the physical environment, competition with fisheries for common prey, predation, disease, and human-caused mortality (Atkinson et al. 2008). Glacier Bay harbor seal populations have primarily, but not exclusively, been impacted by the decline of sea ice, which provides a majority

1 of their haulout sites (Womble et al. 2010). Population declines have also been associated with
2 increased numbers of tour vessels, particularly in glacier fjords that provide important nursing
3 and whelping habitat (Jansen et al. 2015, Matthews et al. 2016). The differences in pinniped
4 population trends across the Gulf of Alaska and Bering Sea suggest varied environmental and
5 ecological drivers underlying these dynamics. Interestingly, harbor seals and Steller sea lions that
6 occur in the same geographic region (sympatric) have experienced different population trends
7 over similar time period (Figure 2). Identifying trophic position trends through time that are
8 shared, compared to changes that only impact a specific species or region, can elucidate how
9 widespread ecological forcing versus localized change influence top predators and potentially
10 explain variable population abundance trends.

11 Both harbor seals and Steller sea lions exhibit generalist, piscivorous foraging strategies,
12 although differences in foraging range, body size, and diet exist. Adult harbor seals have high
13 site fidelity, opportunistically forage 5 - 10 km from haulout sites and at depths < 200 m (Lance
14 et al. 2012, Lowry et al. 2001), and weigh up to 300 pounds. Steller sea lions are central place
15 foragers known to migrate to prey aggregations on the continental shelf and oceanographic
16 boundary zones (Sinclair and Zeppelin 2002, Womble and Sigler 2006). Foraging trips can last
17 1-3 days (Maniscalco et al. 2006) with average distances of 133 km for adult females (Merrick
18 and Loughlin 1997), although foraging trips are shorter in the breeding season (Maniscalco et al.
19 2006). Adult females can weigh up to 800 pounds whereas adult males can exceed 2,500 pounds,
20 indicating a higher energetic demand compared to harbor seals. Diet studies of Steller sea lions
21 and harbor seals are spatially and temporally limited, and primarily utilize scat samples. In the
22 Gulf of Alaska, gadids, cephalopods, and forage fishes are prevalent in both harbor seal and

1 Steller sea lion diet (Sinclair and Zeppelin 2002, Geiger et al. 2013), whereas salmonids are also
2 important for harbors seals in Bristol Bay and Iliamna lake (Hauser et al. 2008).

3 Stable isotopes have been used to reconstruct historical differences in diet and trophic
4 position in Alaskan pinnipeds (Hobson et al. 1997, Hiron et al. 2001, Brennan et al. 2019).

5 These previous studies utilized bulk stable isotope analysis exclusively and were therefore
6 limited in their inferential strength. Differences in the bulk $^{15}\text{N}/^{14}\text{N}$ of consumer tissues can
7 indicate either a trophic level change of the consumer or a change in nitrogen resources at the
8 base of the food web. The specific cause of the isotopic variation cannot be ascertained from
9 consumer bulk stable isotope values unless the data are paired with temporal information on
10 $^{15}\text{N}/^{14}\text{N}$ in primary producers. Lack of consistent, concurrent sampling of nitrogen stable isotope
11 composition of primary producers therefore presents a challenge for previous long-term studies
12 of the trophic dynamics of consumers from bulk stable isotope data. CSIA data address this
13 challenge, as amino acids exhibit two distinct patterns in isotopic enrichment: trophic amino
14 acids (i.e., glutamic acid, alanine, proline) become enriched in ^{15}N with each trophic transfer and
15 source amino acids (i.e., phenylalanine) show minimal change and thus are reflective of the base
16 of the food web (McClelland & Montoya, 2002, Chikaraishi et al. 2009, Ohkouchi et al. 2017).

17 With the ability to internally correct for expected changes in $^{15}\text{N}/^{14}\text{N}$ at the base of the food web
18 (Fedder et al. 2021, McMahon et al. 2021), CSIA allows for a more robust retrospective
19 analysis of consumer trophic dynamics on decadal and century scales.

20 The objective of this work is to describe and compare changes in trophic ecology for
21 Alaskan pinnipeds throughout the past century and investigate trophic position differences for
22 sympatric populations. We apply hierarchical Bayesian analyses to 70 years of trophic position
23 data derived from CSIA from pinnipeds (harbor seal and Steller sea lion) in the Gulf of Alaska,

1 Bristol Bay, and a small population of freshwater harbor seals in Iliamna Lake, Alaska which is
2 adjacent to Bristol Bay. We build on previous research examining pinniped nitrogen stable
3 isotope composition (Hobson et al. 1997, Hirons et al 2001, Misarti et al. 2009, Brennan et al.
4 2019) by adding two decades of data to the record (2000s and 2010s) and incorporating a broad
5 spatial scope (Bristol Bay, Iliamna Lake, Gulf of Alaska). Additionally, by analyzing nitrogen
6 stable isotopes derived from amino acids, we were able to control for known changes in nitrogen
7 resources and phytoplankton composition at the base of the food web that can confound trophic
8 position interpretations from bulk stable isotope data collected over decadal scales (Feddern et al.
9 2021). Furthermore, by comparing trophic position dynamics across species and region through
10 time, regional and location-specific ecological responses to a changing ecosystem can be
11 identified.

1 **2. Materials and Methods**

2 *2.1 Sample collection and analysis*

3 Samples were obtained using methods described in Feddern et al. (2021). Briefly, harbor
4 seal and Steller sea lion bones were sampled from specimens curated at the University of Alaska
5 Museum of the North (*Supplementary Information Table S1*). Specimens were treated by
6 maceration in warm water and soaked in a dilute ammonia solution then stored in acid free
7 boxes. Adult specimens were sampled exclusively to avoid dietary differences between adults
8 and juveniles. Specimens were classified based on species and region. We prioritized long-term
9 temporal coverage in four regional classifications of harbor seals (Iliamna Lake, southeast Gulf
10 of Alaska, northern Gulf of Alaska, eastern Bering Sea) and two regional classifications of
11 Steller sea lions (eastern and western stocks) for a total of 6 species x region classifications.
12 Specimens were extremely limited for the eastern Steller sea lion stock (n = 2) and Iliamna Lake
13 harbor seas (n = 3). We also prioritized specimens with sex and age identifications, but these data
14 were not available for some specimens. A total of 106 harbor seal and 21 Steller sea lion
15 specimens were sampled representing the 1950s to 2010s (Figure 1).

16 Steller sea lions were classified according to the National Oceanic and Atmospheric
17 Administration's (NOAA) distinct population segments, where Steller sea lions east of 144°W
18 are considered the eastern stock and west of 144°W are considered the western stock (Figure 1).
19 NOAA has identified twelve stocks of harbor seals in Alaska and, due to limitations of archived
20 specimens, harbor seals were not able to be classified according to NOAA stocks. Instead, they
21 were classified based on their range relative to the Steller sea lion stocks and utilization of
22 marine versus freshwater habitats. Harbor seals that were west of 144°W, which included
23 samples from the Prince William Sound and Cook Inlet/Shelikof Strait stocks (Figure 1), were
24 classified as northern Gulf of Alaska harbor seals. Harbor seals that were located east of 144°W,

1 which included samples from the Glacier Bay/Icy Strait, Sitka/Chatham Strait, Lynn
2 Canal/Stephens Passage, Dixon/Capes Decisions, and Clarence Strait stocks (Figure 1), were
3 classified as southeast Gulf of Alaska harbor seals. The Bristol Bay harbor seal stock was
4 divided into two classifications, Bristol Bay referring to marine harbor seals, and Iliamna Lake
5 referring to freshwater harbor seals (Figure 1). This allowed for comparison of three pairs of
6 geographically overlapping classifications: western stock of Steller sea lions and northern Gulf
7 of Alaska harbors seals, eastern stock of Steller sea lions and southeast Gulf of Alaska harbor
8 seals, and Bristol Bay and Iliamna Lake harbor seals.

9 *2.2 Trophic position calculation*

10 Bone collagen within the samples was decalcified, acid hydrolyzed, derivatized and
11 analyzed for compound-specific stable isotope analysis (CSIA) of nitrogen ($\delta^{15}\text{N}$) for 12
12 individual amino acids following the protocol described in Feddern et al. (2021). $\delta^{15}\text{N}$ was
13 measured as:

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

15 Collagen samples were measured in triplicate with a laboratory standard containing a 12 amino
16 acid mixture of known isotopic composition. Full analytical details are described in
17 Supplementary Information Appendix S1.

18 Trophic position was calculated using a harbor seal-specific trophic discrimination factor
19 (difference in $^{15}\text{N}/^{14}\text{N}$ between trophic and source amino acids in consumers for a trophic
20 transfer; Germain et al. 2013). This approach assumed trophic discrimination factors (TDF)
21 derived from controlled feeding studies of harbor seals were similar to Steller sea lions.
22 Applying a "multi-TDF" approach that combines both average and taxa-specific TDF can
23 improve trophic position estimates in marine predators including pinnipeds (Germain et al. 2013,

1 McMahon et al. 2019). The following equation was used to determine the trophic position of
 2 each sampled individual:

$$3 \quad 2. \text{ Trophic Position} = \left(\frac{\delta^{15}\text{N}_i - \delta^{15}\text{N}_o - \overline{TDF}_{(i-o),j} - \bar{\beta}_{(i-j)}}{\overline{TDF}_{(i-o)}} \right) + 2$$

4 where, $\delta^{15}\text{N}_i$ is the measured stable isotope composition of a trophic amino acid i in a sample and
 5 $\delta^{15}\text{N}_o$ is the stable isotope composition of a source amino acid o in a sample. $\overline{TDF}_{(i-o)}$ is the
 6 mean difference between given trophic amino acid i and source amino acid o across all
 7 consumers described in Nielsen et al. (2015). $TDF_{(i-o),j}$ is the trophic discrimination factor
 8 between trophic amino acid i and source amino acid o from a controlled feeding study of a
 9 specific consumer j ; here we use harbor seals from Germain et al. (2013; Table 1). $\bar{\beta}_{(i-o)}$ is the
 10 mean difference in $\delta^{15}\text{N}$ across aquatic phytoplankton between a specific trophic amino acid i
 11 and source amino acid o (Nielsen et al. 2015; Table 1). Nielsen et al. (2015) also determined
 12 using multiple amino acids to estimate trophic position improves precision. Therefore, we used
 13 multiple trophic amino acids i (alanine, glutamic acid, aspartic acid and proline) and one source
 14 amino acid o (phenylalanine) to calculate trophic position (Table 1). These amino acids were
 15 chosen based on their prevalence in previous studies to derive parameters for equation 2, and
 16 their concentrations in bone collagen (see Supplementary Information Appendix S1).

17 *2.3 Model framework*

18 Sex was considered as a predictor for trophic position, however, sex metadata were not
 19 available for all specimens. In order to evaluate difference in trophic position by sex, we fit
 20 linear statistical models to each individual trophic amino acid, by classification (species x
 21 region). These models took the following form:

$$22 \quad 3. y_i = \alpha + \beta x_i + \epsilon_i, \epsilon_i \sim N(0, \sigma)$$

1 where, y_i is trophic position for an individual amino acid and β is a vector of coefficients for the
 2 predictor, in this case sex, and epsilon are residual errors assumed to be normally distributed
 3 with mean 0 and standard deviation sigma. There was not sufficient metadata for the eastern
 4 stock Steller sea lion population or the Iliamna Lake population and these two classifications
 5 were omitted from this analysis.

6 A Bayesian hierarchical mixed effects model was used to identify decadal change across
 7 pinniped classifications (species x region), and the degree to which these changes were shared by
 8 testing the effects of classification, decade, and a classification-decade interaction as either
 9 population-level (fixed) or group-level (random) effects (see candidate models in Table 2).
 10 Hierarchical models share information across ‘groups’ to identify common responses, which
 11 refers to both decade and classification in this study. The interaction term allows for increased
 12 flexibility, letting each classification have slight departures from the group-level means. The
 13 mean and variance of pinniped trophic position for each region-species classification and decade
 14 were estimated using a generalized linear Bayesian hierarchical model with decade, population,
 15 and trophic amino acid as predictors:

$$16 \quad 4. y_i = \alpha + \beta x_i + \epsilon_i, \epsilon_i \sim N(0, \sigma_y)$$

$$17 \quad \alpha_{k=1:k} \sim N(\mu_{\alpha,k}, \sigma_{\alpha,k})$$

18 where, for data point i , β is a vector of coefficients for the unpooled predictors (fixed effects,
 19 Table 2) and α is a vector of coefficients for the partially pooled group-level predictors (random
 20 effects, Table 2) for group k (amino acid, decade or classification). At minimum, the α included a
 21 random term for the amino acid corresponding to data point i , and depending on the model
 22 included up to a total of 4 random effects (also effects of decade, classification, and their
 23 interaction, Model 6 in Table 2). For each random effect included, $\mu_{\alpha,k}$ and $\sigma_{\alpha,k}$ are

1 hyperparameters representing the mean and standard deviation of group-level effects on trophic
2 position, for random effect k . For models with more than one random effect, we assumed the
3 deviations to be independent and uncorrelated. We considered models that included decade,
4 classification, and the interaction between decade and classification either as fixed or random
5 effects (e.g. Model 4 v Model 6, Table 2), but did not consider models that included both as fixed
6 and random (Table 2). Parameter estimates were obtained using the brms package (Bürkner
7 2017, version 2.14.4) in R (R Core Development Team 2021, version 3.6.2), which implements a
8 Hamiltonian Monte Carlo sampler and its extension no-U-turn sampler (Hoffman & Gelman
9 2014) through Stan (Stan Development Team 2020). Minimally informative priors were used for
10 random effects (normal distributions with a mean of 0 and variance of 10) and fixed effects
11 (Student's t-distribution with a mean of 0, standard deviation of 2.5 and 3 degrees of freedom).
12 Trophic amino acid was included as a random effect for all models (Table 2). Selection of the
13 best models (Table 2) given the data was based on approximate leave-one-out cross-validation
14 (LOOIC) using the loo package (Veharci et al. 2017, version 2.4.1).

1 **Results**

2 We found no differences between the average male and female pinniped trophic position
3 over the 50-year study period (Figure 3) for the four tested species-region classifications. This
4 finding was consistent for all trophic amino acids-source amino acid pairs (Figure 3). Based on
5 glutamic acid trophic position estimates, both western stock Steller sea lions (2.6 ± 0.5 ; mean \pm
6 sd) and eastern stock Steller sea lions (2.7 ± 0.16) had similar trophic positions. Harbor seals in
7 the Gulf of Alaska foraged higher in the food web than their Steller sea lion counterparts (Figure
8 3). Harbor seals in the southeast region had a higher trophic position on average than any other
9 pinniped in this study (3.5 ± 0.3) but were similar to harbor seals in the northern region ($3.3 \pm$
10 0.5). Bristol Bay (3.1 ± 0.4) and Iliamna lake (3.0 ± 0.3) harbor seals had a lower trophic
11 position than their Gulf of Alaska counterparts on average (Figure 3).

12 *Common trends in Alaskan pinniped trophic position*

13 The best performing model (Table 2, model 6) of pinniped trophic position included both
14 species-region classification and decade as random effects (shared trends) along with an
15 interaction between population and decade (Table 2). Based on the support for decade and
16 classification to be included as group-level effects, these data support consistent differences
17 between classifications over time, as well as differences between trophic position for all
18 classifications. The supported interaction between population and decade (Table 2) indicates
19 distinct decadal changes in trophic position for species-region classifications exist. The model
20 that included decade, classification, and the interaction between decade and classification as
21 fixed effects (model 4) was also supported based on the models LOOIC (Table 2). Therefore, the
22 inclusion of the interaction term was more important for improving model performance than
23 inclusion of decade and classification as fixed versus random effects.

1 There were consistent differences in trophic position that varied by species and ocean
2 basin for the model with the most support. Harbor seals in the Gulf of Alaska had higher trophic
3 position than their Steller sea lion counterparts. The mean difference of the posterior
4 distributions indicated southeast Gulf of Alaska harbor seals have historically fed at 0.32 [-0.01,
5 0.61] (highest density 80% credible interval) trophic levels higher than sympatric eastern stock
6 Steller sea lions (Figure 4). Similarly, the mean difference of posterior distributions showed
7 northern Gulf of Alaska harbor seals fed 0.28 [-0.03, 0.50] trophic levels higher than the
8 sympatric western stock Steller sea lions. Within the Gulf of Alaska, the posterior distributions
9 for trophic position overlapped 39% between harbor seals and Steller sea lions in both the
10 eastern and western regions (Figure 4). Iliamna Lake harbor seals have historically fed at a lower
11 trophic level (mean posterior difference 0.16 [-0.11, 0.41]) than harbor seals in Bristol Bay, but
12 these two classifications have 66% overlap of the group-level posterior distributions for trophic
13 position (Figure 4). The 80% credible intervals included 0 for most region-species classifications
14 thus the posterior probabilities support marginal evidence for consistent differences in trophic
15 position between classifications. Regardless, the differences in posterior means were large,
16 although the distributions were wide.

17 There were no consistent decadal differences in trophic position across the region-species
18 classification (Figure 5). Pinniped trophic position in the 2000s was slightly higher for all
19 classifications (mean posterior difference 0.03 [-0.09, 0.16]) on average compared to 1990 and
20 the posterior distributions for 1990 and 2000 had an 85% overlap (Figure 5). Similarly, posterior
21 distributions in between 2000 and 2010 had a mean difference of -0.1 [-0.27, 0.08] with a 65%
22 overlap (Figure 4). Overall, decadal differences in pinniped trophic position through time were

1 smaller than the region-species classification effects and were likely ecologically
2 inconsequential.

3 *Spatial and temporal differences in pinniped trophic structure*

4 Distinct decadal changes in trophic position were observed for each species-region
5 classification and varied more than the shared decadal changes (Figure 6) as indicated by the
6 decade-classification interaction. Most, but not all, pinniped classifications experienced
7 substantial trophic level change in 2000 or 2010 but the magnitude and direction of this change
8 varied by region-species classification based on the combined effects of decade, classification,
9 and the decade-classification interaction (Figure 6). The recent decadal change in trophic
10 position was most prominent for the western stock of Steller sea lions which had a mean trophic
11 level decrease of 0.43 [-0.25, -0.60] from 1990 to 2000 (a percent decrease of 0.15) with only a
12 21% overlap between the posterior distributions (Figure 6E). This decline in trophic position
13 remained in the 2010s. A similar decline was observed in the southeast Gulf of Alaska harbor
14 seals. This population experienced relatively stable trophic position from 1960-1990, which then
15 declined on average by 0.31 [-0.19, -0.45] trophic levels in 2000 (33% posterior overlap) (Figure
16 6C). In contrast, harbor seals in the northern Gulf of Alaska had variable trophic position across
17 decades and had the highest trophic position in 2000 in contrast to their southeast Gulf of Alaska
18 harbor seals and Steller sea lion counterparts (Figure 6B). Data were only available for 2000 and
19 2010 for the eastern stock Steller sea lions, and trophic position was similar for this population
20 during both of these decades (Figure 6F). Both Bristol Bay and Iliamna Lake harbor seals had
21 relatively stable trophic position from 1950s until 2010s (Figure 6A & B). Bristol Bay harbor
22 seals experienced their lowest trophic level in the 1990s with a 0.24 [-0.54, 0.00] trophic level

- 1 decrease compared to the 1970s and 2000s, but the posterior distribution still overlapped 54%
- 2 with other decades (Figure 6A).

1 **Discussion**

2 Over the past 70 years, Alaskan pinnipeds have exhibited both common and distinct
3 differences in trophic position across region-species classification on decadal scales (Table 2).
4 While potential drivers of change in trophic position were not tested in this study due to data
5 limitations, our results support a combination of local-scale (i.e., vessel traffic, reduction of
6 glacial ice, local foraging) and regional-scale (i.e., environmental condition, basin-wide prey
7 abundance) changes may be influencing pinniped trophic ecology. Furthermore, the largest
8 decadal changes in pinniped trophic position were distinct for each region-species classification
9 and were most apparent during the most recent two decades (2000s and 2010s). These patterns
10 are more pronounced in the Gulf of Alaska compared to Bristol Bay (Figures 5 & 6).

11 *Regional and species trends in harbor seal trophic position*

12 Both Steller sea lions and harbor seals exhibit generalist foraging patterns (Lance et al.
13 2012, Geiger et al. 2013). Diets of Alaskan pinnipeds consist of similar prey species but vary
14 between species, population, and local availability of prey (Iverson et al. 1997, Hiron et al.
15 2001). Bulk stable isotope studies in the Gulf of Alaska have shown that Steller sea lions feed
16 lower in the food web compared to harbor seals (Iverson et al. 1997). Our CSIA analysis
17 confirms the interpretation of these previous studies that isotopic differences can be attributed to
18 trophic position changes and not isotopic shift of basal phytoplankton resources. Both western
19 and eastern stock Steller sea lions have lower trophic position compared to sympatric harbor seal
20 populations but have similar trophic position compared to other populations such as Iliamna
21 Lake. However, despite known differences in both diet (Sinclair and Zeppelin 2002, Geiger et al.
22 2013) and nearshore versus offshore foraging (Merrick and Loughlin 1997, Lowry et al. 2001)

1 between the two species, our results also show historical overlap in trophic position, indicating
2 potential trophic redundancy between harbor seals and Steller sea lions in the Gulf of Alaska.

3 Harbor seals in Bristol Bay and Iliamna Lake are managed as a single population (Muto
4 et al. 2020) despite lack of evidence of migration by the freshwater population and utilization of
5 different resources (Brennan et al. 2019). A previous study of strontium and carbon stable
6 isotopes showed Iliamna Lake harbor seals utilize freshwater-derived resources (resident lake
7 fishes), particularly early in life, and exhibit an ontogenetic shift to more marine resources
8 (returning sockeye salmon) later in life (Brennan et al. 2019). Based on CSIA nitrogen data,
9 Iliamna Lake harbor seals also forage lower in the food web compared to Bristol Bay harbor
10 seals. In addition, both classifications exhibited trophic stability, with the Bristol Bay harbor
11 seals only experiencing a trophic shift in the 1990s relative to the 1960s and 1970s. This
12 coincided with the lowest sockeye salmon returns to Iliamna Lake on record (Hilborn et al.
13 2003). Interestingly, the decrease in trophic position in the 1990s occurred simultaneously with
14 decreases in basin wide Bristol Bay harbor seal abundance in the late 1990s, which then
15 stabilized and increased in the 2000s and 2010s (Figure 2). Data were not available for the
16 freshwater harbor seals between 1990 and 2000 and thus it is unclear whether the freshwater
17 population also experienced a trophic position change during the 1990s when sockeye salmon
18 returns were low. While quantitative comparisons to salmon abundance were not made in this
19 study, salmon population abundance and harbor seal trophic ecology and population trends are
20 seemingly interrelated.

21 *Recent trophic position changes in the Gulf of Alaska*

22 Trophic position changes were observed in all pinniped classifications in the Gulf of
23 Alaska during the past two decades, although the direction of these changes varied on more local

1 scales. During the past two decades (2000-2020), harbor seals in the Gulf of Alaska have
2 experienced stabilization of most monitored populations following long-term declines that
3 persisted from the 1950s through the 1990s (Figure 2, Muto et al. 2020). During this same time
4 period, harbor seals in both southeast and northern Gulf of Alaska experienced a shift in trophic
5 position that was particularly prominent in the 2000s compared to historic estimates of trophic
6 position (Figure 6B & C). It is possible that the observed trophic position shift may have
7 contributed to the population stabilization of Gulf of Alaska harbor seals, either by an increase in
8 prey availability or opportunistically foraging on a novel prey source. Gagne et al. (2018)
9 observed similar trophic position declines in seabird populations, which were attributed to a shift
10 in diet from fish to squid. A similar dietary shift could explain the observed trophic position shift
11 in southeast Gulf of Alaska harbor seals and western stock Steller sea lions.

12 Recent regional change in the Gulf of Alaskan food webs has been well documented in
13 other species and primarily attributed to bottom-up effects of climate (Barbeaux et al. 2020,
14 Litzow et al. 2020). These region-wide trends likely altered prey availability for pinniped
15 populations in the Gulf of Alaska. How pinniped populations have adapted their foraging
16 ecology, however, indicates regional and species trophic divergence, which could be attributed to
17 either local-scale foraging adaptations or differences in prey availability. Pinniped groups that
18 overlap in space (Figure 1) revealed divergent trends in trophic position between Steller sea lions
19 and harbor seals in recent decades (Figure 6B & E). For example, trophic position of northern
20 Gulf of Alaska harbor seals increased in the 2000s while the western stock of Steller sea lions
21 decreased. For western stock Steller sea lions, this shift also persisted into the 2010s (Figure 6E).
22 Posterior distributions of western stock Steller sea lions and northern Gulf of Alaska harbor seals
23 overlapped by 63% in the 1950s but only overlapped by 3% in the 2000s (Figure 6B & E). The

1 recent change in pinniped trophic position within the Gulf of Alaska coincided with population
2 abundance stabilization, albeit at lower than historical abundance for most populations. This
3 trophic divergence indicates there could be increased competition for resources between northern
4 Gulf of Alaska harbor seals and western stock Steller sea lions resulting in diet adaptations.
5 Similar comparisons were challenging to make for the eastern stock of Steller sea lions and
6 southeast Gulf of Alaska harbor seals due to limitations in historical data for the former.
7 However, trophic position in the 2000s showed a 38% overlap (Figure 6C & E) between the two
8 species, indicating any trophic divergence between them may be less pronounced in this region,
9 if existent.

10 The observed divergent trends indicate differences in how Alaskan pinnipeds are
11 adapting to environmental and ecological changes. Trophic position changes from stable isotope
12 data can be accounted for by: 1) prey switching between different species, 2) consuming
13 different sizes of the same prey, or 3) consuming different quality prey. These changes can occur
14 at the consumer level (pinnipeds) or lower in the food web and still be reflected in consumer
15 stable isotope signature and thus trophic position. In recent decades, Pacific salmon and halibut
16 in Alaska have both declined in size (Holsman et al. 2019, Oke et al. 2020). These changes in
17 size distributions of prey have been attributed to changes in marine mammal populations
18 (Groskreutz et al. 2019) and likely contributed to the observed trophic position declines in
19 western Steller sea lion and southeast Gulf of Alaska harbor seals. In contrast, consuming low-
20 quality prey with lower protein content and greater amino acid imbalance between consumer and
21 prey increases the amino acid trophic enrichment factor of nitrogen (McMahon et al. 2015). If
22 not accounted for in trophic position equations, this increase in trophic enrichment factor can
23 result in erroneously high trophic position estimates. This may explain the observed increase in

1 estimated trophic position in northern Gulf of Alaska harbor seals where this population may be
2 consuming a greater proportion of lower quality prey (i.e., crustaceans, shrimp, cephalopods) in
3 recent decades rather than feeding on prey species that are higher in the food web.

4 *Considerations and limitations for CSIA analyses*

5 The data in this study were limited in sample size primarily due to the availability of
6 archived specimens. As a result, we were not able to discern between known fine scale
7 differences in populations or annual trends. For example, harbor seals in the southeast Gulf of
8 Alaska consist of 13 individual stocks. Due to limitations in the number of archived specimens,
9 these stocks were pooled and analyzed as a single classification despite known differences in
10 genetic structure (Muto et al. 2020). Given the observed broad range in trophic position of these
11 generalist predators, it is unlikely that inclusion of finer spatial dynamics would have changed
12 the supported model, although variation in temporal trends within a classification may have been
13 identified. Similarly, data were only available for eastern stock Steller sea lions for 2000s and
14 2010s. As a result, no historical comparisons were possible and the conclusions about this
15 population are tentative. Nonetheless, this dataset offers historic documentation of pinniped
16 trophic position that can be updated with future samples or additional archived specimens.

17 Trophic position estimates in this study were low compared to known foraging strategies
18 of these pinnipeds. For example, Steller sea lions eat primarily walleye pollock and Atka
19 mackerel (Hobson et al. 1997, Trites et al. 2007), which would indicate a trophic position of 3 or
20 higher. Mean trophic position for Steller sea lions was closer to 2.7 in this study, which is lower
21 than expected based on known foraging ecology. It is common for CSIA to underestimate
22 trophic position of marine predators (Germain et al. 2013, McMahon et al. 2019) and the
23 inclusion of multiple amino acid pairs and a multi-trophic enrichment factor framework did not

1 fully resolve this issue. Nielsen et al. (2015) found trophic position estimates can be highly
2 sensitive to the applied β values in equation 2. In our trophic position calculation, we assumed a
3 constant β represented by marine diatoms. However, β values differ by more than 11 per mille
4 between seagrasses and diatoms (Vander Zanden et al. 2013) which has been attributed to
5 differences between vascular and nonvascular plants (Choi et al. 2017,). If vascular plants, such
6 as seagrasses, contribute to the food web in addition to non-vascular algae, the applied β would
7 be too high and would result in underestimation of trophic position of marine consumers (Choi et
8 al. 2017, Ramirez et al. 2021). Even a 10% contribution of vascular plant-derived nitrogen to the
9 food web would result in an underestimation of 0.2 trophic position. It is likely that vascular
10 plants at least partially contribute to the Alaskan food web, as seagrass beds provide essential
11 habitat and food for many fish species and invertebrates. Consideration for variable β values may
12 be helpful in resolving trophic position underestimation of future studies, especially in cases
13 where consumer carbon stable isotope data is available and contributions of seagrasses to the
14 food web are well documented.

15 *Conclusions and Implications*

16 Marine ecosystems in Alaska are experiencing unprecedented environmental change that
17 has altered abundance and size distributions of many fish species consumed by pinnipeds
18 (Barbeaux et al. 2020, Holsman et al. 2019, Oke et al. 2020, Suryan et al. 2021). Heterogeneity
19 in diet and foraging locations allow top predators to adjust to availability of resources by altering
20 their foraging. Based on the observed region-species specific changes in trophic position over the
21 past two decades, pinnipeds are experiencing different food web conditions than in the past, even
22 those that occur in similar geographic regions. This may be the result of adapting foraging
23 strategies to exploit other prey resources or a change that is occurring lower in the food web and

1 is measurable in predators. While our results cannot discern between these two mechanisms of
2 trophic level change, we can conclude that recent food web dynamics have impacted pinniped
3 trophic ecology in Alaska. Future responses of pinnipeds to food web change will likely be
4 locally variable between species, even those that occur within similar geographic regions.

5

1

2 **Tables**

3 **Table 1:** Parameter values for trophic discrimination factors between a trophic amino acid (i)
 4 and phenylalanine (o) for harbor seals ($TDF_{(i-o),j}$), for an average consumer ($\overline{TDF}_{(i-o)}$), and for
 5 primary producers ($\overline{\beta}_{(i-o)}$) derived from previous studies to apply a multi amino acid
 6 framework to equation 2.

Trophic Amino Acid (i)	Equation 2 Parameter Values		
	$\overline{\beta}_{(i-o)}$	$TDF_{(i-o),j}$	$\overline{TDF}_{(i-o)}$
Glutamic acid (Glu)	2.9	3.4	6.6
Alanine (Ala)	2.8	2.5	6.8
Aspartic Acid (Asp)	1.8	3.5	5.4*
Proline (Pro)	2.7	5.5	5.0
Data Sources	Nielsen et al. 2015	Germain et al. 2013	Nielsen et al. 2015

7
 8 **Table 2:** Candidate models for identifying spatial and temporal trophic structure of Alaskan
 9 pinnipeds. Assumptions define how the model describes trophic structure with regards to decade
 10 and classification and LOOIC describes the support of each candidate models. The best model
 11 (6) is italicized.
 12

	Fixed Effects	Random Effects	Assumption	LOOIC (Standard error)
1.	Decade	Trophic Amino Acid	Trophic position varies by decade but not classification	878.8 (52.3)
2.	Classification	Trophic Amino Acid	Trophic position varies by classification but not decade	816.5 (52.3)
3.	Classification, Decade	Trophic Amino Acid	Trophic position varies by both classification and decade	816.6 (52.1)
4.	Classification*Decade	Trophic Amino Acid	Trophic position varies by classification and decade; decadal change is distinct for each classification	797.9 (53.1)
5.	-	Classification, Decade, Trophic Amino Acid	Trophic position varies with classification and decade but common trends exist across classification and decade	813.7 (52.6)
6.	-	<i>Classification*Decade, Trophic Amino Acid</i>	<i>Trophic position varies by classification and decade; decadal change is distinct for each classification. Common trends exist across classification and decade</i>	<i>771.4 (53.1)</i>

13

Figure Captions

Figure 1: Spatial and temporal distribution of harbor seal and Steller sea lion specimens. ‘n’ denotes the number of specimens sampled for each decade. The dashed line shows 144°W, which delineates the distinct population segments of eastern and western Steller sea lion stocks.

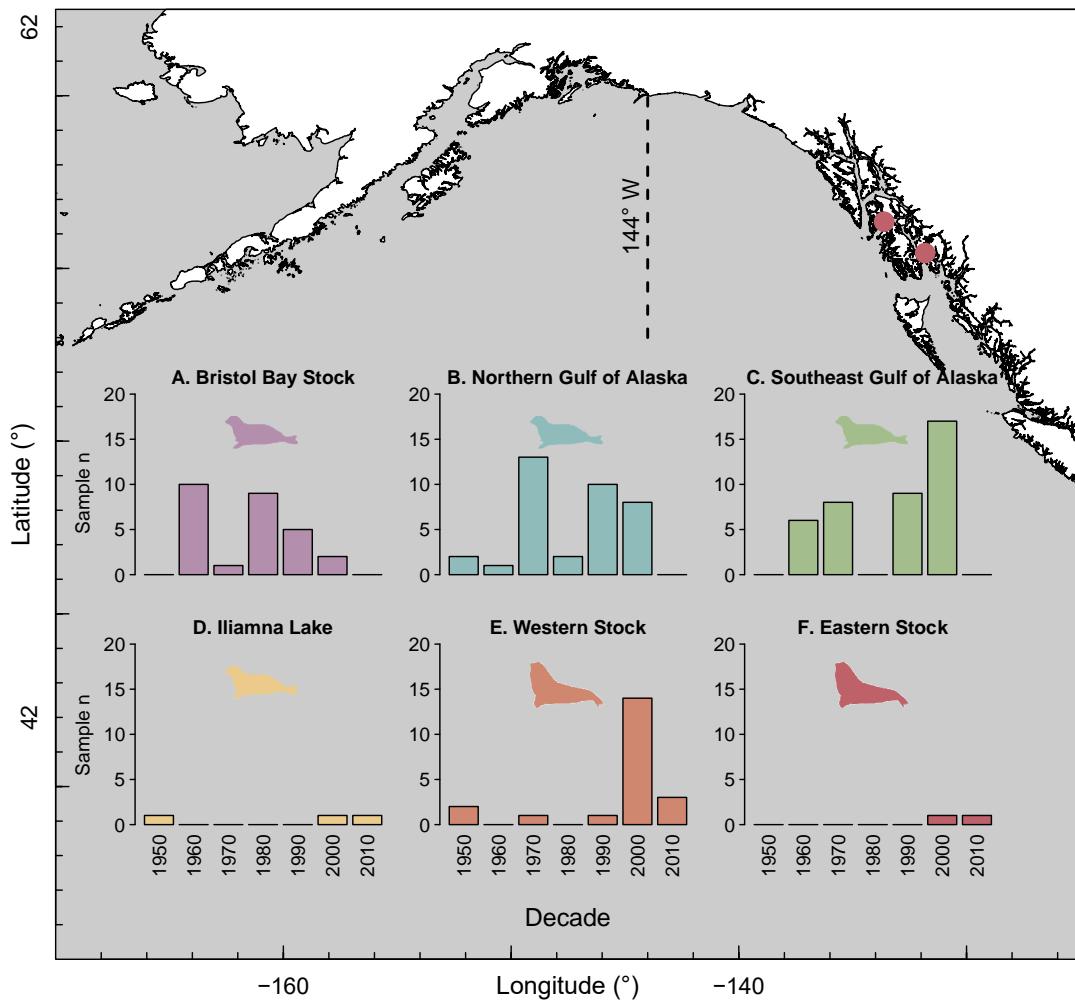
Figure 2: General trends in pinniped population abundance summarized by the six species-region classifications described in this study.

Figure 3: Distribution of harbor seal trophic position data for male (M) and female (F) pinnipeds pooled over the past century and calculated using five different trophic amino acids (glutamic acid, alanine, aspartic acid, valine, and proline) for a) Bristol Bay harbor seals, b) northern Gulf of Alaska harbor seal, c) southeast Gulf of Alaska harbor seals and d) western Steller sea lion stock. Eastern Steller sea lion stock and Iliamna Lake harbor seals did not have sufficient sample sizes; no significant differences between males and females were observed ($\alpha = 0.05$).

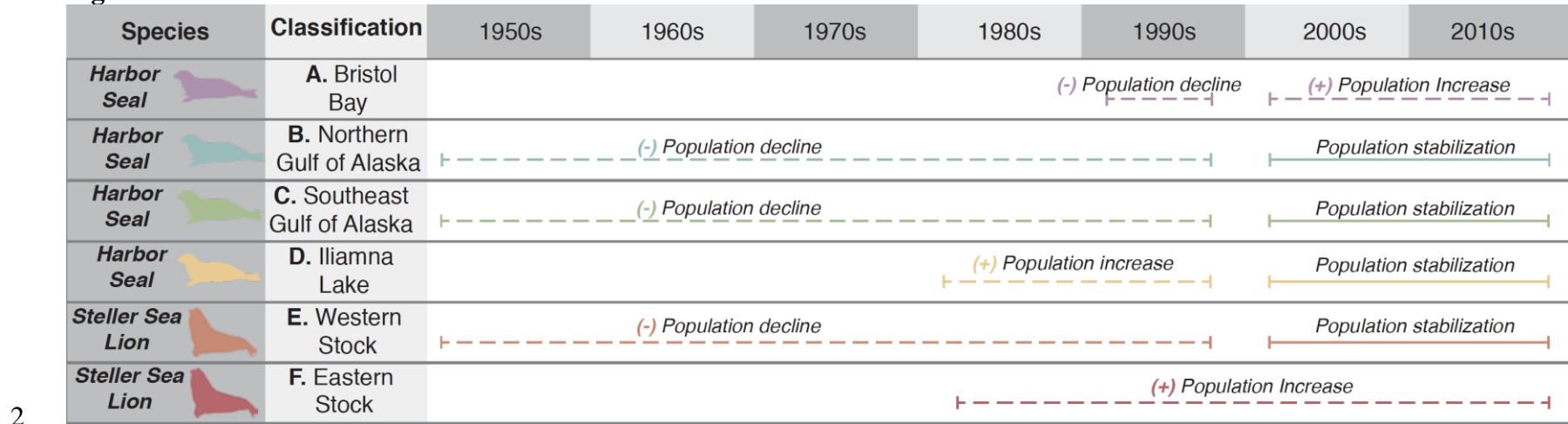
Figure 4: Model estimated posterior distributions for group-level effects of the region-species classification included as a random effect (k) in the best performing model (Model 6, Table 2). Distributions denote medians (black bold line) and 80% credible intervals (colored shaded region) in units of trophic position (x-axis).

Figure 5: Model estimated posterior distributions for group-level effects of decade included as a random effect (k) in the best performing model (Model 6, Table 2). Distributions denote medians (black bold line) and 80% credible intervals (colored shaded region) in units of trophic position (x-axis).

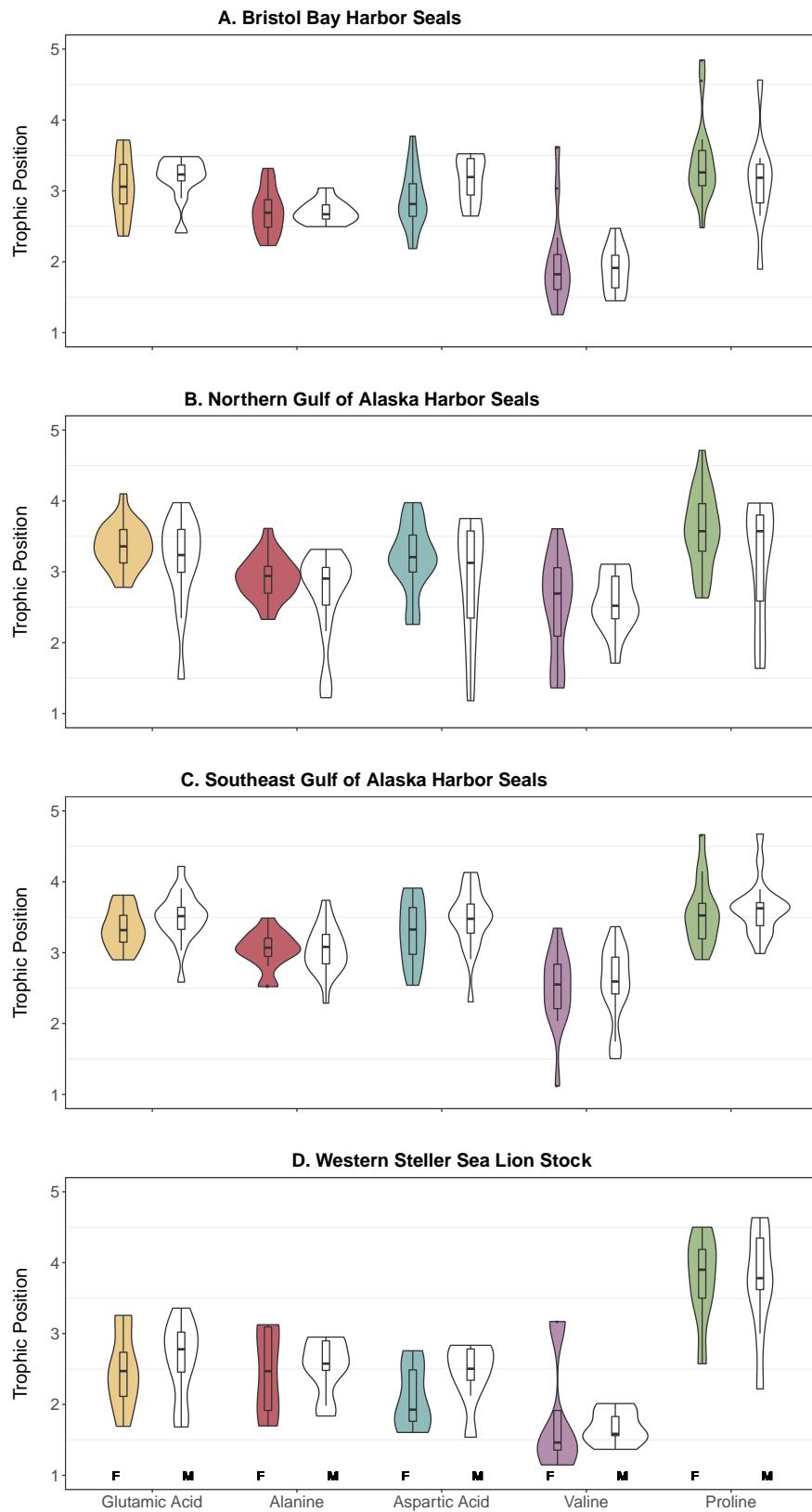
Figure 6: Median of the posteriors for combined decade, classification, and the decade-classification interaction effect on pinniped trophic position from the best performing model (Model 6, Table 2). Tails denote 80% credible interval and dashed line is the long-term mean for each pinniped classification.

1 **Figure 1**

2

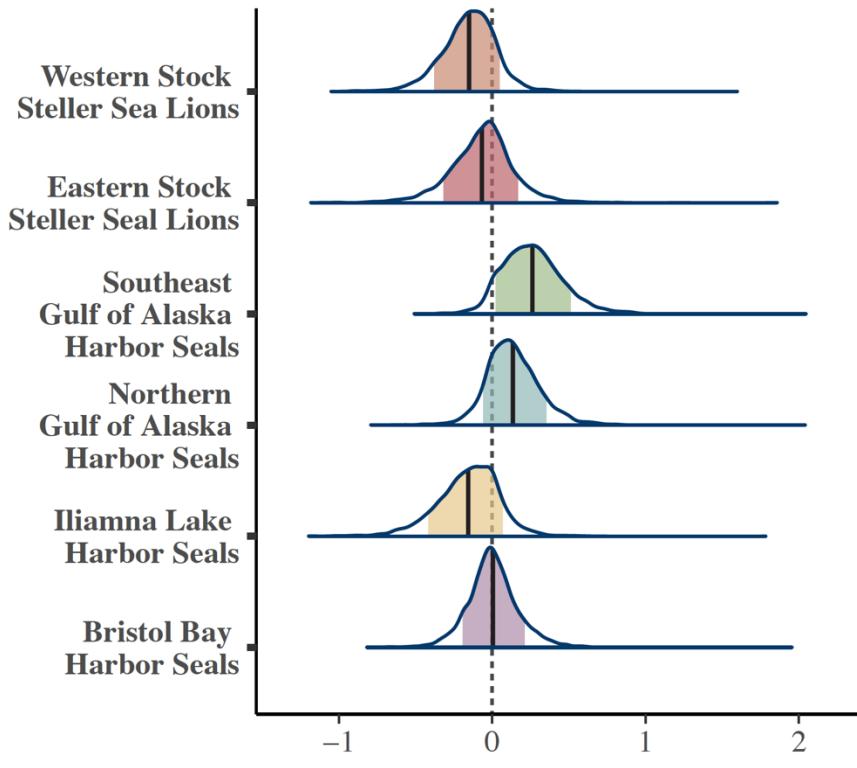
1 **Figure 2**

1 **Figure 3**
2



1 **Figure 4**

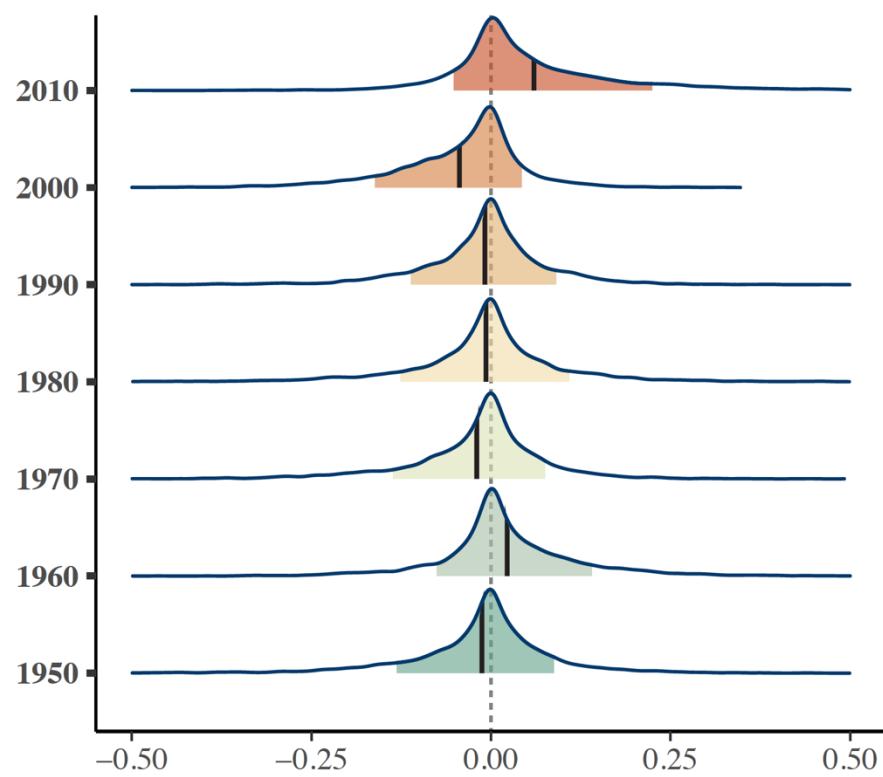
Region-Species Classification



2

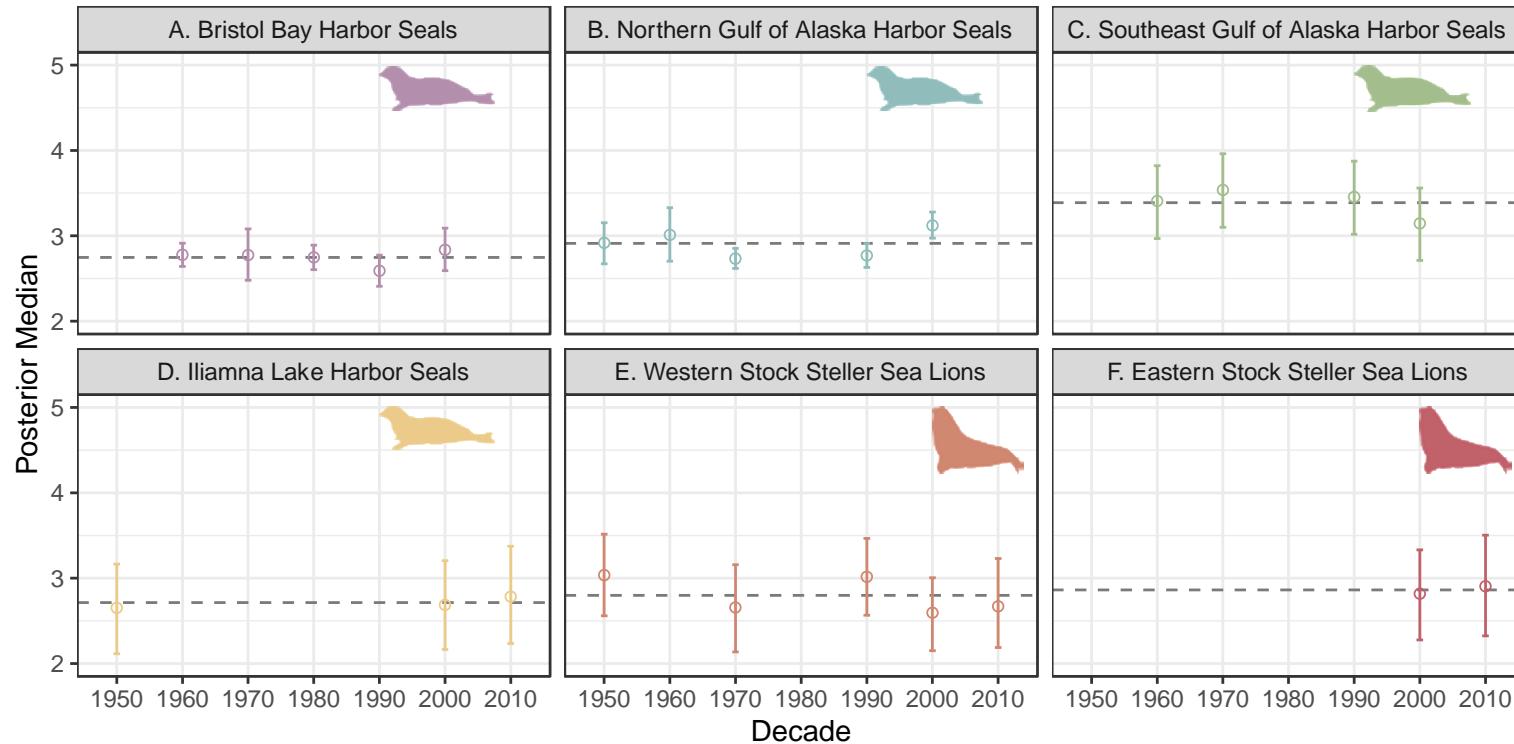
1 **Figure 5**

Decade



2

1
2 **Figure 6**



3

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14

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Appendix S1. Methods for compound specific stable isotope analysis

Collagen samples were analyzed for using 5 mg of purified collagen from approximately 50 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 (mandible, internal occipital shelf, temporal process). All produced similar stable isotope measurements. Samples were primarily taken from the internal occipital shelf at the back of the skull 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 dried under a stream of N₂ 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 available for most (n = 107) samples used as a measure of the quality for nitrogen analyses of bone collagen for stable isotope analysis (van Klinken 1999). No samples within this subset were outside the acceptable C:N range of 2.7-3.6 (by mass), indicating there was no substantial loss of glycine or addition of nitrogen due to microbial processing from mortality, decay, curation, and analysis. We therefore assumed samples without C:N data (n = 20) also were within the acceptable range as they were subject to the same storage and processing procedures at the same museum institution (University of Alaska Fairbanks, Museum of the North).

$\delta^{15}\text{N}$ of eleven amino acids (alanine, glycine, proline, aspartic acid, leucine, isoleucine, valine, threonine, serine, glutamic acid, phenylalanine, tyrosine) were measured in the UW Facility for Compound-Specific Isotope Analysis of Environmental Samples. The composition of of amino acids in bone collagen is highly variable across amino acids (Gauza-Włodarczyk et al.

2017). Tyrosine, isoleucine, valine, and threonine are not abundant in bone collagen, whereas glycine is 20 times more abundant in bone collagen than most amino acids on a gram amino acid per 100 g of protein basis. 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. 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 μ m Agilent Technologies DB-35 capillary column with 35% Phenyl and 65% polysiloxane stationary phase and moderate polarity was used (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. Tyrosine and isoleucine for most samples were not discernable and thus were omitted from this analysis. Leucine and isoleucine also co-eluted for many samples and thus leucine stable isotope measurements were deemed unreliable and also omitted from this dataset. 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. $\delta^{15}\text{N}$ 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:

$$S2. \quad Std_{aa} = m_{aa}t + b_{aa}$$

Where m represents the slope of the precision drift, t represents the injection number since last column oxidation, and Std represents the $\delta^{15}\text{N}$ of an individual amino acid for a standard observation. The data was then corrected using the following equations:

$$S3. \quad D_{aa,t} = Std_{aa,t} - True_{aa}$$

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:

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

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 S1). Conditioning injections were omitted from this calculation.

Table S1: Mean standard precision for amino acids calculated from the standard deviation of the external standard injections for a given run after drift correction and omitting conditioning injections. The mean of standard deviations for multiple runs was taken.

Amino Acid	Mean Precision (%)
Phenylalanine	0.34
Glutamic Acid	0.56
Alanine	0.46
Proline	0.48
Valine	0.38
Aspartic Acid	0.83
Glycine	0.35
Serine	0.89
Threonine	0.37
Norleucine	0.40

Table S2: Catalogue number, collection year, sex, species, and $\delta^{15}\text{N}_x$ of individual amino acids from sampled museum pinniped specimens from University of Alaska Fairbanks Museum of the North (UAM). Region Codes: Southeast Gulf of Alaska harbor seals (SE), Northern Gulf of Alaska harbor seals (SC), Southeast Bristol Bay harbor seals (BB), Iliamna Lake harbor seals (IL), western stock of Steller sea lions (WG), and eastern stock of Steller sea lions (EG). Additional archived metadata associated with specimen catalogue numbers and institution codes is available through: <http://vertnet.org/>. NA indicates data was not available for a given amino acid for a given specimen, in most cases this was due to low concentration of an amino acid (valine, threonine) or co-elution (glycine).

Institution Code	Catalogue Number	Year	Region Code	Sex	Species	$\delta^{15}\text{N}_{\text{Alanine}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{Valine}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{Aspartic Acid}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{Phenylalanine}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{Glutamic Acid}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{Threonine}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{Serine}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{Proline}} (\text{\textperthousand})$	$\delta^{15}\text{N}_{\text{Glycine}} (\text{\textperthousand})$
UAM	110281	2008	WG	F	Sea Lion	26.31	NA	22.85	13.47	28.12	NA	9.69	32.61	22.01
UAM	110284	2010	WG	F	Sea Lion	23.62	NA	19.68	16.53	26.16	NA	13.09	31.97	23.74
UAM	110328	2008	IL	NA	Harbor Seal	21.48	NA	18.87	14.63	26.22	NA	14.25	29.07	23.76
UAM	11475	1962	SC	M	Harbor Seal	22.65	24.63	25.64	11.30	28.06	-24.99	15.09	27.39	10.07
UAM	11712	1972	SE	M	Harbor Seal	22.86	24.09	23.81	10.11	26.77	-32.35	16.16	26.35	7.26
UAM	11713	1965	SE	NA	Harbor Seal	24.18	24.32	23.74	11.36	27.19	-32.52	14.49	26.41	9.01
UAM	11738	1973	SC	F	Harbor Seal	22.79	25.03	23.43	8.29	25.33	-24.62	15.01	20.08	8.98
UAM	11740	1973	SC	F	Harbor Seal	22.06	23.92	23.14	9.31	26.69	-25.50	14.55	25.55	8.10
UAM	11742	1973	SC	F	Harbor Seal	21.69	24.75	23.71	10.13	25.80	-24.72	15.63	26.66	9.01
UAM	11743	1973	SC	M	Harbor Seal	21.54	23.36	23.96	21.50	24.46	-27.58	21.31	27.94	10.70
UAM	11747	1973	SC	F	Harbor Seal	21.73	22.53	22.61	13.49	26.40	-19.71	16.40	24.81	8.81
UAM	11770	1972	SC	M	Harbor Seal	22.61	24.69	18.92	13.01	27.09	-9.32	16.80	24.88	9.58
UAM	11771	1980	SC	F	Harbor Seal	23.25	21.52	24.24	13.37	28.32	-25.67	15.49	26.08	9.47
UAM	11774	1972	SC	F	Harbor Seal	22.89	25.23	25.19	9.24	26.78	-25.88	15.86	27.22	10.19
UAM	11777	1972	SE	F	Harbor Seal	24.94	27.90	26.47	10.86	28.88	-25.52	18.05	26.80	11.60

UAM	11778	1972	SE	F	Harbor Seal	21.85	24.69	24.46	9.12	22.92	-26.71	16.11	30.59	26.44	
UAM	11779	1972	SE	F	Harbor Seal	22.47	23.82	23.60	8.83	23.40	-28.18	11.63	22.87	9.56	
UAM	11816	1973	SC	F	Harbor Seal	23.14	25.34	22.80	9.62	25.96	-24.04	16.34	29.27	11.04	
UAM	11817	1973	SC	F	Harbor Seal	21.19	25.17	22.84	10.92	24.72	-23.85	14.78	26.21	8.43	
UAM	102605	2010	WG	NA	Sea Lion	23.86	26.48	18.00	13.48	28.78	-16.28	16.60	11.50	NA	
UAM	11827	1975	BB	M	Harbor Seal	22.99	24.60	26.80	13.67	28.96	-24.41	15.79	27.40	9.96	
UAM	11836	1973	SC	M	Harbor Seal	19.93	23.04	20.51	13.51	22.15	-19.78	14.80	21.64	9.54	
UAM	11920	1975	SC	F	Harbor Seal	22.13	24.27	22.73	11.05	24.66	-31.29	14.78	26.74	7.42	
UAM	11921	1972	SC	F	Harbor Seal	22.49	22.86	21.72	14.94	26.45	-25.17	16.21	31.36	9.57	
UAM	134119	2016	EG	F	Sea Lion	24.66	22.83	23.46	12.18	23.78	-30.59	19.33	29.14	26.72	
UAM	138278	2017	IL	NA	Harbor Seal	19.95	22.38	21.42	8.34	22.59	-18.00	19.73	26.83	25.11	
UAM	19119	1972	SE	M	Harbor Seal	26.30	26.27	29.17	12.68	31.61	-31.23	19.05	28.96	9.57	
UAM	19122	1972	SE	M	Harbor Seal	20.86	23.32	23.84	8.19	25.53	-29.55	16.36	24.72	7.05	
UAM	19123	1972	SE	M	Harbor Seal	26.17	27.64	27.30	10.50	28.88	-28.73	18.10	32.02	11.74	
UAM	19124	1972	SE	F	Harbor Seal	23.78	23.98	22.61	12.96	27.78	-33.23	19.61	29.82	10.65	
UAM	19159	1981	BB	M	Harbor Seal	25.83	26.98	27.23	16.93	30.79	-22.27	19.51	31.42	13.86	
UAM	19160	1981	BB	F	Harbor Seal	24.46	28.51	23.20	10.18	27.88	-25.23	17.08	32.57	28.34	
UAM	19161	1981	BB	M	Harbor Seal	25.86	26.15	27.71	17.17	26.21	-27.49	19.22	24.80	10.59	
UAM	19172	1981	BB	M	Harbor Seal	25.49	25.80	27.57	14.41	28.94	-30.74	20.04	29.62	12.53	
UAM	19173	1981	BB	F	Harbor Seal	25.09	26.21	23.61	15.02	28.91	-13.94	19.08	28.93	12.71	
UAM	19174	1981	BB	M	Harbor Seal	23.64	25.11	25.51	13.31	25.57	-23.91	15.50	24.71	11.36	
UAM	19175	1981	BB	F	Harbor Seal	25.80	25.28	25.58	15.36	29.33	-24.52	16.81	29.32	12.09	

UAM	21485	1965	SE	F	Harbor Seal	24.38	25.47	24.00	11.03	27.61	-30.75	13.94	27.44	9.37		
UAM	28932	1965	SE	F	Harbor Seal	27.32	25.73	27.09	11.89	30.20	-37.04	20.15	30.69	11.88		
UAM	28933	1965	SE	F	Harbor Seal	23.61	24.36	22.87	11.43	26.52	-30.01	10.66	27.21	8.53		
UAM	28934	1966	BB	F	Harbor Seal	26.66	NA	24.28	13.19	29.60	NA	17.62	34.11	21.21		
UAM	28935	1966	BB	M	Harbor Seal	24.53	23.19	26.14	14.86	28.82	-34.46	19.92	29.30	12.22		
UAM	28936	1966	BB	F	Harbor Seal	26.27	28.10	27.69	18.89	28.56	-23.48	19.05	31.61	12.48		
UAM	28937	1966	BB	F	Harbor Seal	25.26	25.81	28.01	18.39	29.02	-22.52	20.95	31.86	11.73		
UAM	28938	1966	BB	F	Harbor Seal	25.33	28.09	27.28	12.42	30.06	-18.18	18.51	28.28	12.49		
UAM	28939	1966	BB	F	Harbor Seal	27.44	28.13	25.92	17.49	29.96	-21.86	20.68	33.93	27.79		
UAM	28940	1966	BB	F	Harbor Seal	26.05	23.45	26.56	14.89	29.97	-35.19	19.69	30.00	12.78		
UAM	28941	1966	BB	M	Harbor Seal	25.32	24.09	23.17	14.39	29.77	-6.95	19.29	27.46	11.53		
UAM	28942	1966	BB	F	Harbor Seal	26.55	25.89	26.01	16.88	29.70	-32.82	13.94	33.68	25.14		
UAM	28943	1966	BB	NA	Harbor Seal	25.90	25.93	26.20	14.52	30.47	-29.78	20.35	29.42	13.45		
UAM	28950	1980	SC	F	Harbor Seal	23.17	25.64	23.86	9.31	26.99	-26.81	14.37	27.22	9.20		
UAM	31904	1995	WG	F	Sea Lion	24.73	28.01	20.18	11.77	26.09	-31.51	9.14	30.82	26.41		
UAM	3409	1957	IL	NA	Harbor Seal	21.08	24.11	17.65	12.79	24.51	-29.38	10.35	22.89	20.29		
UAM	35432	1995	SE	M	Harbor Seal	23.56	25.62	24.87	13.51	26.69	-24.45	16.56	27.64	11.24		
UAM	35434	1996	SE	M	Harbor Seal	21.20	24.81	24.65	10.36	26.40	-19.40	13.55	25.20	10.04		
UAM	35437	1996	SC	M	Harbor Seal	23.65	25.25	24.84	10.18	27.12	-28.38	16.53	27.84	9.59		
UAM	35438	1996	SC	M	Harbor Seal	22.57	26.30	21.51	13.88	26.48	-22.51	16.08	24.71	10.01		
UAM	35439	1996	SC	F	Harbor Seal	21.83	22.54	21.84	11.26	25.85	-30.18	21.24	30.62	8.53		
UAM	35440	1996	SC	M	Harbor Seal	21.89	25.80	21.00	20.13	30.67	-19.24	18.22	26.47	11.10		

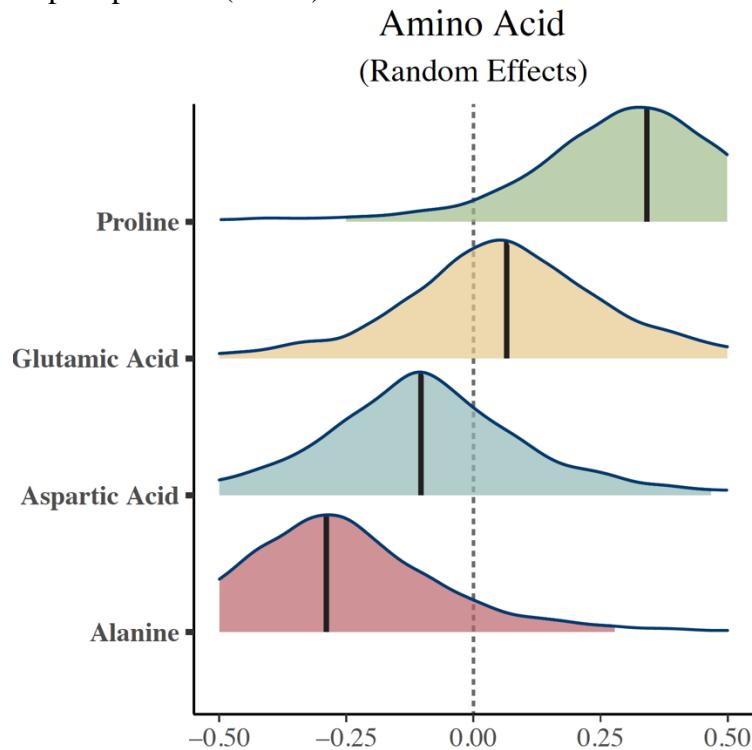
UAM	35442	1996	SC	M	Harbor Seal	23.61	25.40	22.88	12.04	25.88	-31.72	15.70	27.98	8.81		
UAM	35445	1996	SC	F	Harbor Seal	23.89	25.56	24.59	12.45	27.92	-30.06	16.76	26.90	9.75		
UAM	35446	1996	SC	M	Harbor Seal	24.94	25.49	24.96	12.46	28.49	-21.04	16.75	28.99	11.01		
UAM	35447	1996	SC	M	Harbor Seal	23.29	26.70	24.46	10.75	27.85	-29.09	15.34	28.10	14.46		
UAM	35449	1996	SC	F	Harbor Seal	26.42	27.50	20.83	14.16	25.89	-21.99	15.29	27.60	9.51		
UAM	35450	1996	SC	M	Harbor Seal	22.41	23.89	22.47	10.72	25.67	-27.84	15.88	25.79	7.95		
UAM	36254	1965	SE	M	Harbor Seal	22.82	25.68	23.72	10.05	26.40	-24.84	14.33	26.48	10.58		
UAM	36262	1965	SE	F	Harbor Seal	24.34	NA	20.59	12.39	27.45	NA	15.63	31.28	20.92		
UAM	3702	1955	SC	F	Harbor Seal	24.01	27.08	23.69	12.02	27.39	-23.72	15.84	31.22	10.26		
UAM	37032	1975	WG	F	Sea Lion	23.15	26.82	23.46	18.27	25.51	-8.00	13.09	34.15	25.47		
UAM	3716	1880	IL	NA	Harbor Seal	21.63	20.54	21.55	9.22	24.33	-32.75	13.36	24.73	6.13		
UAM	37972	1996	SE	M	Harbor Seal	22.69	27.11	25.19	11.95	28.15	-34.57	17.57	31.58	9.01		
UAM	37973	1995	SE	F	Harbor Seal	22.63	24.84	23.53	10.04	26.34	-24.00	19.78	26.17	9.22		
UAM	37974	1995	SE	M	Harbor Seal	23.90	25.53	23.53	9.78	26.77	-25.09	16.53	26.52	9.02		
UAM	41613	1996	SE	M	Harbor Seal	24.46	22.47	24.88	9.46	28.02	-33.65	15.06	26.39	9.60		
UAM	41615	1995	SE	F	Harbor Seal	22.36	23.66	22.20	9.75	22.04	-32.32	16.52	23.32	7.97		
UAM	41616	1995	SE	F	Harbor Seal	22.99	20.62	22.30	8.88	26.52	-28.70	17.96	24.25	8.45		
UAM	41617	1996	SE	M	Harbor Seal	24.73	NA	22.08	7.59	28.58	NA	13.82	31.12	22.45		
UAM	42151	1996	BB	F	Harbor Seal	23.65	24.00	25.55	12.63	26.95	-30.26	19.30	26.72	9.35		
UAM	42152	1996	BB	F	Harbor Seal	24.02	25.98	26.02	16.28	25.02	-20.68	21.15	29.13	12.11		
UAM	4233	1956	WG	M	Sea Lion	25.53	26.13	25.81	16.06	28.30	-34.69	8.75	33.12	10.64		
UAM	43044	1996	BB	F	Harbor Seal	25.38	26.81	25.73	16.65	26.44	-25.19	17.25	30.19	11.85		

UAM	47510	1985	BB	M	Harbor Seal	26.57	25.31	25.98	16.89	31.33	-12.05	19.55	28.95	13.70	
UAM	47511	1985	BB	M	Harbor Seal	24.23	27.18	27.57	14.16	30.31	-28.43	23.79	29.65	12.86	
UAM	5011	1958	WG	NA	Sea Lion	24.81	19.72	23.68	13.46	27.90	1.64	11.86	31.30	17.75	
UAM	52183	1997	BB	F	Harbor Seal	23.62	23.16	22.28	15.24	27.46	-2.86	19.11	25.80	9.43	
UAM	52184	1997	BB	F	Harbor Seal	26.16	27.00	25.63	14.58	31.35	-20.69	20.27	29.41	11.83	
UAM	5260	1952	SC	F	Harbor Seal	23.23	22.35	20.95	13.23	27.00	-6.19	16.64	30.47	17.91	
UAM	62888	2001	WG	M	Sea Lion	25.80	24.76	23.39	20.61	26.30	-34.52	17.89	33.76	24.97	
UAM	62889	2001	WG	M	Sea Lion	25.42	NA	20.73	21.21	25.46	NA	14.06	30.46	25.15	
UAM	62890	2001	WG	F	Sea Lion	24.08	23.38	24.00	19.78	26.46	-26.12	19.68	37.44	26.49	
UAM	62891	2001	WG	M	Sea Lion	26.98	25.69	23.71	17.75	29.24	-4.29	21.13	34.93	14.16	
UAM	62892	2001	WG	F	Sea Lion	26.72	24.11	26.81	23.46	27.78	7.86	19.78	34.49	16.18	
UAM	62893	2001	WG	F	Sea Lion	24.85	21.86	22.69	14.93	25.11	NA	17.23	NA	24.71	
UAM	62894	2001	WG	M	Sea Lion	26.14	NA	24.15	14.72	28.33	NA	19.02	36.05	23.05	
UAM	62896	2001	WG	M	Sea Lion	25.00	24.97	23.65	16.14	25.50	NA	11.01	32.40	22.53	
UAM	84943	2002	SC	M	Harbor Seal	24.06	25.72	24.54	9.80	27.81	-28.76	15.19	27.69	9.60	
UAM	84950	2002	SC	F	Harbor Seal	24.33	29.49	24.40	12.46	27.73	NA	19.03	30.76	11.04	
UAM	84958	2002	SC	F	Harbor Seal	22.49	24.46	21.81	6.21	26.42	-28.76	15.60	27.93	7.01	
UAM	84959	2002	SC	F	Harbor Seal	21.70	8.94	22.62	12.03	25.76	-28.41	15.27	27.83	29.30	
UAM	85206	2006	SE	M	Harbor Seal	22.48	23.79	22.15	15.21	25.43	-28.42	23.88	29.55	11.85	
UAM	85207	2006	SE	M	Harbor Seal	23.29	20.90	23.25	11.83	26.82	-33.89	12.67	28.13	10.37	
UAM	85208	2006	SE	M	Harbor Seal	23.67	13.02	22.43	9.53	25.13	-28.17	15.08	27.17	9.90	
UAM	85212	2005	SE	M	Harbor Seal	22.64	24.17	22.84	11.39	26.56	-28.57	10.77	26.10	8.01	

UAM	86877	2006	EG	M	Sea Lion	25.85	21.88	26.13	18.08	28.17	2.18	15.05	32.37	28.60	
UAM	86989	2006	WG	M	Sea Lion	25.18	24.32	23.19	13.41	28.72	9.75	13.51	33.30	NA	
UAM	87032	2003	SC	F	Harbor Seal	23.39	25.48	22.72	11.44	28.02	-20.97	16.53	26.53	8.75	
UAM	87054	2002	BB	M	Harbor Seal	26.46	24.92	27.58	14.06	30.14	-5.89	22.71	35.04	12.24	
UAM	87056	2002	BB	F	Harbor Seal	28.14	NA	25.64	19.36	31.48	NA	19.26	34.89	29.33	
UAM	92552	2000	WG	M	Sea Lion	25.27	25.63	24.24	16.69	26.69	-6.93	12.44	32.94	14.13	
UAM	92554	2000	WG	F	Sea Lion	27.37	22.86	19.23	14.65	23.93	-19.09	13.86	35.30	NA	
UAM	92555	2000	WG	M	Sea Lion	26.11	NA	23.03	14.56	27.65	NA	15.94	35.04	21.43	
UAM	99535	2003	SE	F	Harbor Seal	22.48	25.77	23.27	13.50	26.31	-30.79	11.84	27.72	8.64	
UAM	99536	2003	SE	NA	Harbor Seal	20.67	22.14	21.16	11.55	23.92	-29.33	15.88	22.39	8.77	
UAM	99537	2003	SE	F	Harbor Seal	23.65	18.90	23.63	12.10	25.14	-32.58	14.95	27.61	8.40	
UAM	99543	2003	SE	M	Harbor Seal	23.74	26.91	24.00	10.95	27.96	-35.93	10.83	27.00	7.63	
UAM	99544	2003	SE	M	Harbor Seal	22.35	23.66	24.05	10.79	25.88	-27.66	12.34	26.50	10.21	
UAM	99563	2003	SE	NA	Harbor Seal	22.16	22.68	23.65	9.91	26.16	-26.05	16.69	25.04	8.07	
UAM	99566	2003	SE	NA	Harbor Seal	23.37	25.69	23.56	12.19	26.48	-27.83	17.32	23.45	10.41	
UAM	99570	2003	SE	NA	Harbor Seal	23.36	22.03	23.94	11.84	27.06	-32.09	15.29	26.98	8.97	
UAM	99572	2003	SE	NA	Harbor Seal	23.41	25.89	23.11	10.95	27.24	-31.52	13.83	28.04	8.24	
UAM	99575	2005	SC	M	Harbor Seal	23.75	25.40	23.79	9.96	29.35	-23.41	16.79	27.96	9.58	
UAM	99641	2004	SC	F	Harbor Seal	22.98	23.83	23.07	10.72	27.72	-26.53	15.03	26.24	8.76	
UAM	99657	2004	SE	F	Harbor Seal	19.89	23.13	20.32	11.04	25.10	-28.62	19.76	23.71	6.99	
UAM	99658	2004	SE	F	Harbor Seal	21.82	21.17	20.93	9.60	25.52	-34.40	10.62	23.54	8.95	
UAM	99665	2006	SE	M	Harbor Seal	19.89	21.78	21.82	8.59	25.41	-30.56	14.66	24.99	6.04	

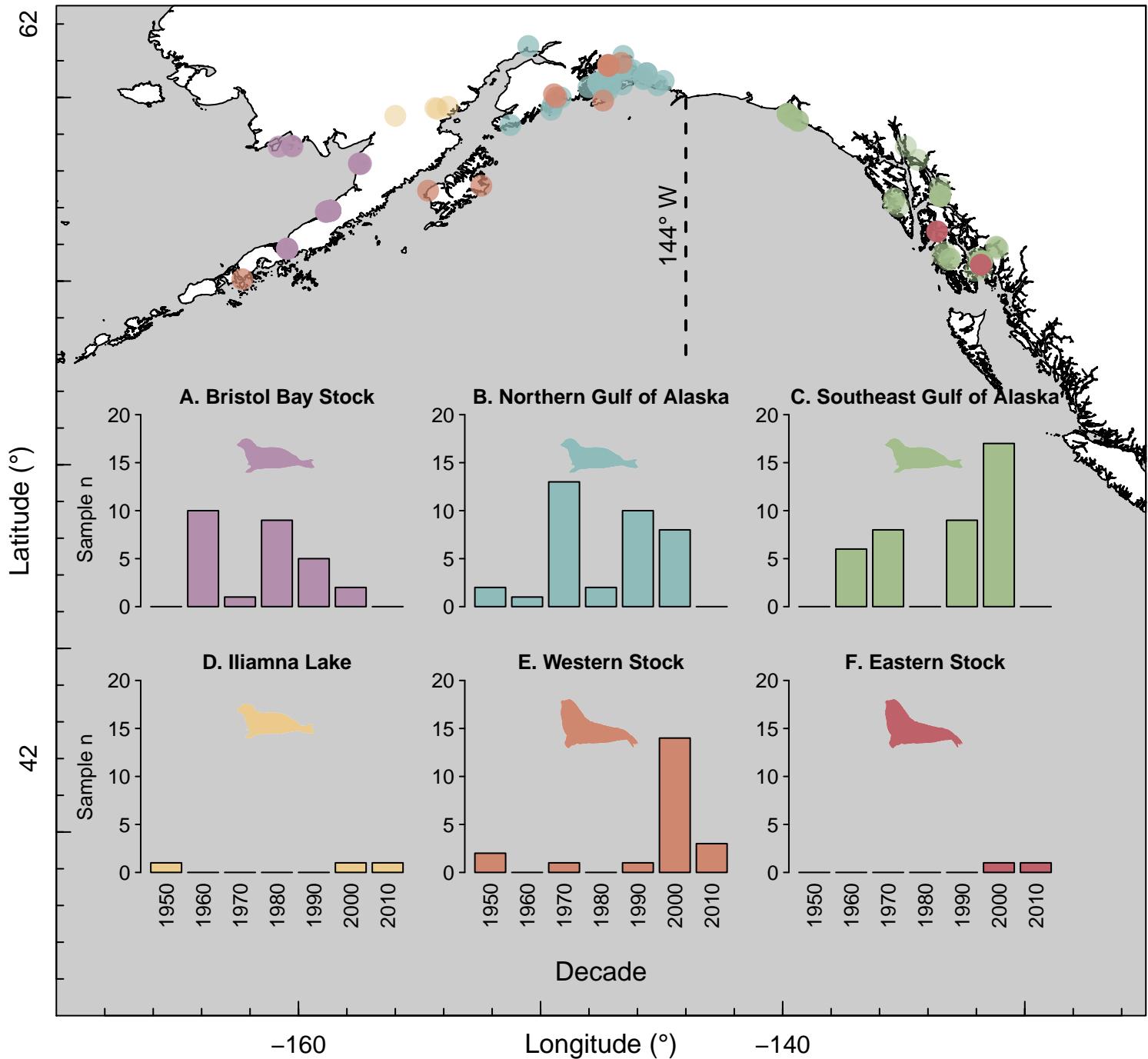
UAM	99667	2005	SE	M	Harbor Seal	21.20	20.90	21.41	11.22	25.58	-17.01	16.64	24.31	11.25
UAM	99693	2003	SC	M	Harbor Seal	23.83	24.83	23.44	12.48	26.35	-25.29	17.94	29.05	9.68

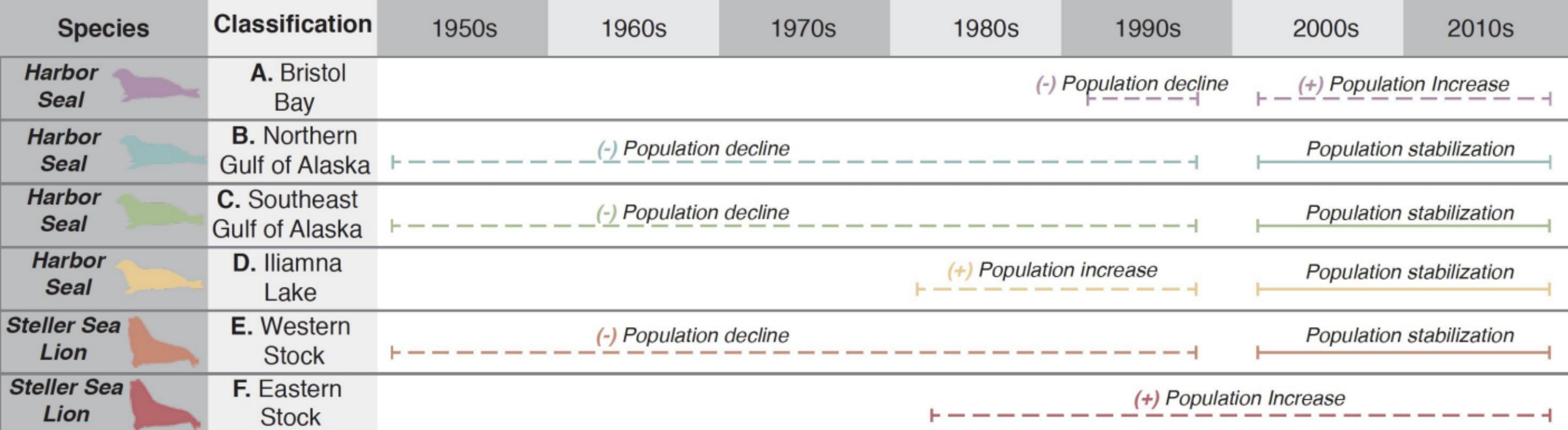
Figure S1: Model estimated posterior distributions for group-level effects of amino acid included as a random effect (k) in the best performing model (Model 6, Table 2). Distributions denote medians (black bold line) and 95% credible intervals (colored shaded region) in units of trophic position (x-axis).



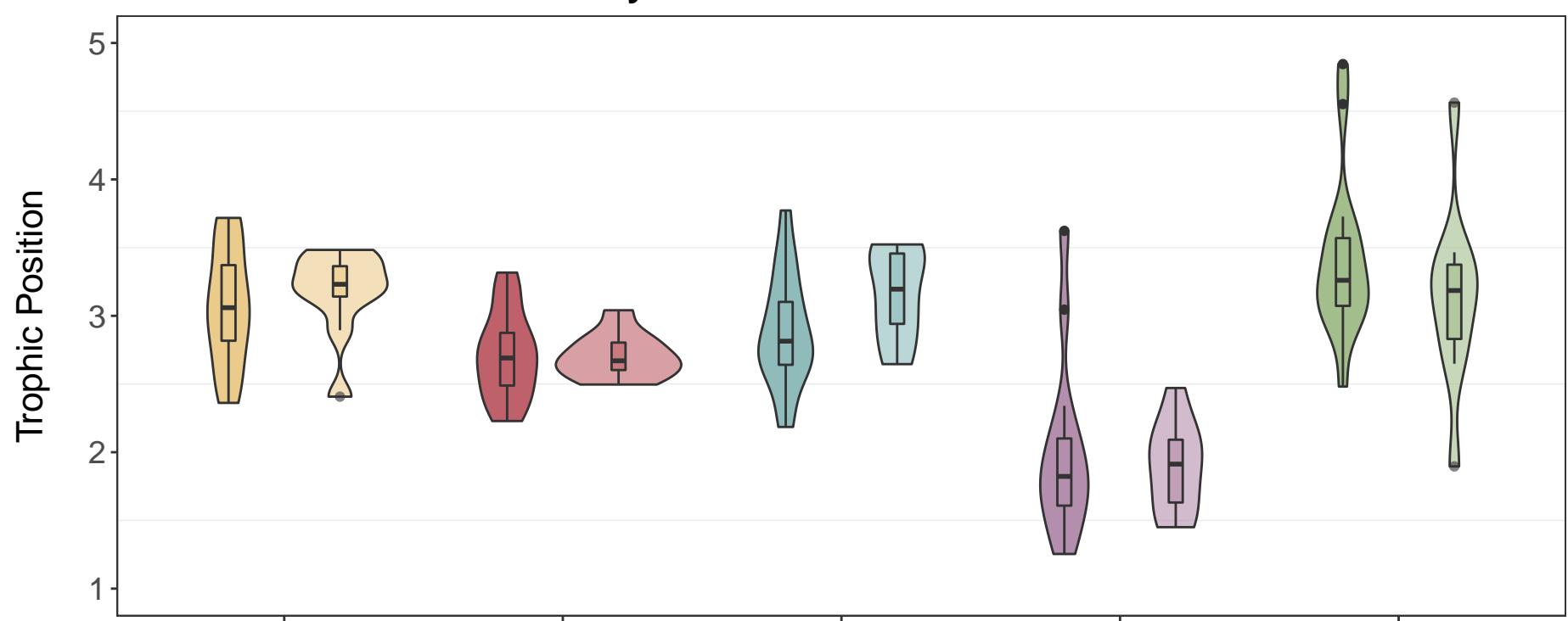
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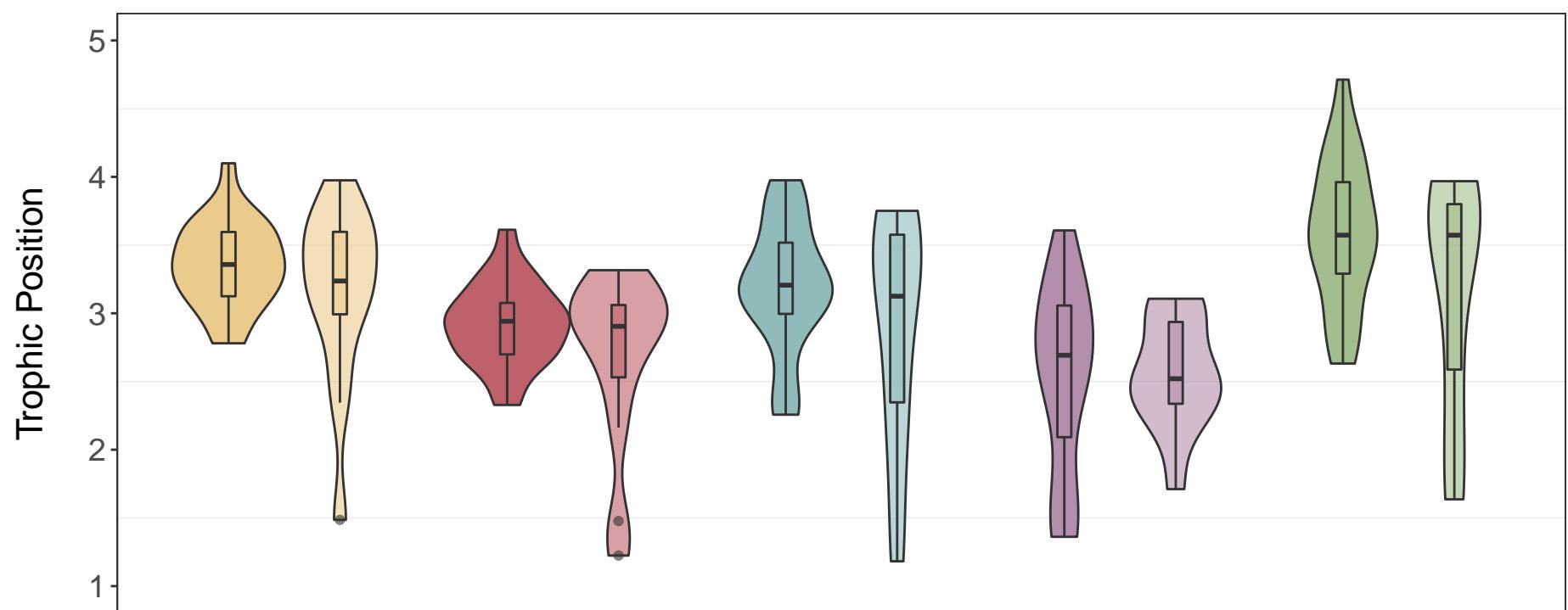




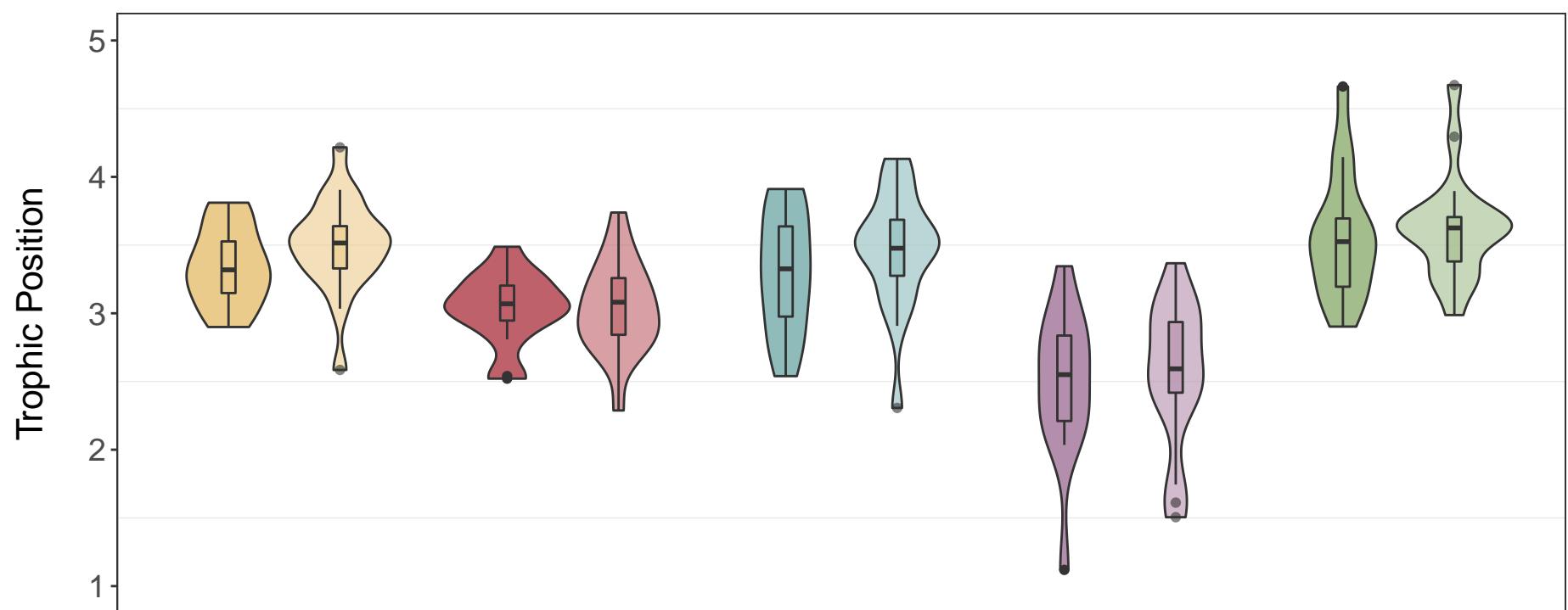
A. Bristol Bay Harbor Seals



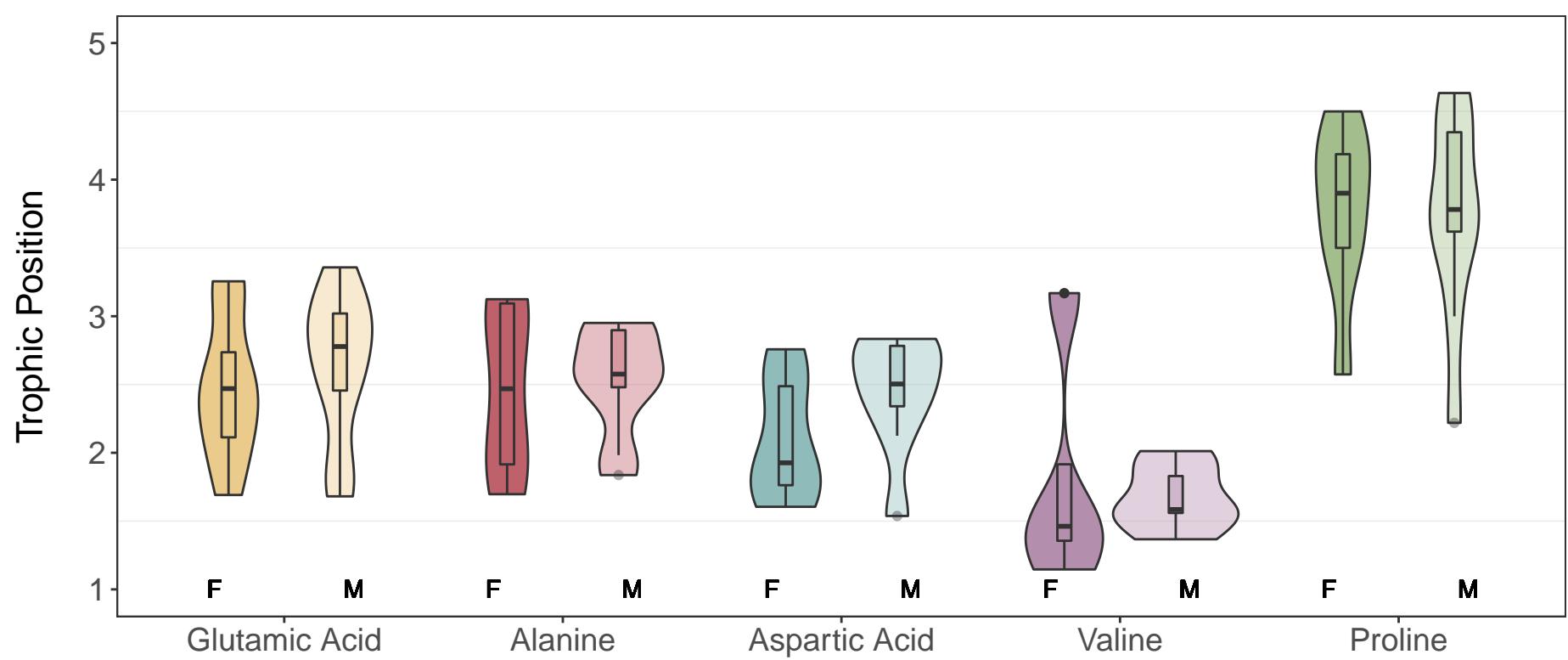
B. Northern Gulf of Alaska Harbor Seals



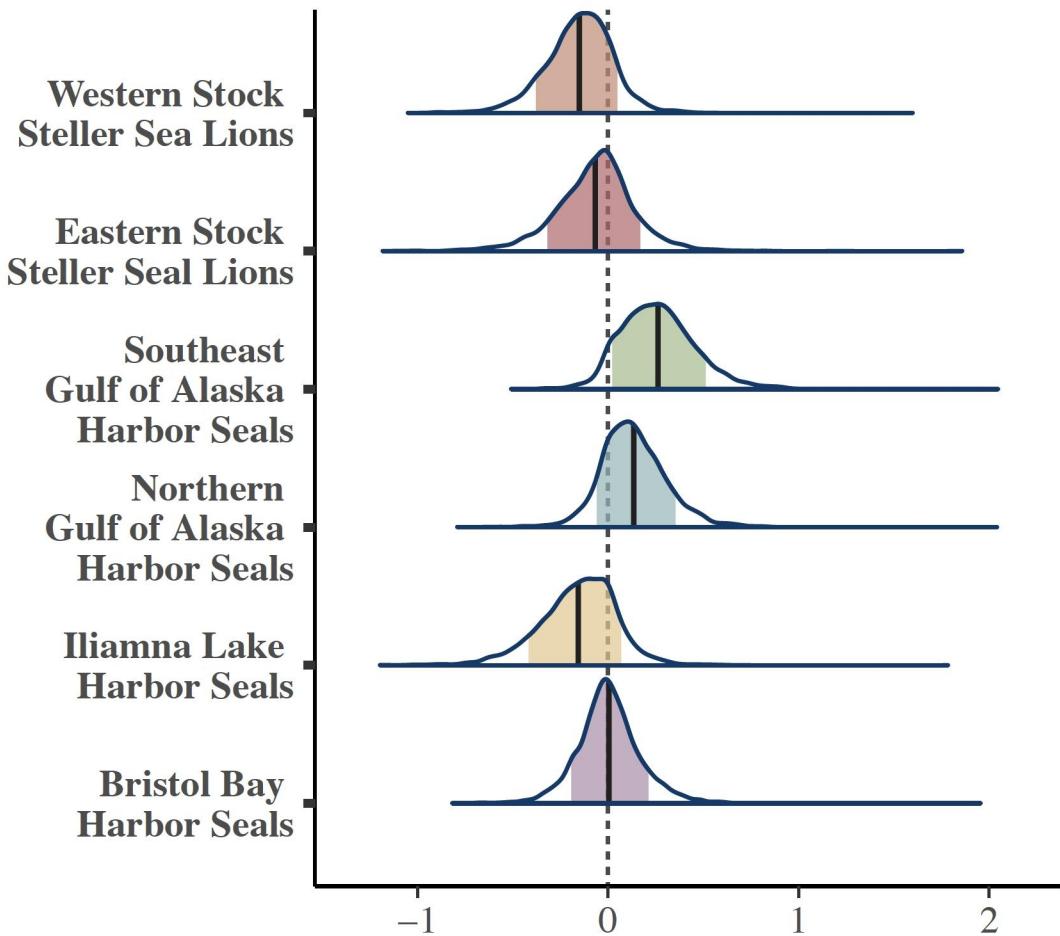
C. Southeast Gulf of Alaska Harbor Seals



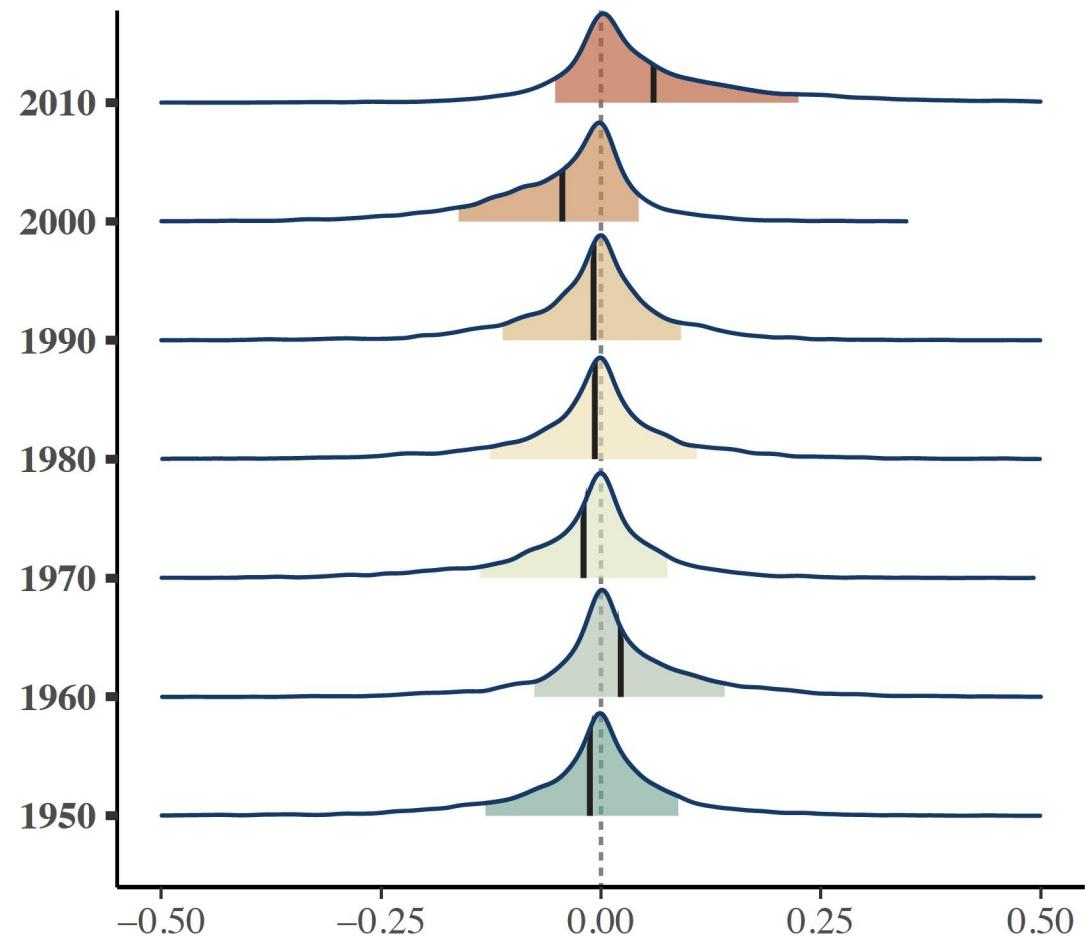
D. Western Steller Sea Lion Stock



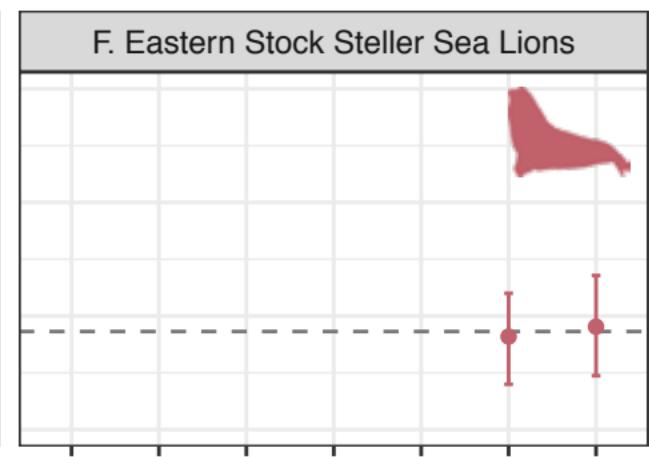
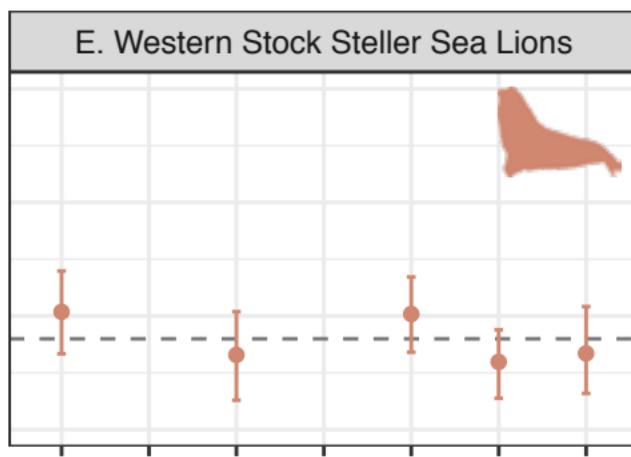
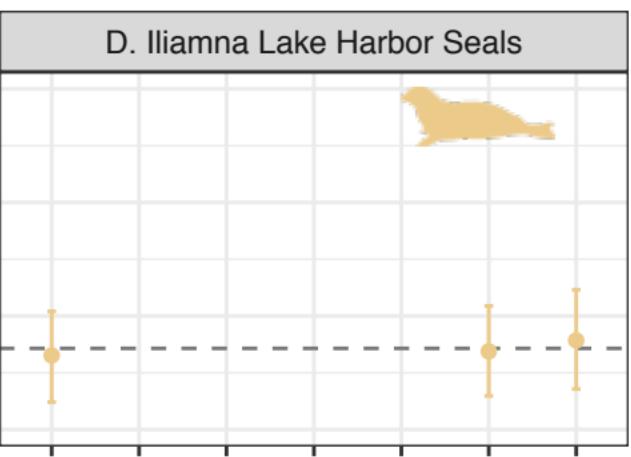
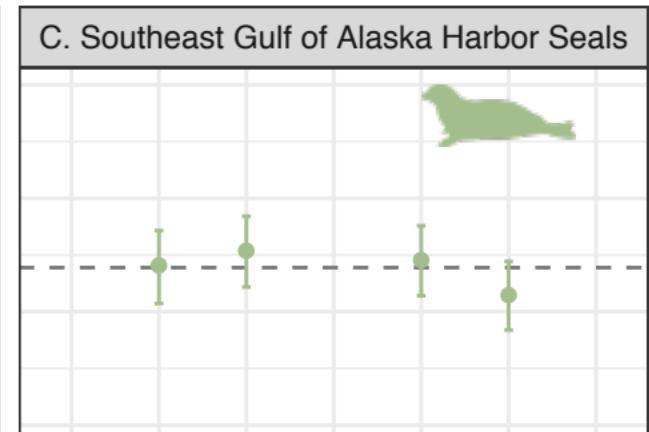
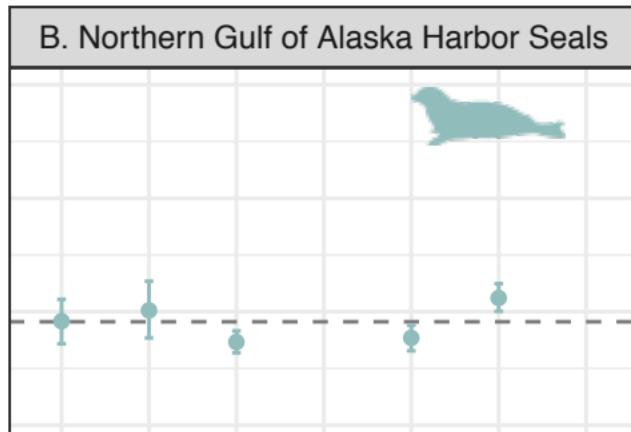
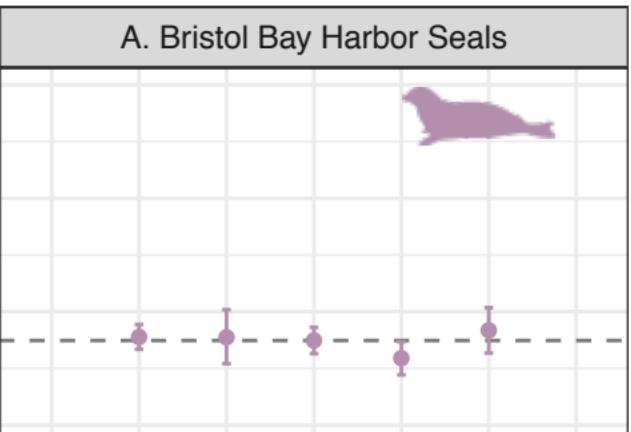
Region-Species Classification



Decade



Posterior Median



Decade