



Recent divergent changes in Alaskan pinniped trophic position detected using compound-specific stable isotope analysis

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ABSTRACT: Over the past century, Alaskan pinnipeds have experienced dramatic changes in abundance, but these changes have been highly variable across species and regions. In recent decades, changes in atmospheric forcing and sea surface temperature have been particularly pronounced in the Gulf of Alaska and eastern Bering Sea, impacting the food webs in which Alaskan pinnipeds forage. We used compound-specific stable isotope analysis of nitrogen in amino acids to estimate historic and modern trophic positions of harbor seals *Phoca vitulina* and Steller sea lions *Eumetopias jubatus* in the Gulf of Alaska and Bristol Bay. We applied a Bayesian hierarchical framework to determine whether shared trends through time exist across pinnipeds (classified by region and species) on decadal scales. Model results identified both shared trends through time and classification-specific decadal changes in pinniped trophic position. The largest change in trophic position occurred in the 2000s and 2010s and was observed in both Steller sea lions (median: 2.8) and harbor seals (median: 3.1) in the Gulf of Alaska, but not harbor seals in Bristol Bay or Iliamna Lake. Divergent trophic position patterns in the 2000s were identified in the western stock of Steller sea lions, which increased in trophic position, and sympatric harbor seals in the northern Gulf of Alaska, which decreased in trophic position. Our results indicate that these species have been experiencing unique food web conditions in recent decades in the Gulf of Alaska, likely in response to recent climate-induced ecological change in the region.

KEY WORDS: Harbor seal · Steller sea lion · Compound-specific stable isotope analysis · Trophic position · Alaska · *Phoca vitulina* · *Eumetopias jubatus*

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1. INTRODUCTION

Over the past century, pinniped populations in the northeast Pacific Ocean have experienced changes in adult and pup abundances (Muto et al. 2020). Understanding specific drivers of these population trends is important for management, as multiple stocks have been listed as threatened or endangered over the past 2 decades (Muto et al. 2020). The observed population dynamics have also corresponded with shifts in both the physical and ecological marine environment,

which frequently occur simultaneously. As a result, disentangling drivers of population trends is complex, as multiple factors (environmental conditions, prey availability) can change in tandem and potentially act synergistically on pinniped populations.

Trophic position of marine predators can be used to understand ecological conditions. Decadal trophic position trends have identified changes in krill availability for Antarctic penguins (McMahon et al. 2019), dietary shifts from fishes to squid in North Pacific seabirds (Gagne et al. 2018), and water mass circula-

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tion changes in the Arctic Ocean in ringed and harp seals (de la Vega et al. 2020). Due to their generalist foraging strategies, the trophic position of pinnipeds derived from stable isotopes is particularly well suited to identifying food web shifts driven by prey availability, prey quality, or nitrogen resources. By measuring trophic position in top predators, broad ecological changes that span the entire food web can be identified.

Examining long-term trends in trophic position across regions and species is one potential way to assess how pinnipeds in Alaska have experienced and responded to food web changes. This approach can also identify how broad shifts in foraging ecology or resources correspond to changes in abundance and population dynamics. More specifically, examining trophic position during periods of declining versus increasing pinniped abundance can provide insight into whether foraging behavior and prey availability are important drivers of population dynamics. In this study, we aim to identify whether common temporal trends in trophic position exist across harbor seals *Phoca vitulina* and Steller sea lions *Eumetopias jubatus* and their locations by deriving 70 yr of trophic position data from compound-specific stable isotope analysis (CSIA) of museum specimens.

Following climatic changes in the 1970s that altered ocean currents and sea surface temperature (Hare & Mantua 2000), most Gulf of Alaska and Bering Sea pinniped populations experienced declines that persisted through the 1990s (Muto et al. 2020). However, since 1990, population trajectories have 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% yr⁻¹ from 1990 to 2017 (Fig. 2, Muto et al. 2020, Pitcher et al. 2007; see our Fig. 1). More recently, atmospheric circulation anomalies in the northeast Pacific Ocean have resulted in unprecedentedly warm sea surface temperatures during the past decade (Walsh et al. 2018), and this environmental shift has altered fish abundances (Bond et al. 2015, Litzow et al. 2019). For example, the 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 the past decade, many pinniped populations have experienced increases or stabilization of population abundance (Muto et al. 2020, our Fig. 1), although changes in population dynamics for some Gulf of Alaska Steller sea lion populations were observed following the marine heat wave (Suryan et al. 2021).

Variable changes in Alaskan pinniped populations over the past 50 yr may not 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 in 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 of their haulout sites (Womble et al. 2010). Population declines have also been associated with increased numbers of tour vessels, particularly in glacier fjords that provide important nursing and whelping habitat (Jansen et al. 2015, Mathews et al. 2016). The differences in pinniped population trends across the Gulf of Alaska and Bering Sea suggest varied environmental and ecological drivers underlying population abundance trends. Interestingly, harbor seals and Steller sea lions that occur in the same geographic region (sympatric) have experienced different population trends over similar time periods (Fig. 1). Identifying trophic position trends through time that are shared, compared to changes that only impact a specific species or region, can elucidate how widescale ecological forcing versus localized food web conditions influence top predators and potentially explain variable population abundance trends.

Both harbor seals and Steller sea lions exhibit generalist, piscivorous foraging strategies, although differences in foraging range, body size, and diet exist. Adult harbor seals have high site fidelity, opportunistically forage 5–100 km from haulout sites at depths <200 m (Lowry et al. 2001, Blundell et al. 2011, Lance et al. 2012), and weigh up to 150 kg. Steller sea lions are central-place foragers known to migrate to prey aggregations on the continental shelf and oceanographic boundary zones (Sinclair & Zeppelin 2002, Womble & Sigler 2006). Foraging trips can last 1–3 d







Species	Classification	1950s	1960s	1970s	1980s	1990s	2000s	2010s
Harbor Seal 	A. Bristol Bay					(-) Population decline	(+) Population Increase	
Harbor Seal 	B. Northern Gulf of Alaska		(-) Population decline				Population stabilization	
Harbor Seal 	C. Southeast Gulf of Alaska		(-) Population decline				Population stabilization	
Harbor Seal 	D. Iliamna Lake				(+) Population increase		Population stabilization	
Steller Sea Lion 	E. Western Stock		(-) Population decline				Population stabilization	
Steller Sea Lion 	F. Eastern Stock				(+) Population Increase			

Fig. 1. General trends in pinniped population abundance summarized by the 6 region–species classifications described in this study

(Maniscalco et al. 2006), with average distances of 133 km for adult females (Merrick & Loughlin 1997), although foraging trips are shorter in the breeding season (Maniscalco et al. 2006). Adult females can weigh up to 350 kg, whereas adult males can exceed 1150 kg, indicating a higher energetic demand compared to harbor seals. Diet studies of Steller sea lions and harbor seals are spatially and temporally limited, and primarily utilize scat samples. In the Gulf of Alaska, gadids, cephalopods, and forage fishes are prevalent in both harbor seal and Steller sea lion diet (Sinclair & Zeppelin 2002, Geiger et al. 2013). Salmonids are also an important dietary component for harbor seals in Bristol Bay and freshwater harbor seals that reside in Iliamna Lake, Alaska, which is adjacent to Bristol Bay (Hauser et al. 2008).

Stable isotopes have been used to reconstruct historical differences in diet and trophic position in Alaskan pinnipeds (Hobson et al. 1997, Hirons et al. 2001, Brennan et al. 2019). These previous studies utilized bulk stable isotope analysis exclusively and were therefore limited in their inferential strength. Differences in the bulk $^{15}\text{N}/^{14}\text{N}$ of consumer tissues can indicate either a trophic level change of the consumer or a change in nitrogen resources at the base of the food web. The specific cause of the isotopic variation cannot be ascertained from consumer bulk stable isotope values unless the data are paired with temporal information on $^{15}\text{N}/^{14}\text{N}$ in primary producers. Lack of consistent, concurrent sampling of nitrogen stable isotope composition of primary producers therefore presents a challenge for previous long-term studies of the trophic dynamics of consumers from bulk stable isotope data. CSIA data address this challenge, as amino acids exhibit 2 distinct patterns in isotopic enrichment: trophic amino acids (i.e. gluta-

mic acid, alanine, proline) become enriched in ^{15}N with each trophic transfer, and source amino acids (i.e. phenylalanine) show minimal change and thus are reflective of the base of the food web (McClelland & Montoya 2002, Chikaraishi et al. 2009, Ohkouchi et al. 2017). With the ability to internally correct for expected changes in $^{15}\text{N}/^{14}\text{N}$ at the base of the food web (Feddern et al. 2021, Ramirez et al. 2021), CSIA allows for a more robust retrospective analysis of consumer trophic dynamics, particularly on decadal and century scales.

The objective of this work is to describe and compare changes in trophic position for Alaskan harbor seals and Steller sea lions throughout the past century and investigate trophic position differences for sympatric populations. We apply hierarchical Bayesian analyses to 70 yr of trophic position data derived from CSIA from pinnipeds (harbor seal and Steller sea lion) in the Gulf of Alaska and Bristol Bay, and freshwater harbor seals in Iliamna Lake. We build on previous research examining pinniped nitrogen stable isotope composition (Hobson et al. 1997, Hirons et al. 2001, Misarti et al. 2009, Brennan et al. 2019) by adding 2 decades of data to the record (2000s and 2010s) and incorporating a broad spatial scope (from latitude $55^{\circ}2'60''\text{N}$ to $61^{\circ}24'3''\text{N}$ and from longitude $131^{\circ}6'45''\text{W}$ to $162^{\circ}19'00''\text{W}$). Additionally, by analyzing nitrogen stable isotopes derived from amino acids, we were able to control for known changes in nitrogen resources and phytoplankton composition at the base of the food web that can confound trophic position interpretations from bulk stable isotope data collected over decadal scales (Feddern et al. 2021). Furthermore, by comparing trophic position dynamics across species and region through time, regional and species-specific food web responses to a changing ecosystem can be identified.

2. MATERIALS AND METHODS

2.1. Sample collection and classification

Samples were obtained using methods described in Feddern et al. (2021). Briefly, harbor seal and Steller sea lion bones were sampled from specimens curated at the University of Alaska Museum of the North (Table S2 in the Supplement at www.int-res.com/articles/suppl/m688p153_supp.pdf). The specimens were treated by maceration in warm water and soaked in a dilute ammonia solution, then stored in acid-free boxes. Adult specimens were sampled to avoid dietary differences between adults and juveniles. Specimens were classified based on region and species. We prioritized long-term temporal coverage

in 4 regional classifications of harbor seals (Iliamna Lake, southeast Gulf of Alaska, northern Gulf of Alaska, eastern Bering Sea) and 2 regional classifications of Steller sea lions (eastern and western stocks) for a total of 6 region \times species classifications. Specimens were extremely limited for the eastern Steller sea lion stock ($n = 2$) and Iliamna Lake harbor seals ($n = 3$). We also prioritized specimens with sex and age identifications, but these data were not available for some specimens. A total of 106 harbor seal and 21 Steller sea lion specimens were sampled, representing the 1950s to 2010s (Fig. 2).

Steller sea lions were classified according to the National Oceanic and Atmospheric Administration's (NOAA) distinct population segments. Steller sea lion specimens from east of 144°W are considered

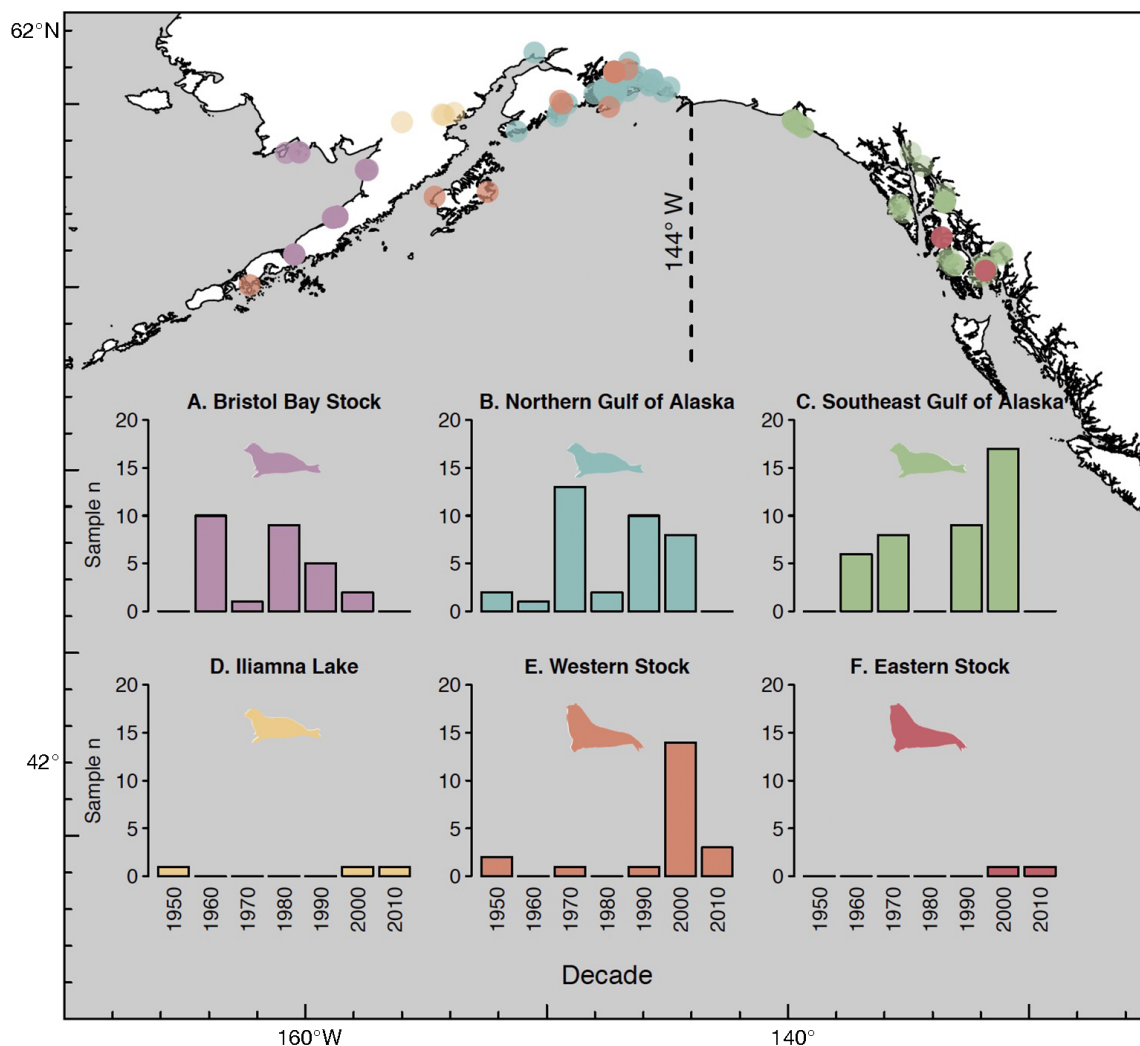


Fig. 2. Spatial and temporal distribution of specimens of (A) Bristol Bay, (B) northern Gulf of Alaska, (C) southeast Gulf of Alaska, and (D) Iliamna Lake harbor seals, and (E) western and (F) eastern Steller sea lion stock. n: number of specimens sampled for each decade. Dashed line: 144°W , which delineates the distinct population segments of eastern and western Steller sea lion stocks. Colors correspond to Fig. 1

the eastern stock and samples were from southeast Alaska. Steller sea lion specimens from west of 144°W are considered the western stock and samples were from central and western Gulf of Alaska (Fig. 2). In 2010, NOAA divided 3 Alaskan harbor seal stocks (Bering Sea, Gulf of Alaska, Southeast Alaska) into 12 stocks based primarily on genetic differences (Muto et al. 2020). Due to limitations of archived specimens, we were not able to classify harbor seals according to current NOAA stock delineations. Instead, they were classified based on their range relative to the Steller sea lion stocks, stock delineations prior to 2010, and utilization of marine versus freshwater habitats. Harbor seals that were west of 144°W, which included samples from the Prince William Sound and Cook Inlet/Shelikof Strait stocks (Fig. 2), were classified as northern Gulf of Alaska harbor seals. Harbor seals that were located east of 144°W, which included samples from the Glacier Bay/Icy Strait, Sitka/Chatham Strait, Lynn Canal/Stephens Passage, Dixon/Capes Decisions, and Clarence Strait stocks (Fig. 2), were classified as southeast Gulf of Alaska harbor seals. The Bristol Bay harbor seal stock was divided into 2 classifications: Bristol Bay referring to marine harbor seals, and Iliamna Lake referring to freshwater harbor seals (Fig. 2). This allowed for comparison of 3 pairs of geographically overlapping classifications: western stock of Steller sea lions and northern Gulf of Alaska harbors seals, eastern stock of Steller sea lions and southeast Gulf of Alaska harbor seals, and Bristol Bay and Iliamna Lake harbor seals.

2.2. CSIA and trophic position calculation

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

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

Collagen samples were measured in triplicate with a laboratory standard containing a 12 amino acid mixture of known isotopic composition. Full analytical details are described in Text S1 and Table S1.

Based on previous research, stable isotope values of seal bone collagen reflect diet over the past 1–2 yr of the individual's life. Experiments directly measuring the turnover time of bone collagen are limited, but Hobson & Clark (1992) found the half-life of carbon

stable isotopes in bone collagen of crows is 173.3 d based on controlled feeding experiments. Indirect measurements of nitrogen stable isotope turnover in adult northern elephant seal skulls found $\delta^{15}\text{N}$ values of bone collagen was significantly correlated with $\delta^{15}\text{N}$ values of the most recent 2 growth layers in tooth dentin (Riofrío-Lazo & Aurióles-Gamboa 2013). Complete turnover of $\delta^{15}\text{N}$ in bone collagen for northern fur seal young-of-the-year was 8–10 mo (Newsome et al. 2006), although complete turnover of adult seals is likely slower (Kurle & Worthy 2002). Seasonal diet changes and periodic fasting may impact pinniped $\delta^{15}\text{N}$ values. Given bone collagen is integrated over a year or more, the month specimens were collected should not affect comparison among samples.

Trophic position estimates from CSIA are sensitive to the parameterization of the trophic position equation, specifically the trophic enrichment factor (TEF, the difference between trophic and source amino acid $^{15}\text{N}/^{14}\text{N}$ values between consumers and prey for each trophic transfer) and β -value (the difference between trophic and source amino acid $^{15}\text{N}/^{14}\text{N}$ values in the primary producers). TEF varies based on nitrogen excretion pathways, feeding ecology (omnivorous, carnivorous, herbivorous), and taxa (Nielsen et al. 2015). Best practices for constraining TEF in trophic position equations apply a multi-TEF framework that incorporates a taxon-specific value for the consumer of interest in addition to a TEF value that represents consumers lower in the food web (Germain et al. 2013, McMahon et al. 2019) which are derived from controlled feeding experiments. In addition, β -values (Nielsen et al. 2015) vary based on the contributions of vascular (i.e. seagrass) versus non-vascular (i.e. phytoplankton, macroalgae) plants to the food web (Ramirez et al. 2021). Changes in the relative contributions of these primary production pathways can impact the trophic position estimate of consumers due to poorly constrained β -values. Additional ecological information (i.e. changes in abundance of vascular versus non-vascular primary producers) or chemical tracers (i.e. carbon stable isotope values) should be used to either constrain β -values or interpret trophic position estimates from CSIA data.

We calculated trophic position using a harbor seal-specific TEF (Germain et al. 2013). This approach assumed TEFs derived from controlled feeding studies of harbor seals were similar to Steller sea lions. Harbor seal TEFs are expected to closely approximate Steller sea lions, given both species are piscivorous and excrete urea. The following equation was used to determine the trophic position of each sampled individual:

Trophic Position =

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

where $\delta^{15}\text{N}_i$ is the measured stable isotope value of a trophic amino acid i in a sample, and $\delta^{15}\text{N}_o$ is the stable isotope value of a source amino acid o in a sample. Applying a ‘multi-TEF’ approach that combines both average and taxon-specific TEF can improve trophic position estimates in marine predators, including pinnipeds (Germain et al. 2013, McMahon et al. 2019). $\overline{\text{TEF}}_{(i-o)}$ is the mean difference between a given trophic amino acid i and source amino acid o across all consumers described in Nielsen et al. (2015) representing other consumers in the food web. $\text{TEF}_{(i-o),j}$ is the TEF between trophic amino acid i and source amino acid o from a controlled feeding study of a specific consumer j ; here, we use harbor seals from Germain et al. (2013; our Table 1). $\bar{\beta}_{(i-o)}$ is the mean difference in $\delta^{15}\text{N}$ values across aquatic phytoplankton between a specific trophic amino acid i and source amino acid o (Nielsen et al. 2015; our Table 1). Nielsen et al. (2015) also determined that using multiple amino acids to estimate trophic position improves precision. Therefore, we used multiple trophic amino acids, i (alanine, glutamic acid, aspartic acid, and proline) and 1 source amino acid, o (phenylalanine) to calculate trophic position (Table 1). These amino acids were chosen based on their prevalence in previous studies to derive parameters for Eq. (2), and their concentrations in bone collagen (see Text S1).

2.3. Model framework

Sex was considered as a predictor for trophic position; however, sex metadata were not available for all specimens. Samples without sex data were omitted from this analysis. In order to evaluate difference in trophic position by sex, we fit linear statistical models to each individual trophic amino acid, by classification (region \times species). These models took the following form:

$$y_i = \alpha + \mathbf{b}\mathbf{x}_i + \varepsilon_i, \varepsilon_i \sim N(0, \sigma) \quad (3)$$

where y_i is trophic position for an individual amino acid; \mathbf{b} is a vector of coefficients for the predictor \mathbf{x} , in this case sex; α is the intercept coefficient for each amino acid; and ε is the residual error for sample i assumed to be normally distributed with mean 0 and SD σ . There was not sufficient metadata for the eastern stock Steller sea lion population or the Iliamna Lake population, and these 2 classifications were omitted from this analysis.

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

$$y_i = \alpha + \mathbf{b}\mathbf{x}_i + \varepsilon_i, \varepsilon_i \sim N(0, \sigma_y) \quad (4)$$

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

where, for data point i , \mathbf{b} is a vector of coefficients for the unpooled predictors (fixed effects, see Table 2) and α is a vector of coefficients for the partially pooled group-level predictors (random effects, see Table 2) for group k (amino acid, decade, or classification). At minimum, the α included a random term for the amino acid corresponding to data point i , and depending on the model included up to a total of 4 random effects (also effects of decade, classification, and their interaction, Model 6, see Table 2). For each random effect included, $\mu_{\alpha,k}$ and $\sigma_{\alpha,k}$ are hyperparameters representing the mean and SD of group-level effects on trophic position, for random effect k . For models with more than 1 random effect, we assumed the deviations to be independent and uncorrelated. We considered models that included decade, classification,

Table 1. Parameter values for trophic enrichment factors between a trophic amino acid (i) and phenylalanine (o) for harbor seals ($\text{TEF}_{(i-o),j}$), for an average consumer ($\overline{\text{TEF}}_{(i-o)}$), and for primary producers ($\bar{\beta}_{(i-o)}$) derived from previous studies to apply a multi-amino-acid framework to Eq. (2)

Trophic amino acid (i)	Eq. (2) parameter values		
	$\bar{\beta}_{(i-o)}$	$\text{TEF}_{(i-o),j}$	$\overline{\text{TEF}}_{(i-o)}$
Glutamic acid	2.9	3.4	6.6
Alanine	2.8	2.5	6.8
Aspartic acid	1.8	3.5	5.4
Proline	2.7	5.5	5.0
Data source	Nielsen et al. (2015)	Germain et al. (2013)	Nielsen et al. (2015)

and the interaction between decade and classification either as fixed or random effects (e.g. Model 4 vs. Model 6, see Table 2), but did not consider models that included both as fixed and random effects (see Table 2). Parameter estimates were obtained using

the brms package (Bürkner 2017; version 2.14.4) in R (R Core Team 2021, version 3.6.2), which implements a Hamiltonian Monte Carlo sampler and its extension no-U-turn sampler (Hoffman & Gelman 2014) through Stan (Stan Development Team 2020). Minimally informative priors were used for random effects (normal distributions with a mean of 0 and variance of 10) and fixed effects (Student's *t*-distribution with a mean of 0, SD of 2.5, and 3 degrees of freedom). Trophic amino acid was included as a random effect for all models (see Table 2). Selection of the best models (see Table 2), given the data, was based on approximate leave-one-out cross-validation (LOOIC) using the loo package (Vehtari et al. 2017; version 2.4.1), where the lowest value indicates the best model. Model performance was compared using the difference between theoretical expected pointwise predictive density (elpd_{100}) for each model compared to elpd_{100} of the best model. Unlike model selection criteria such as the Akaike information criterion (AIC), estimates of Bayesian predictive accuracy can generate SEs. A number of criteria may be developed to determine whether 2 models are substantially different; we assumed if the difference in elpd_{100} for a model was within 3 SEs of the best model, it was considered to be statistically supported relative to the best model. We also tested how the inclusion of low sample-size classifications (Iliamna Lake harbor seals and eastern stock Steller sea lions) impacted model selection and posterior distributions by omitting them from the analysis and repeating the same model selection process (Table S3, Fig. S2).

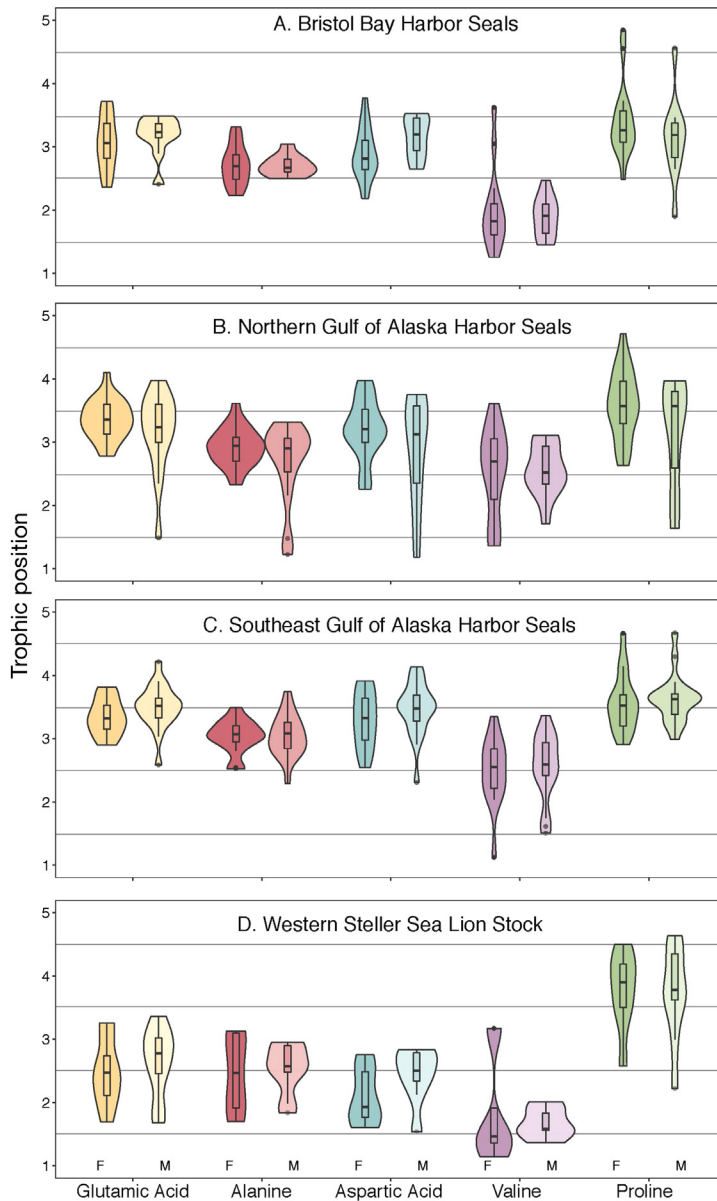


Fig. 3. Distribution of trophic position data for male (M) and female (F) pinnipeds pooled over the past century and calculated using 5 different trophic amino acids represented by color (glutamic acid, alanine, aspartic acid, valine, and proline) for (A) Bristol Bay, (B) northern Gulf of Alaska, and (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 M and F were observed ($\alpha = 0.05$). The box represents the interquartile range (middle 50 % of data) with the median represented by the horizontal line. Whiskers show the lower 25 % and upper 25 % of the data and dots represent outliers. Violin width shows the distribution of observations

3. RESULTS

We found no differences between the average male and female pinniped trophic position over the 50 yr study period (Fig. 3) for the 4 tested region–species classifications. This finding was consistent for all trophic amino acid–source amino acid pairs (Fig. 3). Based on glutamic acid trophic position estimates, both western stock Steller sea lions (2.6 ± 0.5 , mean \pm SD) and eastern stock Steller sea lions (2.7 ± 0.16) had similar trophic position. Harbor seals in the Gulf of Alaska foraged higher in the food web than their Steller sea lion counterparts (Fig. 3).

Harbor seals in the southeast region had a higher trophic position on average than any other pinniped in this study (3.5 ± 0.3) but were similar to harbor seals in the northern region (3.3 ± 0.5). Bristol Bay (3.1 ± 0.4) and Iliamna Lake (3.0 ± 0.3) harbor seals had a lower trophic position than their Gulf of Alaska counterparts on average.

3.1. Common trends in Alaskan pinniped trophic position

The best-performing model (Table 2, Model 6) of pinniped trophic position included both region–species classification and decade as random effects (shared trends) along with an interaction between classification and decade (Table 2). Based on the inclusion of decade and classification as group-level effects, these data support consistent changes over time across classifications. The supported interaction between population and decade (Table 2) indicates that distinct decadal changes in trophic position for region–species classifications also exist. The model that included decade, classification, and the interaction between decade and classification as fixed effects (Model 4) was also supported based on the difference in elpd_{100} (within 3 SEs; Table 2). Therefore, the inclusion of the interaction term was more important for improving model performance than inclusion of decade and classification as fixed versus random effects. The model selection results (Tables 2 & S2) and the posterior distributions (Figs. S2 & S4) were not sensitive to the inclusion of the 2 low sample-size classifications, Iliamna Lake harbor seal ($n = 3$) and eastern stock Steller sea lions ($n = 2$). Models had

similar support when the low sample-size classifications were omitted compared to when they were included (Tables 2 & S3).

There were consistent regional differences in trophic position for the model with the most support. The mean difference of the posterior distribution for the region–species random effect indicated southeast Gulf of Alaska harbor seals have historically fed at 0.32 ($-0.01, 0.61$) (highest-density 80 % credible interval) trophic levels higher than sympatric eastern stock Steller sea lions (Fig. 4). Similarly, the mean difference of posterior distributions showed northern Gulf of Alaska harbor seals fed 0.28 ($-0.03, 0.50$) trophic levels higher than the sympatric western stock Steller sea lions. Within the Gulf of Alaska, the posterior distributions for trophic position overlapped 39 % between harbor seals and Steller sea lions (Fig. 4). Iliamna Lake harbor seals have historically fed at a lower trophic level (mean posterior difference: 0.16 [$-0.11, 0.41$]) than harbor seals in Bristol Bay, but these 2 classifications have 66 % overlap of the posterior distributions for the region–species random effect on trophic position (Fig. 4). The 80 % credible intervals included 0 for all region–species random effects, thus the posterior probabilities only support marginal evidence for consistent differences in trophic position between classifications across decades.

There were no consistent decadal differences in trophic position across region–species classifications based on the posterior distribution of the decade random effect (Fig. 5). Pinniped trophic position in the 2000s was similar across classifications (mean posterior difference: 0.03 [$-0.09, 0.16$]) on average compared to 1990, and the posterior distributions for 1990 and 2000 had an 85 %

Table 2. Candidate models for identifying spatial and temporal trophic structure of Alaskan pinnipeds based on decade and region–species classification. ‘Interpretation’: how the model describes trophic structure with regards to decade and classification; leave-one-out information criterion (LOOIC): the support of each candidate model where lower values indicate best model; difference in theoretical expected pointwise predictive density (elpd_{100}): used to compare model predictive capacity relative to the best model (Model 6, *italicized*)

Fixed effects	Random effects	Interpretation	LOOIC (SE)	Difference elpd_{100} (SE)
1 Decade	Trophic amino acid	Trophic position varies by decade but not classification	878.8 (52.3)	–51.6 (9.9)
2 Classification	Trophic amino acid	Trophic position varies by classification but not decade	816.5 (52.3)	–21.6 (5.6)
3 Classification, Decade	Trophic amino acid	Trophic position varies by both classification and decade	816.6 (52.1)	–21.0 (5.6)
4 Classification × Decade	Trophic amino acid	Trophic position varies by classification and decade; decadal change is distinct for each classification	797.9 (53.1)	–11.8 (4.6)
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)	–21.9 (5.4)
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>	–

overlap (Fig. 5). Similarly, posterior distributions between 2000 and 2010 had a mean difference of -0.1 (-0.27 , 0.08), with a 65 % overlap (Fig. 5). Overall, decadal differences in pinniped trophic position through time were smaller than the region–species classification effects and were likely ecologically inconsequential.

3.2. Spatial and temporal differences in pinniped trophic structure

Distinct decadal changes in trophic position were observed for each region–species classification and varied more than the shared decadal changes (Fig. 6), as indicated by the decade–classification interaction. Most, but not all, pinniped classifications experienced substantial trophic level change in 2000 or 2010 but the magnitude and direction of this change varied by region–species classification based on the combined effects of decade, classification, and the decade–classification interaction (Fig. 6). The recent decadal change in trophic position was most prominent for the western stock of Steller sea lions, which had a mean trophic level decrease of -0.43 (-0.24 , -0.60) from 1990 to 2000 (a 15 % decrease), with only a 21 % overlap between the posterior distributions (Fig. 6E). This decline in trophic position remained in the 2010s. A similar decline was observed in the southeast Gulf of Alaska harbor seals. This population experienced relatively stable trophic position from 1960 to 1990, which then declined on average by -0.31 (-0.19 , -0.45) trophic levels in 2000 (33 % posterior overlap) (Fig. 6C). Harbor seals in the northern Gulf of Alaska had variable trophic position across decades and had the highest trophic position in 2000, in contrast to their southeast Gulf of Alaska harbor seals and Steller sea lion counterparts (Fig. 6B). Data were only available for 2000 and 2010 for the eastern stock Steller sea lions, and the individual sampled in the 2010s had a higher trophic position than the individual sampled in the 2000s (Fig. 6F). Bristol Bay harbor seals had a relatively stable trophic position from the 1950s until the 2010s (Fig. 6A) but experienced their lowest trophic level in the 1990s, with a -0.24 (-0.54 , 0.00) trophic level decrease compared to the 1970s and 2000s. Notably, the posterior distribution still overlapped 54 % with other decades (Fig. 6A). The individual harbor seals sampled from Iliamna Lake in the 1950s and 2000s had similar trophic position estimates, but the single harbor seal sampled in the 2010s was 0.5 trophic level higher than the other individuals.

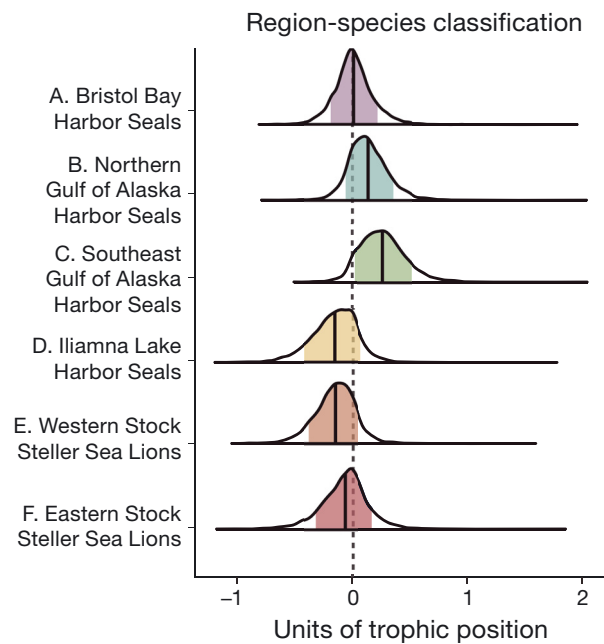


Fig. 4. Model-estimated posterior distributions for group-level effects of the region–species classification included as a random effect (k) in the best-performing model (Model 6, Table 2) for (A) Bristol Bay, (B) northern Gulf of Alaska, (C) southeast Gulf of Alaska, and (D) Iliamna Lake harbor seals, and (E) western and (F) eastern Steller sea lion stock. Distributions denote median (black bold line) and 80 % credible interval (colored shaded region) in units of trophic position (x-axis). Colors correspond to Figs. 1 & 2

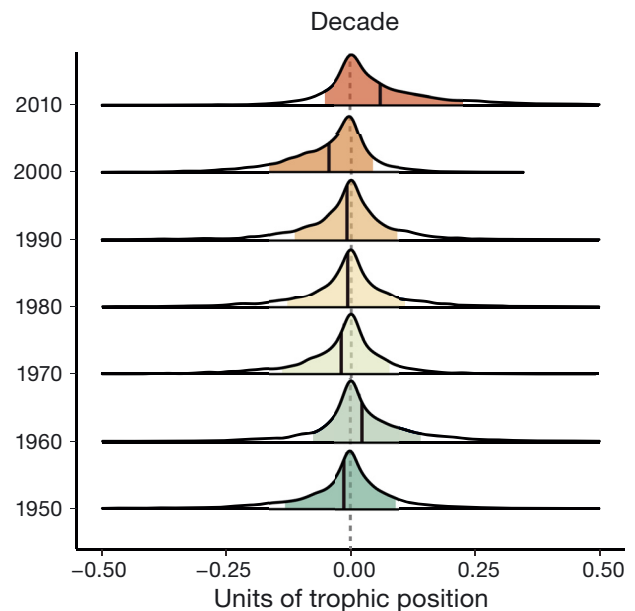


Fig. 5. Model-estimated posterior distributions for group-level effects of decade included as a random effect (k) in the best-performing model (Model 6, Table 2). Distributions denote median (black bold line) and 80 % credible interval (colored shaded region) in units of trophic position (x-axis). Colors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

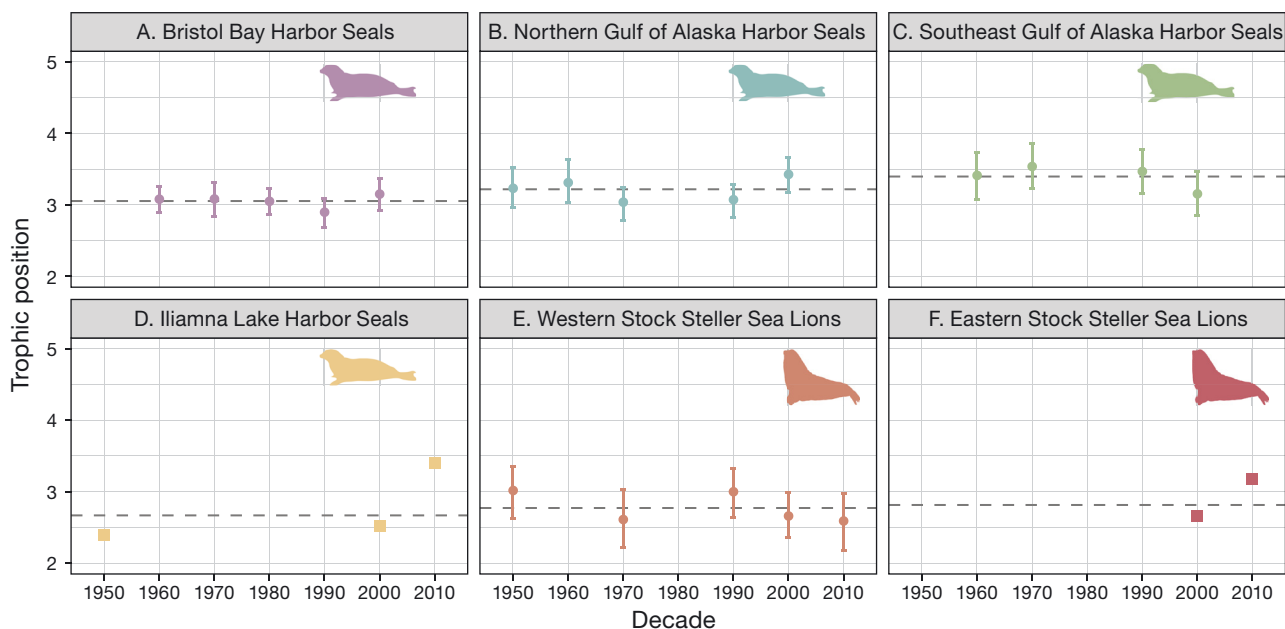


Fig. 6. Model-estimated pinniped trophic position for the combined effects of region–species classification, decade, and decade \times classification interaction from the best-performing model (Model 6, Table 2) for (A) Bristol Bay, (B) northern Gulf of Alaska, (C) southeast Gulf of Alaska, and (D) Iliamna Lake harbor seals, and (E) western and (F) eastern Steller sea lion stock. Distributions denote median (circles), 80% credible interval (error bars), and long-term mean (dashed line) for each pinniped classification (A–C & E). Unmodeled trophic position estimates (square) are plotted for classifications with low sample size (D & F) and are averaged across trophic amino acid. Colors correspond to Figs. 1 & 2

4. DISCUSSION

Over the past 70 yr, Alaskan pinnipeds have exhibited both shared and distinct differences in trophic position across region–species classification on decadal scales (Table 2). While potential drivers of trophic position were not tested in this study due to data limitations, our results suggest that a combination of local-scale (i.e. reduction of glacial ice, local foraging) and regional-scale (i.e. environmental condition, basin-wide prey abundance) food web changes may be influencing pinniped trophic position. Furthermore, the largest decadal changes in pinniped trophic position were distinct for each region–species classification and were most apparent during the recent 2 decades (2000s and 2010s). These patterns are more pronounced in the Gulf of Alaska compared to Bristol Bay (Figs. 4 & 6).

4.1. Regional and species trends in harbor seal trophic position

Both Steller sea lions and harbor seals exhibit generalist foraging patterns (Lance et al. 2012, Geiger et al. 2013). Diets of Alaskan pinnipeds consist of simi-

lar prey species but vary between species, population, and local availability of prey (Iverson et al. 1997, Hirons et al. 2001). Bulk stable isotope studies in the Gulf of Alaska have shown that Steller sea lions feed lower in the food web compared to harbor seals (Iverson et al. 1997). Our CSIA suggests that both western and eastern stock Steller sea lions have lower trophic position compared to sympatric harbor seal classifications but have similar trophic position compared to other classifications such as Iliamna Lake. Despite known differences in both diet (Sinclair & Zeppelin 2002, Geiger et al. 2013) and nearshore versus offshore foraging (Merrick & Loughlin 1997, Lowry et al. 2001) between the 2 species, our results also show potential historical overlap in trophic position between harbor seals and Steller sea lions in the Gulf of Alaska.

Harbor seals in Bristol Bay and Iliamna Lake are managed as a single population (Muto et al. 2020) despite lack of evidence of migration by the freshwater population and utilization of different resources (Brennan et al. 2019). A previous study of strontium and carbon stable isotopes showed Iliamna Lake harbor seals utilize freshwater-derived resources (resident lake fishes), particularly early in life, and exhibit an ontogenetic shift to more marine

resources (returning sockeye salmon) later in life (Brennan et al. 2019). Based on CSIA of nitrogen data, Iliamna Lake harbor seals also forage lower in the food web compared to Bristol Bay harbor seals, which could be a result of their reliance on freshwater resources (Hauser et al. 2008, Brennan et al. 2019). Generally, bulk $\delta^{15}\text{N}$ values in salmon can increase by 1.2–5.3‰ as they grow (Kaeriyama et al. 2004). Consumption of freshwater species that are available when adult salmon are not spawning, such as juvenile sockeye salmon *Oncorhynchus nerka* or smelt (*Osmerus eperlaus* and *Hypomesus olidus*), could explain observed trophic position differences. In addition, the Bristol Bay harbor seals exhibited trophic stability and only experienced a trophic shift in the 1990s relative to the 1960s and 1970s. This coincided with the lowest sockeye salmon returns to Iliamna Lake on record (Hilborn et al. 2003). Interestingly, the decrease in trophic position in the 1990s occurred simultaneously with decreases in basin-wide Bristol Bay harbor seal abundance in the late 1990s, which then stabilized and increased in the 2000s and 2010s (Fig. 1). Data were not available for the freshwater harbor seals between 1990 and 2000 and thus it is unclear whether the freshwater population also experienced a trophic position change during the 1990s when sockeye salmon returns were low. While quantitative comparisons to salmon abundance were not made in this study, salmon population abundance, harbor seal trophic position, and harbor seal population trends may be interrelated, but require further analysis.

4.2. Recent trophic position changes in the Gulf of Alaska

Trophic position changes were observed in all pinniped classifications in the Gulf of Alaska during the past 2 decades, although the direction of these changes varied on local scales. Pinniped classifications that overlap in space (Fig. 2) revealed divergent trends in trophic position between Steller sea lions and harbor seals in recent decades (Fig. 6B,E) which coincided with population stabilizations, albeit at lower than historical abundance for most populations (Muto et al. 2020; our Fig. 1). Trophic position of northern Gulf of Alaska harbor seals increased in the 2000s while the western stock of Steller sea lions decreased. Posterior distributions of western stock Steller sea lions and northern Gulf of Alaska harbor seals overlapped by 63 % in the 1950s, but only overlapped by 3 % in the 2000s (Fig. 6B,E).

Recent regional changes in the Gulf of Alaskan food webs have been well documented in other species and primarily attributed to bottom-up effects of climate (Litzow et al. 2019, Barbeaux et al. 2020). The observed divergent trends indicate differences in how Alaskan pinnipeds are experiencing or adapting to environmental and ecological changes. Consumer trophic position changes from CSIA data can be accounted for by: (1) consuming different sizes of the same prey, (2) prey switching between different species, (3) consuming different quality prey, or (4) changes in the relative contribution of vascular versus non-vascular primary producers to the food web resulting in poorly constrained β -values. These changes can occur at the consumer level (pinnipeds) or lower in the food web and still be reflected in consumer stable isotope signature and thus trophic position.

Pacific salmon, which are pinniped prey species, have declined in size in recent decades in Alaska (Oke et al. 2020). Pacific salmon can increase by 1 trophic level as they grow from juvenile to adult (Kaeriyama et al. 2004). Changes in size distributions of prey have been attributed to nutritional stress in killer whales (Groskreutz et al. 2019) and potentially contributed to the observed trophic position declines in western Steller sea lion and southeast Gulf of Alaska harbor seals. Alternatively, pinnipeds may be switching prey species altogether. Prey switching by Gulf of Alaska seabirds resulted in trophic position declines over the same period, which were attributed to a shift in diet from fish to squid (Gagne et al. 2018). A similar dietary shift, such as a greater dietary proportion of forage fish or juvenile fish, could explain the observed trophic position decline in southeast Gulf of Alaska harbor seals and western stock Steller sea lions. In contrast, consuming prey with lower protein content and greater amino acid imbalance between consumer and prey increases the amino acid TEF of nitrogen (McMahon et al. 2015). If not accounted for in trophic position equations, this increase in TEF can result in erroneously high trophic position estimates. This may explain the observed increase in estimated trophic position in northern Gulf of Alaska harbor seals, where this population may be consuming a greater proportion of lower-quality prey (i.e. crustaceans, shrimp, cephalopods) in recent decades rather than feeding on prey species that are higher in the food web.

4.3. Considerations and limitations for CSIA

The data in this study were limited in sample size primarily due to the availability of archived speci-

mens. As a result, we were not able to discern between known fine-scale differences in populations or annual trends. For example, harbor seals in the southeast Gulf of Alaska consist of 13 individual stocks. Due to limitations in the number of archived specimens, these stocks were pooled and analyzed as a single classification, despite known differences in genetic structure (Muto et al. 2020). Given the observed broad range in trophic position of these generalist predators, it is unlikely that inclusion of finer spatial dynamics would have changed the supported model, although variation in temporal trends within a classification may have been identified. Similarly, data were temporally limited and were pooled by decade for analysis, which could overlook shorter-term changes in trophic position or continuous trends (Fig. S3). Data were only available for eastern stock Steller sea lions for 2000s and 2010s. As a result, no historical comparisons were possible. Nonetheless, this dataset offers historic documentation of pinniped trophic position that can be updated with future samples or additional archived specimens.

Trophic position estimates in this study were low compared to known foraging strategies of these pinnipeds. For example, Steller sea lions eat primarily walleye pollock and Atka mackerel (Hobson et al. 1997, Trites et al. 2007), which would indicate a trophic position of 3 or higher. Mean trophic position for Steller sea lions was closer to 2.7 in this study, which is lower than expected based on known foraging ecology. It is common for CSIA to underestimate trophic position of marine predators (Germain et al. 2013, McMahon et al. 2019), and the inclusion of multiple amino acid pairs and a multi-TEF framework did not fully resolve this issue. Nielsen et al. (2015) found trophic position estimates can be highly sensitive to the applied β -values. In our trophic position calculation, we assumed a constant β -value. Notably, β -values differ by more than 11‰ between seagrasses and diatoms (Vander Zanden et al. 2013), which has been attributed to differences between vascular and non-vascular plants (Choi et al. 2017, Ramirez et al. 2021). If vascular plants, such as seagrasses, contribute to the food web in addition to non-vascular algae, the applied β -value would be too high and would result in underestimation of trophic position of marine consumers (Choi et al. 2017, Ramirez et al. 2021). Even a 10% contribution of vascular plant-derived nitrogen to the food web would result in an underestimation of 0.2 trophic position. It is likely that vascular plants at least partially contribute to the Alaskan food web, as seagrass beds provide essential habitat and food for many fish species and invertebrates.

Long-term seagrass abundance records are not available for Alaska on regional scales, but carbon stable isotope data can serve as a useful tracer of contributions of vascular versus non-vascular primary production pathways to the food web. $\delta^{13}\text{C}$ values increase with an increase in seagrass contribution to the food web (lower β -value), and $\delta^{13}\text{C}$ values would decrease with a decrease in seagrass contribution (higher β -value) (McConnaughey & McRoy 1979, Howe & Simenstad 2015). Feddern et al. (2021) measured bulk $\delta^{13}\text{C}$ values for the same harbor seal skull specimens measured in this study from Bristol Bay, northern Gulf of Alaska, and southeast Gulf of Alaska and found no long-term temporal trends. Hirons et al. (2001) observed similar $\delta^{13}\text{C}$ values for Alaskan harbor seals but observed a 2‰ decline in Alaskan Steller sea lion $\delta^{13}\text{C}$ values from 1950 until 2000. This would indicate a 10% decrease in vascular plant assimilation, an increase in Steller sea lion β -values in recent decades, which could explain the recent change in Steller sea lion trophic position (but not harbor seals). Notably, Hirons et al. (2001) did not consider regional variability in stable isotope values across Alaska or the Suess effect (global depletion in $\delta^{13}\text{C}$ values due to burning of fossil fuels, Quay et al. 1992), which could explain the observed decline in $\delta^{13}\text{C}$ values. Regardless, consideration for vascular and non-vascular primary producers to constrain β -values may be helpful in resolving trophic position underestimation in future studies, especially in cases where consumer carbon stable isotope data is available and contributions of seagrasses to the food web are well documented.

4.4. Conclusions and implications

Marine ecosystems in Alaska are experiencing unprecedented environmental change that has altered abundance and size distributions of many fish species consumed by pinnipeds (Holsman et al. 2019, Barbeaux et al. 2020, Oke et al. 2020, Suryan et al. 2021). Heterogeneity in diet and foraging locations allow top predators to adjust to availability of resources by altering their foraging. Based on the observed region-species-specific changes in trophic position over the past 2 decades, pinnipeds are experiencing different food web conditions than in the past. This may be the result of adapting foraging strategies to exploit other prey resources or a change that is occurring lower in the food web and is measurable in predators. While our results cannot discern between these 2 mechanisms of trophic level change,

we can conclude that recent food web dynamics have impacted pinniped trophic ecology in Alaska. Future responses of pinnipeds to food web change will likely be locally variable between species, even those that occur within similar geographic regions.

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